

## Chapter 16

# Pervasive Themes in Insect Life Cycle Strategies

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Two prominent themes recur as organizing constructs for studies on life history evolution. The first envisions life history variation as adaptations to the relative intensity and/or timing of mortality incurred by various stages of the life cycle (Istock 1967; Murphy 1968; Emlen 1970; Schaffer 1974a,b; Livdahl 1979). The second envisions life histories as adaptations responding to the degree of density dependence experienced by populations (MacArthur 1962; MacArthur and Wilson 1967; Pianka 1970). The theoretical and conceptual offspring of these themes are enormous as any review will reveal (e.g., Wilbur et al. 1974; Giesel 1976; Stearns 1976, 1977; Gould 1977). Direct experiments designed specifically to discriminate between or test these theories have been slower to emerge. Reasonable attempts in the laboratory have been undertaken with bacteria (Luckinbill 1978, 1984), protozoa (Luckinbill 1979), *Drosophila* (Giesel and Zettler 1980; Mueller and Ayala 1981; Barclay and Gregory 1981), and copepods (Bergmans 1984).

Tests of theory among natural populations may be harder to establish, but they exist nonetheless. Bradshaw and Holzapfel (this volume) describe a system in which density-dependent selection operates relatively free of the complications of interspecific competition, predation, or variation in microhabitat over geographical distances. Shapiro (this volume) sought to establish at what systematic levels  $r$  and  $K$  selection might be operating. His examination of pierid butterflies from temperate to tropical and high-elevation populations and species revealed a striking departure from the general pierid pattern in the form of high Andean *Phulia*. Shapiro concluded that the life history tactics of *Phulia* were not surprising in the context of their habitat but what was surprising was the failure of  $r$  and  $K$  selection theory to explain arctic bumblebees, aphids, and *Phulia*. *Phulia* and the combined responses to laboratory selection cited above suggest that the "simple model of  $r$  and  $K$  selection based on the effects of density alone seems inadequate to explain variation in life history features of complex organisms" (Barclay and Gregory 1981). Results do conform more generally to the predictions of bet hedging but without a high degree of accuracy.

Even when some adaptations are consistent with predictions, the specific traits involved appear highly idiosyncratic. Having discarded  $r$  and  $K$  selection and having found a myriad of idiosyncracies surrounding bet hedging, what are the pervasive themes of life cycle evolution?

In even the most thoroughly rejected forms of  $r$  and  $K$  selection theory, there are elements of actual life histories that drew our attention in the first place. The lure of  $r$  and  $K$  selection was and is, I believe, the realization that most life cycles do arrange themselves in suites of apparently co-adapted characters that we call strategies. Similarly, many strategies share patterns in common and, along with Dingle (this volume), I would like to call these patterns "syndromes." Syndrome implies only that if we observe the presence of certain traits, we should be able to predict the presence of others as well without being upset if they do not conform to constants in the logistic equation.

We would be making much better progress if we were, at this point, identifying common syndromes of life cycle strategies rather than each of us comparing our own data to theories we all know are not absolute. We already know a number of life cycle syndromes of which, under the weight of new data, some are crumbling, some are being confirmed, and some are still emerging. Since my emphasis is on conceptual progress, I shall concentrate on the latter two categories.

