# PLASTICITY IN LIFE-HISTORY TRAITS

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### ABSTRACT

We describe the impact of recent life-history plasticity theory on insect studies, particularly on the interface between genetics and plasticity. We focus on the three-dimensional relationship between three key life-history traits: adult size (or mass), development time and growth rate, and the connections to life cycle regulation, host plant choice, and sexual selection in seasonal environments. The review covers fitness consequences of variation in size, development time and growth rate, and effects of sex, photoperiod, temperature, diet, and perceived mortality risk on these traits. We give special attention to evidence for adaptive plasticity in growth rates because of the important effects of such plasticity on the expected relationships between development time and adult size and, hence, on the use of life-history, fitness, and optimality approaches in ecology, as well as in genetics.

## INTRODUCTION

Life-history plasticity is a very large subject, and for a manageable review it is necessary to narrow the subject matter considerably. We chose an area of research that we believe has consequences for many branches of entomology. Recent studies suggest that variation in growth rates in insects and other organisms may often be adaptive (6). This offsets the trade-off between short juvenile development time and large adult size or mass (henceforth for simplicity referred to as body size), a trade-off that forms the basis of many life-history models because an organism that grows at a high rate can achieve both at the same time. In turn, adequate life-history theory is crucial for how we view fitness and, hence, for predictive power in biology (125).

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Consequently, we focus on plasticity shown in the three closely interrelated life-history traits mentioned above: adult size, development time from egg to adult, and the rate of juvenile growth. These traits should typically be of great importance for fitness, not the least because they also correlate with other key life-history traits.

## THEORY

### Life-History Theory

"Life-history theory" in evolutionary biology (105, 126) refers to the body of theory that deals with how the lives of organisms—the way that they develop, reproduce, and die—have been shaped by natural selection. It is a theory of life cycles, but it can also be more than this: It is a theory of fitness. To avoid the circularity and ad hoc nature of fitness definitions stated only in terms of past selection, we need definitions or models of fitness that can be used to generate predictions (125). Such models, e.g. "reproductive success" or "intrinsic rate of increase" of a genotype coding for a certain set of phenotypic traits, are always stated in terms of life-history traits, such as generation time and fecundity. A specific, albeit provisional, model of fitness helps us to find the relevant focus for further studies. A fitness framework also means that some generalization is possible beyond the studied species, to species likely to have experienced similar selection pressures.

### Plasticity Theory

The term phenotypic plasticity refers to cases when a single genotype can produce alternative phenotypes, depending on the environment during ontogeny (110, 138). The set of phenotypes produced in a range of environments is referred to as the reaction norm of the genotype to this specific set of environments (128). The reaction norm is determined by rearing randomly split clones (preferably) or families in several environments. There has been some debate regarding whether reaction norms can be selected for per se or whether they are only the sum of selection in specific environments (141). The current consensus seems to be that both types of selection and genetic determination of reaction norms may occur (140). Plasticity may be adaptive or nonadaptive, and reaction norms (or, rather, a given aspect of them) may or may not qualify as adaptations, in the narrower historical sense, to a variable environment. The distinctions are not always straightforward (46, 82, 122).

Genetic differentiation and phenotypic plasticity are two of the phenomena linking genotype to phenotype. The third is "canalization" (or "developmental homeostasis") (134), the case in which the same phenotype results regardless of environmental variation, i.e. a flat reaction norm. It seems reasonable to assume

that traits that are tightly linked to fitness should be more strongly canalized as a result of past stabilizing selection (37), and there is some experimental evidence that this is so (127).

Canalization can result from selection in favor of reaction norms that counteract environmental effects. This phenomenon, i.e. selection upwards in bad environments, downwards in good environments, is "counter-gradient selection" (28) or "antagonistic selection" (37). Stabilizing selection equals antagonistic selection in both directions (37). The reverse of antagonistic selection is "synergistic" or "co-gradient selection" (18, 37).

