

ECOLOGY AND BEHAVIOR OF FIRST INSTAR LARVAL LEPIDOPTERA

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■ **Abstract** Neonate Lepidoptera are confronted with the daunting task of establishing themselves on a food plant. The factors relevant to this process need to be considered at spatial and temporal scales relevant to the larva and not the investigator. Neonates have to cope with an array of plant surface characters as well as internal characters once the integument is ruptured. These characters, as well as microclimatic conditions, vary within and between plant modules and interact with larval feeding requirements, strongly affecting movement behavior, which may be extensive even for such small organisms. In addition to these factors, there is an array of predators, pathogens, and parasitoids with which first instars must contend. Not surprisingly, mortality in neonates is high but can vary widely. Experimental and manipulative studies, as well as detailed observations of the animal, are vital if the subtle interaction of factors responsible for this high and variable mortality are to be understood. These studies are essential for an understanding of theories linking female oviposition behavior with larval survival, plant defense theory, and population dynamics, as well as modern crop resistance breeding programs.

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INTRODUCTION

As has been observed by anyone following the fate of lepidopteran larvae in the field, it is during the first instar, soon after hatching, that most animals disappear and are assumed to have died. That generally high but variable rates of mortality occur in first instar caterpillars has been recognized since at least the 1960s, when formal life-table analysis began in earnest. The causes of this apparent mortality are not always clear, partly because of the small size of first instars. Even live animals are hard to find, and within hours of death the cadavers of neonates desiccate and disappear.

When assessing the fate of first instars, there is a great deal of conjecture and superficial treatment of mortality estimates, causative agents, and precisely when death occurs. This, in part, reflects the limitation of a life-table approach when trying to disentangle the subtle interactions that take place in the first few hours of a neonate's life. Shortly after hatching a neonate needs to establish a feeding site, negotiating some or all of the following: leaf hairs, surface waxes, hard plant parts, laticifers, glands or tissues filled with allelochemicals, locally induced plant changes, variable microenvironments, predators, pathogens, and parasitoids! The life-table paradigm in population ecology has a number of methodological problems (109, 138, 188, 221), ranging from loss of information by averaging mortalities to errors associated with sampling and the inability to assign cause of death. For first instars, which are difficult to find and follow, these methodological problems are exacerbated.

We argue that intensive observation and manipulative experimentation are essential if we are to understand neonate survival and growth. Beginning with a review of life-table studies, we highlight the patterns that such studies yield, but

stress their low explanatory power. We then draw together the growing, but scattered, literature dealing with observational and manipulative studies on neonate caterpillars. As will be apparent to readers in some sections, our review is less than comprehensive. Limitations on space preclude this. We seek merely to alert readers to the factors that need to be considered.

SURVIVAL OF NEONATES AND MORTALITY FACTORS

Data Set and Caveats

From the literature on mortality of early stages of Lepidoptera, we reviewed data from 141 studies for 105 species (Appendix, see the Supplemental Material link at www.annualreviews.org). In some cases early instars were not distinguished, and we took early stage survival to be from egg to established larva (instar III or IV). Most are classic life-table studies of pest species, based only on samples from a single "population" at key points of the life-cycle (104 studies) (Appendix, see the Supplemental Material link at www.annualreviews.org). Alternatively, by regular observation, authors followed a cohort of individuals from birth, or when neonates/eggs were placed on plants, to their time of disappearance (11 studies, mainly of butterflies). Others attempted to closely monitor their subjects (37, 97, 138) or carried out experimental studies that attempted to measure mortality factors by manipulations (12 studies) or through some mixture of experiment and life-table (16 studies). Although most studies are on pest species, a number have been undertaken on nonpest Lepidoptera, mainly butterflies (33 species), particularly Papilionidae (13 species) and Nymphalidae (8 species).