### Adaptation Is Alive and Well

One school of thought, stemming from the work of Eldredge and Gould (1972, Gould 1977), perceives evolution to proceed in temporally sporadic spurts separated by longer periods of relative stasis. When this concept is extended from morphological to life historical traits, major changes in life history tactics (tactic: a set of co-adapted traits, designed by natural selection, to solve particular ecological problems; Stearns 1976) are not likely to occur during the lifetime of a species. A variety of empirical studies on insects, however, have shown that life history traits do vary within species, usually over geographical ranges (Walter and Hacker 1974; Stearns 1976; Giesel 1976; Hegmann and Dingle 1982; Dingle et al. 1982; Giesel et al. 1982; Dingle and Baldwin 1983; Allan 1984; Taylor and Spalding, this volume) or in contrasting subhabitats (Spielman 1957; Crovello and Hacker 1972; Stearns 1976; Hairston and Munns 1984). Fisher's "fundamental theorem of natural selection" (1958) can be interpreted to imply that characters such as life history traits that have a large impact on fitness (fitness characters) should have little or no underlying genetic variability as the result of adaptive depletion of such variability. Perhaps this interpretation would have some validity if directional selection were the only form of selection operating. However, selection in varying directions (Haldane and Jayakar 1963; Levins and MacArthur 1966; Powell 1971; Roughgarden 1972; Bradshaw 1973; Istock 1981) or negative genetic correlations between traits (Williams 1957; Lande 1980, 1982a,b; Rose and Charlesworth 1981a,b; Falconer 1981; Rose 1982, 1983) may serve to maintain genetic variability despite apparently strong

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selective forces. Substantial additive genetic variance persists among fitness characters (Jinks and Broadhurst 1963; Perrins and Jones 1974; Dingle et al. 1977; Istock 1981; Lynch 1984), and even plastic fitness characters may respond rapidly to selection (Stearns 1983; Via 1984).

Still, proponents of evolutionary stasis argue that life history traits are constrained by phylogeny and ontogeny to tight functional and/or genetic units so that more complete understanding of life history evolution is to be gained only by considering the whole organism, not individual traits (Gould and Lewontin 1979; Williamson 1981; Tuomi et al. 1983). I would not argue that evolution, development, and genetic correlations impose constraints to adaptation. However, some traits appear relatively free from genetic correlations (e.g., Dingle et al. 1982; Hegmann and Dingle 1982) and even among those that are genetically correlated with other traits, the degree of genetic correlation may vary from one population to another (Berven and Gill 1983). Thus, the focus of selection may be an independent trait, a complex of genetically correlated traits, and/or the degree of genetic correlation itself.

In a study that provides a model of how we might pursue life cycle strategies, Masaki (this volume) first correlated ovipositor length with body size and then sought causes for deviations from this regression. Ground crickets (*Pteronemobius*) superficially appear constrained by ovipositor length: body size allometry (Masaki, Figure 2.3A, this volume); but, on closer inspection, individual species deviate from the genus mean relationship and these deviations are closely associated with habitat (Masaki, Figure 2.3B, this volume). Within one habitat type, deviations from allometry among *P. taprobanensis* and *P. mikado* are correlated with overwintering stage, latitude, and voltinism (Masaki, Figures 2.5 and 2.6, this volume). Longer ovipositors are then expected in drier habitats among univoltine crickets that overwinter as eggs at northern latitudes; shorter ovipositors are expected for crickets living in the contrasting habitats. Having recognized that there is an allometric correlation between ovipositor length and body size, Masaki did not stop at this relationship but probed further to find that species and populations are able to escape allometric constraints and adapt to their specific habitats.

We should beware of clutching onto convenient, current theory or dogma to explain the latest deviation from our expectations and let our data lead us to new patterns. Several times during the discussion after individual papers or at the end of this symposium, we heard phylo- or ontogenetic constraints invoked to "explain" why an organism cannot do something. I have known for a long time that, whereas a number of insect orders include species that may interpolate instars under poor food conditions, mosquitoes are constrained to only four. I also knew that there was no maternal care among mosquitoes, but, as Lounibos and Machado-Allison have shown (this volume), *Trichoprosopron digitatum* is unaware of its phylogenetic constraints and broods its eggs. I am eagerly awaiting the discovery of a fifth instar mosquito.

I am not advocating the complete dismissal of prior theory. We should continue to measure individual life cycle strategies against known theories and syndromes. But, when results are not congruent with theory, we should not

reject either the theory as being wrong or the organisms as being too idiosyncratic. Rather, we should focus on these deviations from expected to see if they fall into a pattern, which identifies a new theory or syndrome.