## Theory for the Relationship Between Time and Size

DIRECT TIME/SIZE TRADE-OFFS   A trade-off between juvenile development time and size at maturity is a typical component of life-history models (105, 126). Growth rates are explicitly or implicitly assumed to be fixed or are maximized within the constraints set by extrinsic factors. Current theory on optimal insect size typically involves a direct trade-off between the fitness advantages of large size, particularly high fecundity, and the disadvantage of a long development time (102–104). Such a trade-off is also invoked in theory on the relationship between early male emergence (protandry) and sexual size dimorphism (119, 149).

A related body of theory deals with how nonadaptive variation in growth rate affects the outcome of the time/size trade-off. Stearns & Koella (128) and later, after critique of the early models, others (12, 60) have suggested models for optimal age and size at maturity when growth rate varies because of extrinsic factors such as temperature or diet. These models, where mortality patterns in different developmental stages play an important part, suggest that the optimal reaction norm typically should be displaced towards maturing later at a smaller size when growth rate is reduced.

ADAPTIVE GROWTH RATE VARIATION    Case (23), writing in 1978, reviewed the evidence for adaptive growth rate variation in mammals. A comparative effort for other organisms, including insects, has only recently been completed (6). These reviews show compelling evidence that populations and species of organisms that need to grow fast are better adapted to do so. Moreover, evidence is accumulating that many organisms possess plastic reaction norms enabling them to grow fast in situations when they need to do so. Rather than a time/size trade-off there is a three-dimensional network of relationships between time, size, and growth rate (Figure 1) (86, 117, 144).

A model relating all three variables to each other in a seasonal environment has recently been put forward (2). High growth rates are assumed to carry mortality costs, and what decides the predictions of the model is particularly
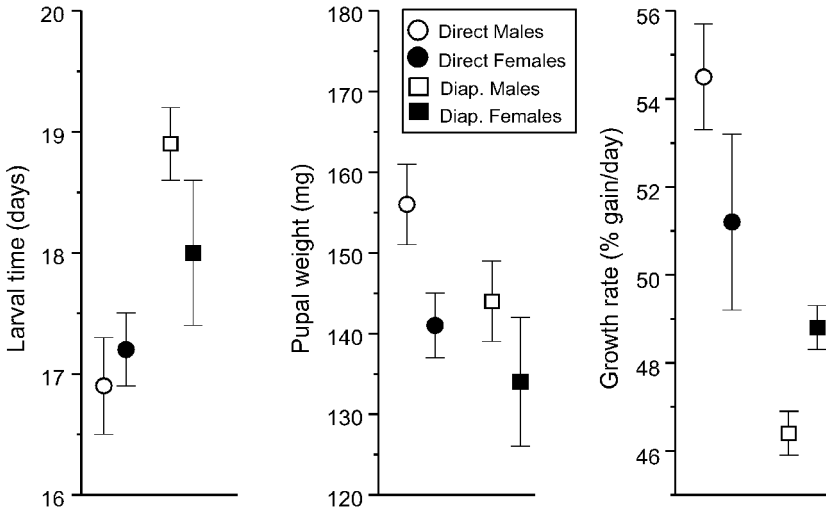
*Figure 1*    Adaptive life-history plasticity in the butterfly *Pieris napi*. Larval development times are shorter (and relatively shorter for males) under direct development to sexual maturation than under development to pupal diapause (*left*). Yet pupae are heavier, and male pupae relatively heavier, under direct development (*center*). This is explained by adaptive variation in growth rates (*right*). Data from Reference 144. Used by permission from *Oikos*.

the type of cost of having a high growth rate. Typically, growth becomes faster and size smaller with less time available. A relatively constant size is, however, probable when the cost of high growth rates increases linearly. Under more stressful circumstances, when growth rates are already close to the maximum that is physiologically possible in a given environment, the cost can be assumed to increase in an accelerating manner. Predictions then come close to those from earlier models because growth rate has little scope for varying adaptively. Sibly et al (117) has proposed a three-dimensional model that assumes a universal accelerating cost function for growth rate.