Life-tables represent a summary of survival data across either time (usually one or many generations within and/or across years) or space (many plants, samples, sites, or experimental blocks). Where many studies have been undertaken on a single species, we quote the average of the mean mortality rate recorded in a stage and the minimum and maximum mortality recorded across the studies (Appendix, see the Supplemental Material link at www.annualreviews.org). We include the egg stage if available, because most studies based on sampling are not sufficiently sensitive to distinguish when mortality actually occurs and so can underestimate first instar mortality and overestimate mortality in the egg stage. Egg mortality will be overestimated because survival in this stage is usually calculated by dividing the number of first instars found by the estimate of the number of eggs. Deaths occurring after egg hatch but before a census would be wrongly attributed to egg mortality (e.g., 56, 124). In cases where authors could not detect first instars, survival is simply quoted from the egg (sometimes estimated from female numbers and potential fecundity) to some later stage, such as the II or III instar (e.g., 4, 19, 119, 229, 235).

Mortality in the early larval stages of Lepidoptera is high. Between 9 and 96% of the first (or early) instar stage(s) are lost, with the usual level of mortality around 25–75% (in 80 species). Generally, some 41% (100 q_x values) of the egg stage and

54% of the first instar are lost (Appendix, see the Supplemental Material link at www.annualreviews.org). Thus, by the end of the first instar a cohort of 100 eggs would have been reduced to 27 individuals on average.

Census data, as are commonly recorded in life-table studies, may underestimate real mortality. In our own research, we have compared survival estimated from regular samples of naturally laid monarch, *Danaus plexippus*, eggs and subsequent first instars, to estimates of first instar mortality based on experiments in which we placed eggs out at the hatching stage onto *Asclepias humistrata* in the field. Based on census estimates, we recorded between 66–82% mortality. From direct experiment we estimated 88–97% mortality of first instars (243).

Patterns in the Level and Distribution of Mortality in Early Stages

Based on a limited number of life-table studies available at the time (including 13 lepidopteran species), Price (187) suggested exposed feeders suffered a much higher mortality rate (average 70%) than concealed feeders (40%). We find a similar tendency (Table 1), but the variation is high and the differences much smaller. Leaf miners (concealed feeders) generally have a lower level of mortality in the first instar (32%), but borers that also “conceal” themselves have a relatively high mortality rate (50%). Mortality of exposed foliage feeders is high (53%), but mortality of foliage feeders that feed in aggregations, and frequently concealed in webs, is also relatively high (41%). The highest mortality was in those species with “mixed” feeding habits (70%; Table 1). One difficulty in this analysis lies in correctly identifying where and how a first instar feeds. Many species change feeding habits (see below), and those that feed on foliage often move to buds and are effectively concealed. A more accurate description of many exposed foliage feeders is that they have “mixed feeding habits” and are frequently concealed in flower buds and leaves, or under leaf hairs that are grazed (Figure 1), as well as feeding on exposed leaf surfaces.

The degree of host “specialization” appears to influence survival. Species feeding on hosts within a single plant family we arbitrarily classified as specialist and those that feed on more than one family as polyphagous. On average, there was 57% mortality in first instars of polyphagous species and 43% in specialists. There was only a slight effect of the mode of egg laying on mortality (batch or egg mass versus single egg layers); species that lay eggs in masses tend to have a high mortality rate in the first instar (60%) (Table 1).

The variance in early-stage mortality is generally high (Appendix, see the Supplemental Material link at www.annualreviews.org). Variability may be high at the one time across space (Figure 2a), over time and space (Figure 2b), over time at one place (Figure 2c), or across host plants at the one time in one place (Figure 2d). This variability makes comparisons between studies difficult, as well as making conclusions about consistent patterns in the level and cause of mortality associated with any particular factor such as host specialization, mode of feeding, and so forth less than convincing.