The potentials for this approach are clear in Brown's chapter (this volume), which has taken perhaps the broadest overview of life history evolution in this symposium. She has asked to what extent the stage of vegetation succession selects for specific herbivore life cycles. From her data (Brown, Table 7.1, this volume) she has been able to test previous theories of Margalef (1968) and Odum (1969) as well as some predictions of MacArthur and Wilson (1967). More importantly, she has established convincingly that insect life cycles show pronounced changes along a successional gradient and that none of these changes are absolute. The latter point means that inhabiting each seral stage are insects whose life histories apparently contradict the general pattern. Rather than despairing these exceptions, I would like to know more about them to see if their life cycles reveal a secondary, underlying pattern. Are the exceptional egg diapausers also exceptional in their other life cycle characters or do they conform to the broader, overlying pattern of life cycles along a successional gradient?

For many years, but especially since Danilevskii's (1965) treatment of photoperiodism and seasonal development, life historians have been aware that photoperiodically mediated diapause represents one of the most consistent eco-geographical relationships: critical photoperiod tends to increase with latitude or altitude. I agree with Taylor and Spalding (this volume) that further "studies directed solely at examining latitudinal trends in the median day length or date of diapause induction response are redundant. It remains of great interest, however, to understand the evolutionary mechanisms maintaining the median response at even a single location." Their plot of latitudinal trends (their Figure 5.2) clearly illustrates considerable variation about the central tendency. Pursuing the theme of this section, I would like to ask what factors are associated with deviations from the overall trend?

The assertion I wish to make is that darkness of habitat can affect the interpretation of day length and, consequently, the timing of diapause. To illustrate this point, I shall use the mosquito species shown in Taylor and Spalding's Figure 5.2 and refer to their species designations in parentheses. Two of the mosquitoes, *Wyeomyia smithii* (4) and *Aedes atropalpus* (V), live in pitcher plants and rock holes, respectively, whereas *Toxorynchites rutilus* (3) and *Aedes sierrensis* (W) live in tree holes. Consequently, diapause in *T. rutilus* and *A. sierrensis* is determined under darker conditions than in *W. smithii* or *A. atropalpus*. At a given latitude (Taylor and Spalding, Figure 5.2) the median day length is lower and the day of the year on which the median day length occurs is later for *T. rutilus* and *A. sierrensis* than for *W. smithii* and *A. atropalpus*. These differences are based on each species' perceiving a day that begins at the onset of civil twilight in the dawn and ends at the termination of civil twilight in the dusk. The effective day length is shorter in tree holes in pitcher plants or rock holes, however, and tree-hole mosquitoes have compensated for this difference with shorter median day lengths than among the more exposed pitcher

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plant and rock hole species. Evidence consistent with this interpretation comes from *T. rutilus*. Fourth instars of *T. rutilus* captured 26 August at 40.3°N (Bradshaw and Holzapfel 1975) were all in diapause. This date is considerably earlier than 20 September estimated by Taylor and Spalding based on Bradshaw and Holzapfel's (1975) laboratory determination of median photoperiod but using as a photoperiodic day sunrise to sunset plus two civil twilights. By contrast, if, due to their dark habitat, the photoperiodic day of *T. rutilus* is based on sunrise to sunset only, the day of median photoperiod advances to 13 August, a date far more consistent with field observations. Thus, taking photic habitat into account can reduce the deviations from the central tendencies in Taylor and Spalding's (Figure 5.2) relationships. Certainly other factors such as generation time and the relationship of the sensitive period to the diapause stage will prove to be important considerations as well.

The important point here is that these considerations would not have been forthcoming without the variation shown in Taylor and Spalding's chapter. The overall trend, the positive correlation of critical day length or date with latitude is clear and familiar but, like ovipositor length in Masaki's crickets, new interesting relationships will be forthcoming by examining deviations from this trend.