# HOW IS FITNESS RELATED TO LIFE-HISTORY TRAITS?

## Adult Size and Fitness

Female fecundity in insects generally shows a strong positive relationship to adult body mass when the number of eggs is assessed as lifetime fecundity under standard conditions or by dissection (54). Size and mass are typically strongly correlated (e.g. 121), but not always, and there are situations when it is

important to decide which is best used as a potential fitness correlate. The functions that relate fecundity to size can also be very different in the field compared with those seen under standard conditions (30). Fecundity of different species show very different types of dependence on environmental variables. The general life-style of the insect and the type of ovaries and oviposition strategies that this has selected for is likely to be of great importance in determining the major features of these connections (15, 36, 54).

Male body size can be important in male-male competition for females (45) as well as for female choice of mates (44), and it can also affect the male's mobility and ability to find females (131). In other cases, bigger males do not seem to do better in these respects (44). Size may not always be the best correlate of overall quality of individuals (148), or females can be too short-lived to afford to practice mate choice (142). There is often a positive relationship between male size and success in sperm competition, e.g. in Diptera (94), Orthoptera (135), and Lepidoptera (22). The mechanisms vary, from simply more sperm transferred to induction of longer periods before females remove the sperm or re-mate.

Small predators take small prey; large predators take large prey. Thus, when predation from insects and other invertebrates is important, selection may favor large body size in adults (98). Insect parasitoids, however, may preferentially attack large hosts (121). Vertebrates, be they fish (74), lizards (33), bats (56), or birds (29), typically prefer large prey, and hence they select for small body size in insects (4).

Predation is not the only selection pressure acting on adult body size through survival. Small individuals may survive and reproduce better when food is limited because they need less food to sustain themselves (14, 34). On the other hand, larger individuals may survive better when there is no food at all, e.g. during hibernation, if body size is correlated with nutrient reserves (93). Larger insects may also survive drought better (25).

Selection in favor of adults surviving to reproduce will sometimes be negatively size-dependent, opposing positively size-dependent selection for, possibly, large potential reproductive success. Such opposing selection pressures have been suggested to maintain size variation in the bee *Centris pallida* (4). Trade-offs of this kind can indicate that there is an optimal body size per se, rather than selection in favor of maximum size constrained only by selection for short development time. This is also suggested by the existence of adaptive variation in growth rates, since direct time-size trade-offs then become less likely (1, 67). Relatively intimate knowledge of a given system is necessary to assess the shape of the size/fitness function in a more exact manner. Because size is often a plastic trait, experimental manipulation of the phenotype is one avenue of investigation (5).

## Development Time and Fitness

In the general case, a short development time is beneficial in nonseasonal environments because this reduces the risk of death before reproduction (116). Even stronger positive effects of a short generation time are expected in species with opportunistic life-styles and fluctuating population dynamics, where the intrinsic rate of increase is a reasonable model of fitness (69). The situation is different in seasonal environments because of the constraint that diapause can only take place in species-specific developmental stages (104). The value of a short development time will then vary with the amount of time left in the favorable season, hence favoring genotypes capable of plasticity in development time. The diapause stage must be reached in time, despite variation in date of oviposition or hatching (65) and despite fluctuations in temperature (100). In some cases there will be more than enough time for the number of generations present and not enough time for an additional generation, leaving individuals with surplus time for development (90, 104).

Besides unfavorable winters, there are several other aspects of time peculiar to seasonal environments. Potential mates (143), host plants (9, 147), and other resources, as well as many natural enemies (76), all occur seasonally. In certain cases, when entering the reproductive population at an early date would mean arriving before mates or food resources are available, or arriving when enemies are still present, short development times will be actively selected against.

## Growth Rate and Fitness

In most situations, a high growth rate is beneficial. In accordance with this, ovipositing females of phytophagous insects typically show a preference for host plants capable of supporting fast larval growth (55, 133). Nevertheless, the degree of importance of high growth rates also varies. For instance, a high growth rate is more important in transitional areas where an additional generation is only barely possible than, for example, in the geographical center of the univoltine populations. It follows that females of phytophagous insects should show a stronger preference for the very best host plants in transitional areas, as seems to be the case in some butterflies (84, 107). Oviposition sites exposed to the sun can also be preferred, exploiting the positive effect of temperature on growth rates (50).

In addition, any costs and trade-offs associated with high growth rates will lead organisms to grow below their physiological maximum. In his recent review, Arendt (6) concluded that rapid growth evolves when a minimum size must be reached rapidly or to compensate for slowed growth due to environmental conditions.