TABLE 1 Mean stage mortality (100 q_x) and standard error (se) for egg and first/early instars among 105 species of Lepidoptera. Values in parentheses beneath the mean are the range in values, minimum to maximum. Data split by mode of egg laying, feeding, and host specialization^a

Mode of egg laying					
Stage	Specials	Batch	Mass	Singly	
Egg	X (se)	X (se)	X (se)	X (se)	
	22 (7)	48 (6)	42 (5)	41 (3)	
	(5–51)	(8–88)	(1–90)	(4–82)	
Firsts	49 (3)	44 (5)	60 (5)	46 (3)	
	(37–60)	(9–88)	(15–96)	(13–95)	
Mode of feeding					
Stage	Borer	Foliage	Colony	Leaf miner	Mixed
Egg	X (se)	X (se)	X (se)	X (se)	X (se)
	34 (7)	46 (3)	35 (6)	36 (7)	37 (8)
	(5–70)	(6–90)	(1–90)	(4–81)	(7–66)
Firsts	50 (5)	53 (3)	41 (5)	32 (4)	71 (5)
	(23–96)	(20–95)	(13–85)	(9–84)	(54–91)
Host specialization					
Stage	Specialist	Polyphagous			
Egg	X (se)	X (se)			
	40 (3)	42 (5)			
	(1–88)	(4–90)			
Firsts	43 (2)	57 (4)			
	(9–96)	(15–95)			

^aSpecials, eggs laid elsewhere, not on the host; batch, a small group of eggs; mass, several hundred eggs; mixed, the animals feed on various plant parts, frequently the flowers as well as leaves; specialist, hosts restricted to one plant family; polyphagy, more than one family.

Causes of Mortality

What factors account for the early-stage mortality found in life-tables? There are numerous descriptors of mortality proffered. Although the terminology may vary, the basic causes supposedly identified that are listed first come down to predators (41 studies), unknown (18 studies), disappearance (14 studies), dispersal (13 studies), weather (12 studies), and failure to establish and host-related factors (28 studies). Cornell & Hawkins (45), using a database similar to ours, accepted the authors' assessments and concluded that "predation is of overwhelming importance." We are more skeptical.

Even with intense observation, it can be difficult to determine cause of death. Most studies can only really say the animals disappeared and died owing to causes "unknown." Predation is often assumed, but predation does not equate to missing or unknown. One would need to study predators, preferably by direct observation, to determine when, how often, and what they eat (e.g., 205) or watch caterpillars and see what eats them (20, 176, 209). Most studies that claim predation as

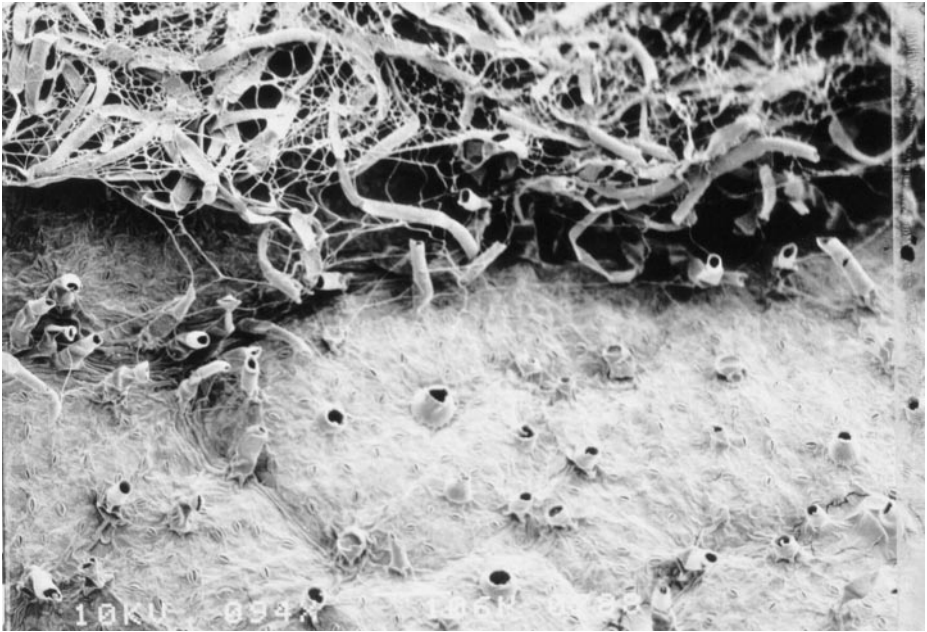


Figure 1 Leaf hairs of *Asclepias syriaca* (background) covered in first instar monarch caterpillar silk and grazed hairs in the foreground. Neonates need to clear a patch of hairs by grazing before they can begin to establish a feeding site on the leaf surface.