Dingle (this volume) has pointed out that among lygaeid bugs of the genus *Oncopeltus*, subgenus *Oncopeltus* produces the more general lygaeid pattern of large clutches of eggs every few days whereas members of the subgenus *Erithrischius* produce small clutches every day. Among the former but not the latter, clutch size is positively correlated with body size. One can then view the dependency of clutch size on body size as a phylogenetic constraint imposed by the timing of oviposition. By contrast, further examination of members of the subgenus *Erithrischius* may reveal that they are the lygaeid equivalent of Shapiro's (this volume) *Phulia* and illustrate that adaptation is flourishing in the genus *Oncopeltus*.

### Life Cycle Delays

In a pivotal paper, Lewontin (1965) showed that the intrinsic rate of natural increase ( $r$ ) was more strongly influenced by a small change in age at first reproduction or in generation time than by an equivalent change in fecundity. Consequently, selection among colonizing species (and subsequently, among  $r$ -selected species) "will have long since shortened development time, but will not have acted as efficiently on fecundity." The direct implication is that whenever intrinsic rate of natural increase is a reasonable index of fitness, organisms should minimize both time to first reproduction and mean generation time. Yet, virtually every insect considered in this volume delays its development and/or reproduction beyond physiologically possible times.

Insect life cycle delays may take place over the span of hours, days, weeks, months, or even years. Some of these delays are extrinsically mediated by the direct effects of the environment; others, although environmentally cued or set,

are the result of endogenous mechanisms. It is the latter type of life cycle delay that proves to be so intriguing because, whether or not we can identify ultimate causality, we must be left with the conclusion that endogenous delays are genetically programmed, adaptive responses to environmental variability.

Many developmental and reproductive events such as hatching, molting, emergence, mating, and oviposition occur at specific times of the day or night; these events usually persist with circadian regularity under constant conditions (Saunders 1982). Eggs having completed embryogenesis or pupae having completed adult development will delay hatching or molting until the time of an internally programmed, externally phased temporal "gate." Although hundreds of examples exist illustrating circadian rhythms among insects, the adaptive significance of only a relative few is known or reasonably inferred.

The adaptive significance of longer life cycle delays is not always so elusive. One of the finest examples of variation in endogenous orchestration of life cycle delays is presented by marine midges of the genus *Clunio* (Neumann, this volume). Marine *Clunio*, although living in an energy-rich environment, are characteristically slower developing than their freshwater counterparts and have very short-lived adults. To coordinate their reproduction with infrequent or variable exposure of their tidal or subtidal habitat, *Clunio* exhibit endogenous circadian emergence and circasemilunar pupation rhythms. Thus, even though individuals may be fully mature, pupation or eclosion may be delayed up to 2 weeks or 24 hr, respectively, if developmental maturity does not coincide with the proper phase of the endogenous oscillator. Phasing of the circasemilunar pupation rhythm is cued by temperature, moonlight, and tidal flux. In the south where the habitat is exposed only during a few days each semilunar cycle, moonlight is the primary cue; in the north where the habitat is exposed part of each day, tidal or temperature flux is the stronger cue. Tidal flux predominates on exposed coastlines and thermal flux in protected fjords. The interaction of endogenous circadian and circasemilunar rhythms with locally reliable zeitgebers thus effects coincidence of oviposition with the optimal habitat exposure between an insect with a complex life cycle and a temporally heterogeneous but highly periodic environment.

By far one of the most pervasive features of temperate insects is that they enter some form of seasonal developmental or reproductive arrest. Diapause generally effects a life cycle delay of several months so that development or reproduction ceases from the end of one growing season through aestival or hibernal harshness until the beginning of the next growing season. Both Dingle (this volume) and Sauer (this volume) point out that insects have an array of mechanisms available to them to arrive at the critical developmental or reproductive interval at the environmentally proper time. This array of mechanisms is wonderfully illustrated by various chapters in this volume. Wardhaugh (this volume) shows how photoperiod interacts with temperature and humidity to elicit an embryonic diapause syndrome characterized by changes in maternal oviposition behavior, egg-pod morphology, and embryonic physiology. Neumann (this volume) shows how hibernal diapause in *Clunio* is cued by photo-