Few studies have explicitly investigated the costs of high growth rates in insects. Costs in the form of higher juvenile mortality from nutritional stress

have been found in many kinds of organisms (6). In Lepidoptera larvae under food stress, high growth rates were associated with poorer survival (47, 130). Antagonistic pleiotropy between developmental rate and juvenile viability was found in *Drosophila melanogaster* (24).

High growth effort may increase the susceptibility to parasitism by bacteria and viruses, for example (111). Costs in terms of increased predation risk are also likely to be common, and they are often assumed in theoretical work (3, 78, 137). Direct evidence is scarce, but there is plenty of circumstantial evidence. In many taxa, active individuals encounter more food and grow faster, but activity also increases vulnerability to predators (77, 137). It seems reasonable to assume a trade-off between growth rate and predation risk. Contrary to earlier beliefs, increased growth rate may also increase risk of parasitoid attack (26).

Even less studied in insects are the possible consequences of high juvenile growth rates for adult quality later in life. In *D. melanogaster*, selection for increased adult longevity led to slower development up to the same size, but there was no correlation among individuals (24). A trade-off between juvenile developmental rate and adult survival seems to be present among species of *Drosophila* (109) and perhaps among populations and sexes of speckled wood butterflies (47). Fluctuating asymmetry in adults as a result of high larval growth rates is an area of research that should be explored. Asymmetry is a good indicator of stress during development (96) and can lead to decreased longevity (80).

## OBSERVED REACTION NORMS

### *Photoperiod*

Photoperiod is the main seasonal cue in insects, i.e. the environmental signal that is used to tell the date and adjust the life cycle accordingly (30, 132). Hence, we expect shorter development times in insects growing at a late date relative to either an approaching winter or an approaching optimal date for adult emergence (2). One of the first to report such low-level regulation was Masaki (75), working on crickets hibernating in the egg stage. He noted that short-day photoperiods induced short nymphal development times and reasoned that this prevented eggs from being laid too late in the autumn. Effects on size were not mentioned, suggesting that the primary mechanism was an increase in growth rate. Similar responses have been reported from other crickets (21).

In one study, aquatic larvae of Odonata grew faster in short daylengths before autumn equinox but faster in long daylengths after this date (73). This synchronized the population so that it all entered the final instar shortly after the equinox.

Short days, or decreasing photoperiods, induced short development times in several butterfly species (67, 85, 87, 90). Size was sometimes affected, but the main mechanisms were an increase in larval growth rate and in pupal

developmental rate. The patterns were seen under direct development as well as in individuals destined for diapause. The reaction norms relating development time to photoperiod had opposing slopes in two species of *Lasiommata* (87). The species differ in the stage used for hibernation, and hence the late larval stages of one species experience increasing photoperiods, and the other, decreasing photoperiods in the field.

The degree of genetic variation in these reaction norms has been investigated to a very limited degree. Variation can be expected to be weak, since regulatory reaction norms of this fundamental nature should be under strong stabilizing selection, but more variation is expected in transitional areas where the optimal phenology can vary from year to year (13, 79).

## Temperature

As a generally accepted guideline, increased temperature results in higher growth rates, shorter development times, and smaller adult size in insects and other ectotherms (114). At least the first two patterns are probably most often seen as examples of purely nonadaptive plasticity. After all, the direct effect of temperature on metabolic rates sets limits for growth rates and, since size is typically less flexible, for development times.

It is not obvious why size should necessarily decrease with increasing temperature. An adaptive explanation cannot be ruled out, especially since the effect on size is in fact not universal. There are examples of insects growing to a larger size in higher temperatures or of size not being affected at all (7, 99). The sexes may also differ in this respect, so that sexual size dimorphism varies between temperatures (32). Finally, reaction norms may be nonlinear, convex (32), or concave (146).

Effects of temperature on the size of ectotherms have been reviewed by Sibly & Atkinson (7, 8, 114). They found few exceptions to the rule of decreasing size with increasing temperature, but there were more such found in studies made under natural photoperiods. Atkinson (7) suggested that reduced size in higher temperatures can be adaptive if this means earlier reproduction, since high temperatures may signal good conditions for future population growth.