the major cause of death did not confirm this with additional experiments (e.g., 19, 28, 51, 98, 174, 213, 223, 228, 231; Appendix, see the Supplemental Material link at www.annualreviews.org). The level of mortality due to predation among first instars can be tested using exclusion (e.g., 50, 82, 118, 165, 212, 221, 230) or other techniques such as chemical treatment (e.g., 67) or precipitin tests (e.g., 54). In the absence of much direct data on the role of predation, we conclude that the overwhelming cause of disappearance and mortality in first instars is agents or factors “unknown.”

For many studies the failure of larvae to establish on host plants is cited as a cause of loss, although here too the causative agent is not always clear. Dispersal from hosts and high losses are not uncommon in some systems (e.g., 14, 18, 29, 52, 54, 59, 76, 89, 134, 143, 177, 178; see Dispersal and Feeding Site Location of First Instars).

In only a few studies have the authors tried to differentiate losses due to predation, dispersal, and host establishment. Dempster (54) used immunoassays to identify a group of predators that had fed on cinnabar moth, *Tyria jacobaeae*, larvae. These results were associated with larvae that were missing from intensive cohort life-table studies. Others have used cadavers (e.g., 165) and cage exclusions to determine the relative contribution of predation (e.g., 50, 82, 118, 165, 212, 221).