period, coordinated with, and perhaps mediated through, endocrine mechanisms similar to those of the circasemilunar pupation rhythm. It is now clear that more than a few insects may diapause at more than one stage. The plague locust, *Chortoicetes terminifera* (Wardhaugh, this volume), may diapause as an embryo or as a nymph; under the influence of short days, eggs that did not diapause have a greater propensity to enter nymphal diapause. The flesh fly, *Calliphora vicina* (Vinogradova, this volume), may diapause twice, as a larva or as an adult. All populations are capable of adult, reproductive diapause but individuals among more northern populations may diapause as a larva as well. The burnet moth, *Zygaena trifolii* (Wipking and Neumann, this volume), may diapause in a variety of successive larval stages. Southern populations are generally bivoltine with an aestival diapause of variable duration. Among northern populations, larvae enter hibernal diapause but may do so up to three times in successive larval stages spanning 3 years or more. Some individuals fail to terminate diapause after the first winter, molt, and develop during the third summer, and diapause again the following winter. The entire range of life cycles from univoltine to 3 years or more "was evident even within the progeny of a single female." Wipking and Neumann propose that females may therefore be "spreading the risk" (den Boer 1968) over several growing seasons as some summers are so inclement that they greatly inhibit reproductive success. Similarly, entry into diapause during successive stages of locusts (Wardhaugh) or flesh flies (Vinogradova) may provide a "fail-safe" mechanism against misinterpretation of environmental cues or against the lack of correlation between environmental cues and weather during a specific year (Lounibos and Bradshaw 1975; Bradshaw and Holzapfel 1977; Holzapfel and Bradshaw 1981).

*Zygaena trifolii* (Wipking and Neumann, this volume) provides an example of apparently inherited life cycle delays that extend beyond a year. Diapause in *Z. trifolii* is entirely different from diapause in the emperor dragonfly, *Anax imperator* (Corbet 1956), which is capable of completing development within one summer but when food is scarce, may enter diapause twice in the same generation during successive winters. Diapause in *A. imperator* reflects the direct effects of the immediate trophic environment on development whereas diapause in *Z. trifolii* can be preprogrammed by endogenous physiological mechanisms, independently of the environment.

Even longer life cycle delays are possible. Cicadas as a group exhibit longer life cycles and slower growth rates than other xylem feeding homopterans (Karban, this volume). In an extreme case, generation time may extend to 17 years. Karban has proposed that this great increase in preadult development relates to increased fitness accruing to individuals of larger size: larger males are more attractive to females than smaller males; larger females produce more eggs than smaller females. Cicadas emerge with great regularity at 17-year intervals. Regardless of the selective forces maintaining this synchrony, it persists over a range of local subhabitats and among cicadas of variable weight. Consequently, some endogenous counter or timer appears to be regulating this periodic emergence. As with *Clunio* and *Zygaena trifolii*, the endogenous nature

of periodic development in cicadas argues that, even if we cannot identify ultimate causality, the periodicity is a genetically programmed response to the environment experienced by the insect during its evolutionary history.

My assertion is that periodic life cycle delays, which are independent of or compensated for the effects of the immediate environment, are characteristic of insect populations in general. When our attention focuses on these delays themselves, we are not likely to belittle their import. When our attention focuses on other life history traits, especially demographic traits, we need to integrate periodic delays into our considerations. Dingle's studies (this volume and literature cited therein) with lygaeid bugs provide a good example of this approach. Traits such as age of first reproduction, mean generation time, clutch size, and clutch frequency are then viewed as part of life cycle syndromes, that is, traits potentially interacting with diapause and migration. A pervasive theme is that insect life cycles are punctuated by exogenously cued but endogenously programmed delays; consequently, these delays must be integrated into any theory of life cycle evolution in insects.