Although it may seem hard to escape the direct consequences of temperature for growth rates and development times, there are in fact many examples of presumably adaptive differences also in such reaction norms. Antagonistic selection has adapted species and populations to the temperatures in their normal environment (10, 70, 146). In the swallowtail butterfly *Papilio canadensis*, Alaskan larvae grew faster than Michigan larvae at low temperatures, primarily because of 40% higher consumption rates (10).

An example of adaptation to temperature and probably of spontaneous antagonistic selection in the laboratory is the work on *D. melanogaster* by Partridge

and colleagues (97), where replicated lines were allowed to evolve at 16.5°C or 25°C for five years. After this time each set of lines performed better when tested at the temperature at which they had been evolving. When compared at the same temperature, larvae of low temperature lines grew faster at both temperatures.

Within populations, interactions with photoperiod can aid synchronization of emergence to the rest of the population, by inducing a steeper time-temperature reaction norm when necessary (73). In the aquatic larvae of the gnat *Chaoborus americanus*, late individuals in the spring displayed steeper reaction norms, taking advantage of the rise in water temperature to catch up to earlier emerging individuals (19).

## *Diet, Density, and Hosts*

Plastic effects of poor diets and high densities of individuals can undoubtedly sometimes be purely nonadaptive, as they strike directly on the base of resources on which growth, maintenance, and reproduction have to be accomplished. However, we can still ask whether there is evidence for adaptive differences in these effects (46, 128). For instance, there is some evidence that size is more plastic in species adapted to fluctuating resources (11, 68).

A commonly observed effect of reduced resources is that the lower growth rate results in both prolonged development time and reduced size, as predicted from theory on nonadaptive growth rate variation (126). To name only one of many such examples from the literature on insect-plant relationships, the rose-hip fruit fly *Rhagoletis alternata* emerged later at a smaller size on its old host species of *Rosa*, compared with a novel host supporting higher larval growth rates (66). In *Drosophila mercatorum* and *D. melanogaster*, Gebhardt & Stearns (42, 43) found that at lower levels of yeast concentration, flies emerged later at a smaller size. They also found that genetic correlations between development time and size switched from negative to positive when going from one environment to another. In the lygeid bug *L. equestris*, populations from northern Italy and Sicily differed in their reaction norms in response to amount of food. At low food levels, individuals of both sexes of both populations attained the same adult size, but at high food levels both of these categories differed (121).

Results like those from *Drosophila* and *Lygaeus* show that the potential exists for evolution of reaction norms relating time and size to resources. Not all organisms decrease steadily in size with decreased growth rates. An alternative response (within limits) is to prolong development time and keep size rather constant, as was seen in the comma butterfly *Polygonia c-album* when reared on a number of natural host plants (84). In this species, size and fecundity were even larger when larvae were reared on *Salix caprea* than on *Urtica dioica*, although the latter host supported a higher growth rate and shorter development

time (55, 88). Such trade-offs between fitness components may help maintain the polyphagy of this and other generalist species (64). In the general case, however, larval growth rate on a particular plant species is probably in itself a good indicator of fitness in host preference studies, as this measure of larval performance usually combines the fitness advantages of a short development time and a large final weight (88).

## Perceived Mortality Risk

Mortality risk in different developmental stages plays an important part in life-history theory, not least for theory on time-rate-size relationships (105, 126). How do insects react to the perceived mortality risk?

We have seen that insects can shorten their development time when seasonal cues alert them that a season is approaching that can only be survived in a stage adapted for diapause. Similarly, larvae of the tree-hole mosquito were expected to react to conditions signaling that their ponds were drying up by metamorphosing earlier and at a smaller size (58). The results only partly corroborated these predictions, and the authors concluded that increasing solute concentration may have speeded up growth, enabling individuals to mature early at a large size.

Theory on consequences of variation in predation risk is complicated by conflicting selection pressures on growth rate. On the one hand, a dangerous juvenile stage should be avoided by growing quickly through it; on the other hand, fast growth may lead to more exposure to predators (71, 78, 137). Probably the most general prediction is that animals should grow slower and mature earlier at smaller size when there is high risk of predation (3).