### Homeostasis, Polymorphism, and Environmental Uncertainty

Taylor (this volume) considers the onset of winter as a variable catastrophe in response to which insects adaptively vary sensitive periods and switching times mediating diapause. A fundamental consideration "is that the catastrophe be predicted by some event so that it can be prepared for in advance" (Taylor, this volume). Principal events used by insects to predict the onset of winter include photoperiod, temperature, and moisture. These cues exhibit a strong correlation with changing seasons, which of these cues provides the highest predicting power varies with geography, both within and between species. No single cue is perfectly correlated with the optimal time to enter diapause and, as we have seen above, insects use combinations of cues to induce diapause or enter diapause in sequential stages to provide a "fail-safe" mechanism against environmental variation. Even a combination of cues may not always provide very reliable indications of impending catastrophe. Yet, insects do develop, diapause, and persist in highly variable environments with few reliable cues. In this section, I shall propose that there is a consistent relationship between environmental predictability and the form of insect variability.

As early as 1953, Levene showed theoretically that multiple subhabitats could provide opportunity for the persistence of a variety of genotypes in a population. Levene's multiple-niche polymorphism has resurfaced over the years in many guises but serves as an organizing concept for all of them. Roff (this volume) proposes that genetic control for wing length should evolve from single- to multi-locus control so that organisms could present a continuously variable array of phenotypes to the environment. Dingle (this volume) reports that in California as opposed to Iowa, some winters are sufficiently mild that they do not kill nymphs of the milkweed bug, *Oncopeltus fasciatus*. Correspondingly, there is extreme variability in diapause response among California as compared

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with Iowa strains of *O. fasciatus* in the laboratory. Thus, there has been a maintenance of genetic variability among California *O. fasciatus* due to the uncertainty of California winters. The important point here is that it is the uncertainty of winter conditions, not their harshness, that selects for variability.

Sauer et al. (this volume) point out that whereas day length is the same every year, the end of the favorable season varies about some mean. The mean end of season at any locality may select for a population level critical day length and/or required day number for the initiation of diapause but the standard deviation in the end of season maintains significant genetic variability for these traits. At the same time, polygenic control provides a means for "genotypes that were completely eliminated by selection in one generation (to) be reconstituted by recombination the following generations" (Sauer et al., this volume). Thus, both genetic variability and the degree of polygenic control underlying life cycle traits should increase with environmental uncertainty (Sauer et al., Roff, this volume).

A lack of genetic variability does not necessarily imply a lack of phenotypic variability. When even very harsh conditions are predictable in advance from environmental cues, individual organisms may make physiological or developmental adjustments for this harshness before it impinges upon them. Thus, when environmental conditions are highly correlated, we may expect individual insects to display elaborate homeostases so that the appropriate phenotypes are deployed at the appropriate times.

The evolution of homeostasis provides a possible explanation for the maintenance of genetic polymorphisms within populations. Suppose (Figure 16.1) that there are two alleles at the  $\alpha$  locus and that when both alleles occur in a population, they are maintained at frequencies greater than expected from mutation alone by heterosis, multiple subhabitats, or other factors (Figure 16.1, middle). This population is then polymorphic at the  $\alpha$  locus. By virtue of its very stability, genetic polymorphism could persist sufficiently long for a variety

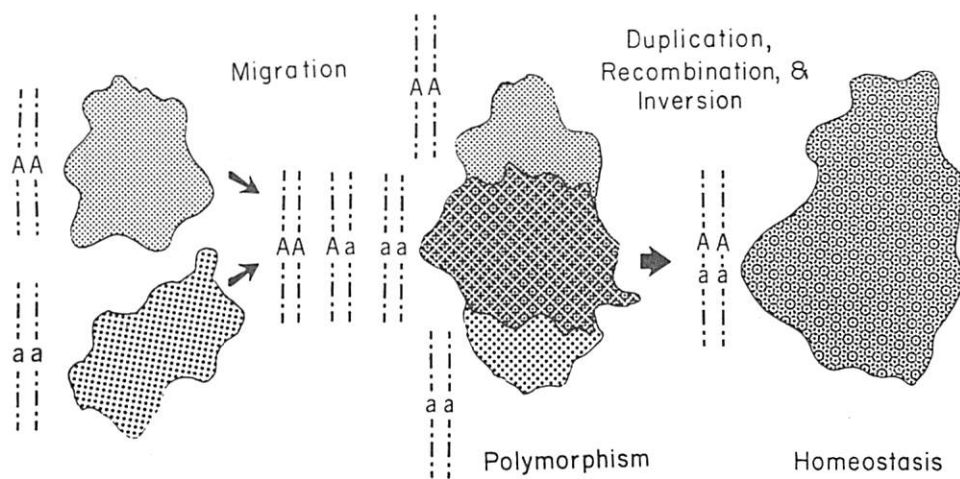


Figure 16.1. Evolution of homeostasis from genetic polymorphism.

of chromosomal events to take place. If these events included duplication, recombination, and inversion, the former alleles could come to occupy separate, homozygous loci protected from recombination (Figure 16.1, right). With a common operator for the two loci, each individual would be effectively heterozygous. But, if each locus was controlled by a separate operator that could respond independently to environmental factors, then each individual in the derived population would be able to assume the phenotypic repertoire of the entire ancestral population without the cost of homozygosity. An individual of the derived, homeostatic, and apparently homozygous population would, on the average, realize greater fitness than an individual of the ancestral polymorphic population. Homeostatic mechanisms should, therefore, replace stable polymorphism.

Why then should not all organisms accumulate progressively elaborate homeostases (Slobodkin 1968)? The answer, I believe, lies in the observation that homeostatic mechanisms enable organisms to overcome specific exigencies only if they can deploy the appropriate phenotype in advance of the exigency. Otherwise, a homeostatic individual has no advantage over an individual with a fixed phenotype. Whether or not polymorphism persists or evolves into a homeostatic mechanism depends on the relative timing of three events (Figure 16.2): (1) the time or age at which organisms must switch between alternate phenotypes, (2) the time of the catastrophe, period of environmental harshness, or other selective force, and (3) the timing of an environmental cue associated with the selective force. If the environmental cue is available at the time of or before the point of developmental decision and both events precede the selective force, then a homeostatic individual will realize greater average fitness than an individual with a fixed phenotype (Figure 16.2A). If the environmental cue occurs after the time of developmental decision (Figure 16.2B), a homeostatic

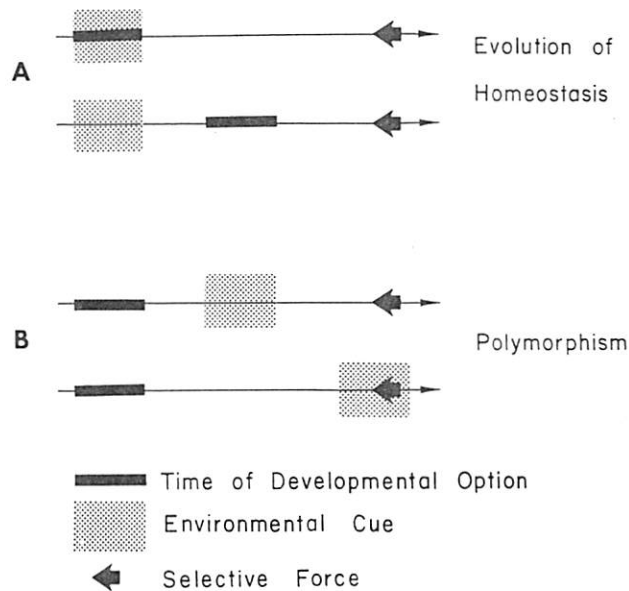


Figure 16.2. Maintenance of genetic polymorphism.