In dragonfly larvae, the presence of fish predators reduced growth rate (74). This was also the case when mayfly larvae were exposed to a model fish (108). The effect on growth was so drastic that the mayflies emerged later at a smaller size, showing clearly decreased fecundity. Lepidoptera larvae altered feeding patterns to reduce exposure when insect predators were present, resulting in reduced growth (123). Lycaenid butterfly larvae grew faster when protected from enemies by ants, although they gave some resources to the ants (38). Because development time was not affected, adults emerged at a larger size.

# SYNTHESIS: LIFE CYCLES

## Time and Size Revisited

SEASON LENGTH    Along a gradient in season length, a "saw-tooth" pattern in adult size is predicted by life-history theory (75, 102, 104). Development time and body size should increase with season length, e.g. going from north to south. However, when there is a shift in voltinism, optimal body size decreases

drastically before increasing anew in areas further to the south. The reason for this pattern is that when an additional generation is only just possible, the season must be "cut" into more parts to provide for all generations. The theory has some support from studies of crickets (75, 79) and butterflies (89).

However, many insects do not fit the expected patterns in all respects. In the water strider *Aquarius remigis*, insects in a northern univoltine population were smaller and developed faster than insects in the southern, transition zone to bivoltinism. The expected fecundity advantage of large size was not found among populations (13). In the butterfly *P. c-album*, individuals of the partially bivoltine English population did have a shorter larval development time than those from the univoltine Swedish population, as predicted from theory, yet they were larger (85). Genetic variations in growth rates and in reaction norms for growth rate among populations are likely to be major sources of the incompatible patterns. In Australian *D. melanogaster*, the correlations between development time and latitude were reversed when the sampled populations were compared at two different temperatures. This was because reaction norms relating development time to temperature changed slope over the latitudinal gradient, probably as a result of local antagonistic selection (146).

DIFFERENCES BETWEEN THE SEXES    Male insects often emerge before females, at a smaller size, which has prompted theories of a direct causal relationship between protandry and sexual size dimorphism (119, 149). This is based on the assumption that the sexes grow at the same rate, which is not always the case. Males grew faster and were able to achieve protandry without loss in adult weight in, for instance, a spider (51), several butterflies (85, 92, 144), and a mosquito (72). In *D. melanogaster*, females instead generally eclose earlier, although they are larger (83). Furthermore, the sexes often have been found to differ in how growth rate responds to environmental factors such as photoperiod (67, 92, 144), temperature (32), diet (42, 121), and mortality risk (38, 58), so that protandry and sexual size dimorphism varied independently between environments.

When there is selection for protandry, males can be expected to display shorter development times than females under direct development to sexual maturation without diapause. This should not necessarily occur under diapause development because males need not enter diapause early in order to display protandry in the following spring (86, 92). Because there is typically also a selective premium on large male size, we can predict larger male-biased differences in growth rate under direct development, as has been found repeatedly in butterflies (85, 92, 136, 144) (cf Figure 1).

The fact that females of most insects are larger than males, with or without protandry, suggests that the fecundity advantage of large female size typically

is more important for fitness than the advantages of large size in males. When in combination with selection for protandry, we should expect males to become relatively smaller in stressful situations. This has been found in a lycaenid butterfly under time stress (67) and in a mosquito (63) and a butterfly under food stress (59). In *D. mercatorum*, however, females decreased more in size when given a poor diet, although they prolonged development time more than did males (42). Such a result could indicate that growth rates were closer to maximum in females than in males, and indeed this is suggested by the fact that females were heavier and protandry was absent. Protandry is not expected in populations with several overlapping generations per year (92, 119).

An interesting comparison can be made with sexes of the butterfly *Pieris napi*, a polyandrous species in which males give large and nutritious spermatophores to females at mating. In this species, males are larger than females. When given a poor diet, females responded more strongly than males in the direction of shorter development time and reduced size, perhaps because they could expect later nutrient compensation from male donations (68).

The genetics of differences in time-rate-size relationships between the sexes have not been studied in much detail. There is some evidence for a sex-linked inheritance of development time in the butterfly *Pararge aegeria* (91). Reeve & Fairbairn (101) selected for size dimorphism in *D. melanogaster*. Body size responded well to selection, but, contrary to theoretical predictions, dimorphism decreased in most selection lines. The authors suggested that changes in dimorphism are caused by the fact that male and female growth trajectories are not parallel. Termination of growth at different points results in dimorphism but at levels that are difficult to predict without detailed knowledge of growth parameters.

## When to Expect Trade-Offs

A trade-off between juvenile development time and adult size must exist at some level because constraints on resource availability and uptake would indicate that an organism cannot grow to a very large size in a very short time (115). This particular trade-off is not necessarily always the most essential part of a life-history model that aims to explain variation among organisms, especially not within species.

One factor influencing the likelihood of trade-offs is whether or not a nonfeeding stage intrudes in the life cycle before sexual maturation. In holometabolous insects such as Lepidoptera or Diptera, the pupal stage acts to a degree as a buffer for selection on development time (83, 85, 92). Similarly, clear trade-offs are not expected in species with an obligatory diapause in the adult stage (119). However, the duration of the larval stage can be the direct target for selection, e.g. when there is a constraint to feed early in the season (9) or when there is scramble competition for resources that are being rapidly depleted (57).

We should expect clearer trade-offs in insects having very short generation times relative to season length, e.g. *Drosophila.* When most generations develop directly (without diapause), the situation approaches the nonseasonal one where *r* is a reasonable model of fitness (103, 120). Development times are expected to be minimized and growth rates to be close to maximum, particularly in opportunistic species, and trade-offs become likely (83).

Among populations, we can expect geographical trends in development time. Because of counter-gradient variation, we may not always see the trends in size with season length that are predicted by theory (102, 104). But, in that case, we should instead see trends in genetic growth rate and clearer trade-offs in short-season areas and in transitional areas where voltinism changes.

Clearer trade-offs are also expected in more stressful situations, as seen in the preceding section for differences between the sexes. We can expect them under time stress or when resources are limited, especially when these factors are piled one upon the other. Larvae of the butterfly *Papilio glaucus* in Alaska displayed fast growth at low temperatures, but the higher respiration of individuals of this population compared with larvae of a Michigan population led to strong interactions with host plant quality (10).

The same type of reasoning applies among individuals within populations. Ignoring genetic variation, we should expect more positive phenotypic time-size correlations under stress because trade-offs become necessary. This has been observed for time stress (87), but for food stress the opposite patterns have been seen (17, 42). One proposed explanation (42) is based on the fact that patterns of genetic correlation change between environments (118, 124). Genotypes may display worse canalization (more divergent reaction norms) under stress (62), so that some genotypes perform better than others in terms of growth rate.

## Egg Size and Maternal Effects

So far, we have taken into account neither variation in the amount of resources given by mothers to the egg nor other maternal effects. Egg size can vary adaptively (16) and is sometimes a plastic trait (39, 40). In seed beetles, adaptive plasticity in egg size has been found in response to competition (61) and host plant characteristics (41). A large egg can conceivably also be an alternative to high growth rate or low adult size when short development times are important (113).

In a bruchid beetle, development time increased when egg size decreased because of maternal age, but increased egg size because of multiple matings or adult feeding did not result in reduced development time (40). Among species of ladybird beetles, species with proportionally small eggs took longer to complete their development than did species with large eggs (129). In a heteropteran

bug, egg size largely determined adult size, suggesting that development time was little affected (53). In butterflies, relationships between egg size and development time were weak (16, 85). There is reason to believe that negative correlations will not be universal, since the egg can carry only a limited amount of the resources needed up to adulthood. In some systems, other types of maternal effects may be of importance for development time, those based on hormonal control of the life cycle rather than on nutrient flow (49).

## *Plasticity at Two Levels*

With insects, it is often useful to make a distinction between life-history plasticity acting at the higher level of life cycle regulation (or "choice" between developmental pathways) and the lower level of environmental effects seen within pathways. In reality, however, the system of regulation is a complex hierarchy (30).