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organism will have no advantage over an individual with a fixed phenotype, regardless of whether the environmental cue precedes or coincides with the selective force and genetic polymorphism will persist in the population. Thus, genetic polymorphisms should abound among loci involved in polygenic systems when environmental predictability is low; varying degrees of homeostases coded for by a few loci or tightly linked, co-adapted gene complexes should predominate when environmental predictability is high.

One has to be careful to identify the focus of selection. In a homeostatic population, it is the ability of the individual to deploy the appropriate phenotype in response to the correlated cue. In a genetically polymorphic population, it may be the degree of genetic variance or degree of gene-gene interaction. Finally, the focus of selection may be the range of phenotypes that an individual can produce among its offspring. Dingle (this volume) has shown how maternal effects in aphids can produce fine tuning to the environment, but there are also more elusive mechanisms. Diapause, as discussed above, may occur in successive stages of the life cycle. Roff (this volume) argues that it may be the pattern of wing length variation that is selected for rather than an optimal wing length alone. Bonner (1965) described what he termed "range variation" whereby the range of variation of a phenotype can be genetically determined but the position of an individual within that range is not. Bonner's range variation encompasses more recent manifestations such as "spreading the risk" (den Boer 1968) or "bet hedging" (Stearns 1976) without the implied ultimate causality of the latter terms. Such a mechanism may be producing the pattern of diapause among *Zygaena trifolii* (Wipking and Neumann, this volume) where individual females apparently produce progeny that, among them, show the entire range of variation from univoltine, single diapause generations to generations spanning more than 3 years, accompanied by up to three periods of diapause. Regardless of the mechanism by which range variation is effected, it is probably a far more widespread adaptive response to unpredictable environments than is presently appreciated.

## Conclusions

The above considerations, well illustrated by Chapters in this volume, lead me to propose the following pervasive themes of insect life cycle strategies.

1. Life cycle delays are characteristic of most, if not all insect populations. Present knowledge concerning their genetic control indicates that they are underlain by high heritabilities and low genetic correlations with demographic traits (Dingle, this volume). Consequently, despite apparent ontogenetic or phylogenetic constraints, life cycle delays have an enormous capacity to respond adaptively to environmental exigencies or opportunities.
2. In well adapted insects, phenotypic adjustment to predictable environmental events will involve little or no genetic change in the population;

phenotypic change in response to unpredictably environmental events will involve greater or predominantly genetic change in the population (Slobodkin 1968).

3. In moderately variable environments, developmental fine tuning may be achieved by facultative life cycle delays in successive stages and/or multiple interacting cues (Vinogradova, Wardhaugh, Wipking and Neumann, Neumann, Dingle, this volume).
4. The number of loci involved in life cycle delays will increase with environmental uncertainty (Roff, Sauer et al., this volume).
5. Phenotypic plasticity surrounding life cycle delays will increase with environmental predictability. Genetic variability and heritability of life cycle delays will increase with environmental uncertainty. Phenotypic plasticity and genetic variance-covariance relationships modulating life cycle events are therefore subject to selection and adaptive in nature.
6. When environments become highly unpredictable, individuals should deploy among their offspring the full array of potentially surviving life cycle phenotypes, i.e., by spreading the risk, hedging their bets, or practicing some other tactic of range variation.

*Acknowledgments* I would especially like to thank Christina Holzapfel for many years of enjoyable discussions concerning insect development, evolution, and life cycle strategies. I have also profited greatly from informal discussions over the years with Hugh Dingle, Fritz Taylor, and L. Phillip Lounibos. I am grateful to all the participants of this symposium for their enthusiastic input in the form of provocative papers and excited discussion in Hamburg and for their prompt submission of the interesting manuscripts that I have been again stimulated by reading. Particularly, I would like to extend my appreciation to Hugh Dingle for helping organize the symposium and to Fritz Taylor and Rick Karban for taking on the large responsibility of editing this volume. Finally, I thank the National Science Foundation for continual financial support, most recently through grant BSR-8114953.

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