HIGH LEVEL PLASTICITY    Insects are often polymorphic, displaying a number of more or less discrete phenotypes within populations (31, 106). The morphs can be determined by genetic differences ("genetic polymorphism") or by plasticity ("polyphenism"), but in the latter case there is often genetic variation for the plasticity (106). Morphs are often distinguished by life-history characteristics as well as by morphology. The most universal kind of insect polymorphism is seasonal polyphenism (110), where the generations seen over the year differ. Commonly, one phenotype is associated with diapause and/or migration and one is not, and the "choice" of developmental pathway is done in response to seasonal cues such as temperature (145), diet, and, above all, photoperiod (30, 132).

Besides cued (hormonal) regulation, environmental effects of the more direct type are important in life cycle regulation (30). Growth rate variation caused by temperature or diet may be what determines whether individuals experience conditions that can induce direct development when they are in a developmental stage that responds to such cues (112, 132). Over the years, selection will act on the thresholds (27) but presumably also on the reaction norms relating development time to environmental variation. The outcome should be a near-optimal interplay between them in the "typical" environment or possibly a bet-hedging strategy in the face of year-to-year fluctuations (48). A still largely unexplored area of research is what type of spatial and temporal variation maintains the genetic variation so often seen in polymorphism and polyphenism (18, 106). Such systems should be prime targets of research on insect life-history plasticity (46).

LOW LEVEL PLASTICITY    As we have seen, growth and development within developmental pathways are also strongly affected by the environment. Some

of these effects are clearly of a cued, regulatory nature, i.e. under hormonal control. Evidently, over time insects adapt to predictable environmental fluctuations and make use of environmental cues to fine-tune development, achieving synchronization to the environment and to conspecifics (30).

The borderline between cued and direct plasticity may in fact not be very sharp because co-gradient selection will favor reaction norms that respond in a suitable manner to environmental variation (18). For instance, consider growth rate variation from extrinsic and intrinsic sources and how this variation interplays with choice of developmental pathway. The optimal development time should be shorter, and the optimal growth rate typically higher, for directly developing individuals (86, 144). This is probably the reason why conditions that lead to long development times (low temperature, poor diet, crowding) also often act as cues for hormonal regulation, forming part of the mechanism for inducing diapause (132, 136). Furthermore, genetic variation in growth rates may co-vary with thresholds for diapause induction, forming co-adapted syndromes (52, 81).

## CONCLUSIONS AND PROSPECTS

It is not really genes but the reaction norms of genotypes that change in evolution (35). Because reaction norms often cross, heritabilities and genetic correlations change between environments (124), but understanding the sources of such complications is the first step towards their clarification. We need a synthesis of ecology and genetics to find out what to expect in terms of the nature and stability of genetic variation, heritabilities, genetic correlations, and trade-offs. Only a combination of the optimality approach of evolutionary ecology and the constraint approach of genetics will cast real light on these subjects (91) and on the evolution of reaction norms (139, 141).

Outside of genetics, a more general recognition is needed that plasticity in the form of direct environmental effects does not preclude adaptation; differences in reaction norms of this type can still be adaptive. Furthermore, we need to study the general rules and the exceptions (8). Is size a more canalized trait in the face of growth rate reductions, when size is itself very important for fitness? Is size a more plastic trait when resources are likely to disappear, enabling development to still be completed? Are there understandable and predictable differences among insects in the minimum (threshold) time and size needed to reach adulthood (20, 99)?

The prevalence of adaptive growth rate variation has its own consequences. Trade-offs between development time and adult size do not always occur (92). Reaction norms for size or development time of different genotypes in a population need not cross, as they are expected to do if there is a tight time/size

trade-off, and hence consistent heritabilities and genetic correlations across environments in these traits become more probable.

Finally, some fundamental questions in evolutionary biology are still in need of an answer. Plasticity seems to provide a wonderful way of adapting the phenotype; so why are not all organisms perfectly plastic? Is the main reason that plasticity is hard to evolve, or is it that it disappears quickly in stable environments? If the latter, are there costs of plasticity (82), or is it the time-lags between induction and expression that select against plastic phenotypes (95)? Is plasticity the raw material for speciation and biodiversity (138)? The subject of phenotypic plasticity still holds many challenges.

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