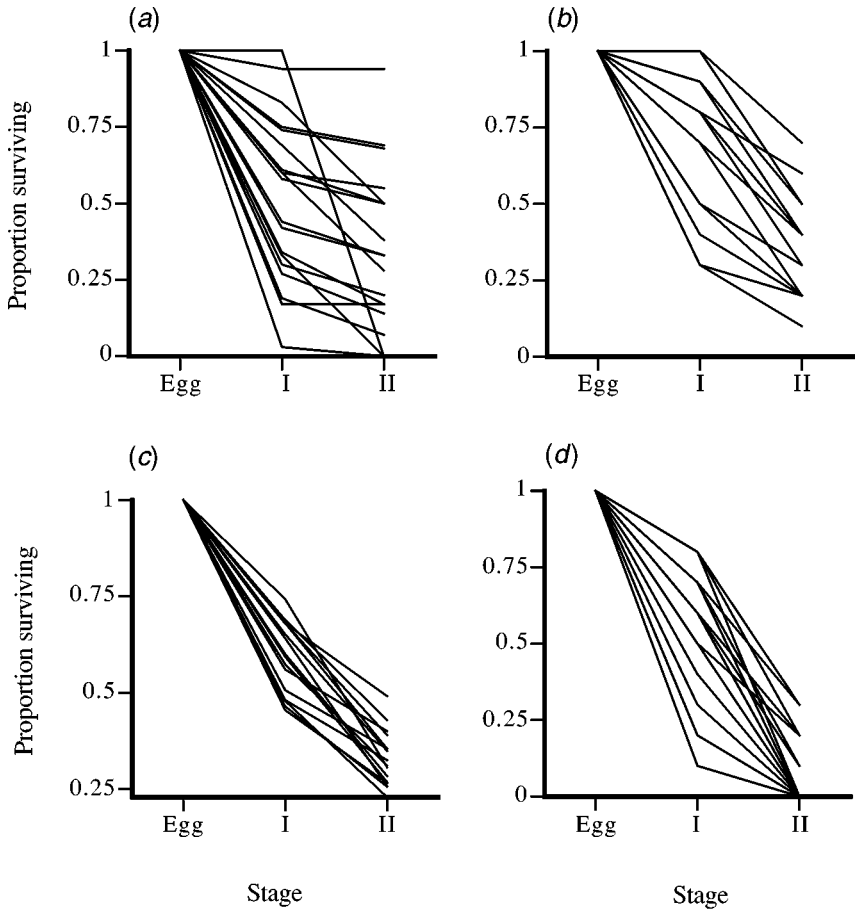


Figure 2 Early stage survival (egg to second instar), expressed as a standardized l_x curve for: (A) *Ochrogaster lunifer*, an egg mass-laying species that does not feed in the first instar and forages as a group from a nest at the base of a host tree. Each curve represents a separate site ($n = 19$ sites) and is based on a complete census of the site over one generation (see 88). (B) *Papilio xuthus*, a single-egg layer that feeds on young foliage. Curves are based on samples from field populations at four sites over four generations (see 114). (C) *Perthida glyphopa*, a leaf miner that lays eggs into leaf tissue. Curves are for one site sampled over 16 years (170). (D) *Helicoverpa* sp., a single-egg layer with mixed feeding habits. Curves recorded at the one site and year across six different host plants (221).

Results can be mixed and differ among broods or time (82, 133, 232) and place or host (86, 192, 212, 221). Mason & Torgersen (165) found that roughly 47% of losses in first instars were due to predators and 40% to dispersal. Protected cohorts of *Omphalocera munroei* suffered 50% mortality (50). Other studies have found high mortality in protected and exposed cohorts in the field (e.g., 82, 230) and the laboratory (138, 234), although this is not always the case (118, 228). As has been noted by others (e.g., 157), one needs to be cautious when using cages to exclude predators. Cages may prevent neonates leaving the plant or plant part (Figure 3), perhaps improving survival.

Generally, parasitism is not a major cause of mortality in neonates (but see 93, 197, 226, 234), although it can be for eggs (see 206a). Weather effects generally include drowning or wash-off owing to rainfall (e.g., 28, 101, 206), high temperature (e.g., 189), and low winter temperatures (e.g., 15, 213). Again, these factors are often assumed to be causative based on correlation or association.

Interactions Between Mortality Factors

Various mortality factors can interact and generate either additive or antagonistic changes in mortality (123). In natural enemy exclusion experiments with neonate *Heliothis virescens* larvae, there was significant synergism between mortality caused by expression of *Bacillus thuringiensis* toxin in genetically engineered tobacco plants and mortality caused by natural enemies.

Different feeding guilds of natural enemies that attack neonates in different ways are likely to interact directly, through intra- and interspecific competition, and indirectly, through their prey. The numbers of neonate corn earworms, *Helicoverpa zea*, that were consumed by lygaeid bug and lynx spider predators varied according to the densities and presence or absence of the other predator (99).

Other factors can also have indirect impacts on neonates. For example, the presence of vesicular-arbuscular mycorrhizae on the roots of soybeans significantly reduced growth rates and survival of neonate larvae of *H. zea* (93a, 190).

A continuing debate invokes the relative significance of either bottom-up or top-down regulation of insect population dynamics. In a test of these processes using neonate larvae of the oecophorid, *Psilocorsis quercicella*, Lill & Marquis (149) concluded that plant quality had a more important direct effect on herbivore survivorship and fecundity than it had an indirect effect on predation. The indirect effect was mediated through increased development time and increased exposure to natural enemies. Benrey & Denno (16) found support for the “slow-growth-high-mortality hypothesis” because slow development of the first two instars of the cabbage white, *Pieris rapae*, resulted in increased attack by a braconid parasitoid. However, the effect was complicated when examined across host-plant species because host plants influenced parasitoid foraging directly (25).

Neonate Defenses

Although there is a large literature that describes chemical, physiological, behavioral, and morphological defenses in lepidopteran larvae against natural enemies,

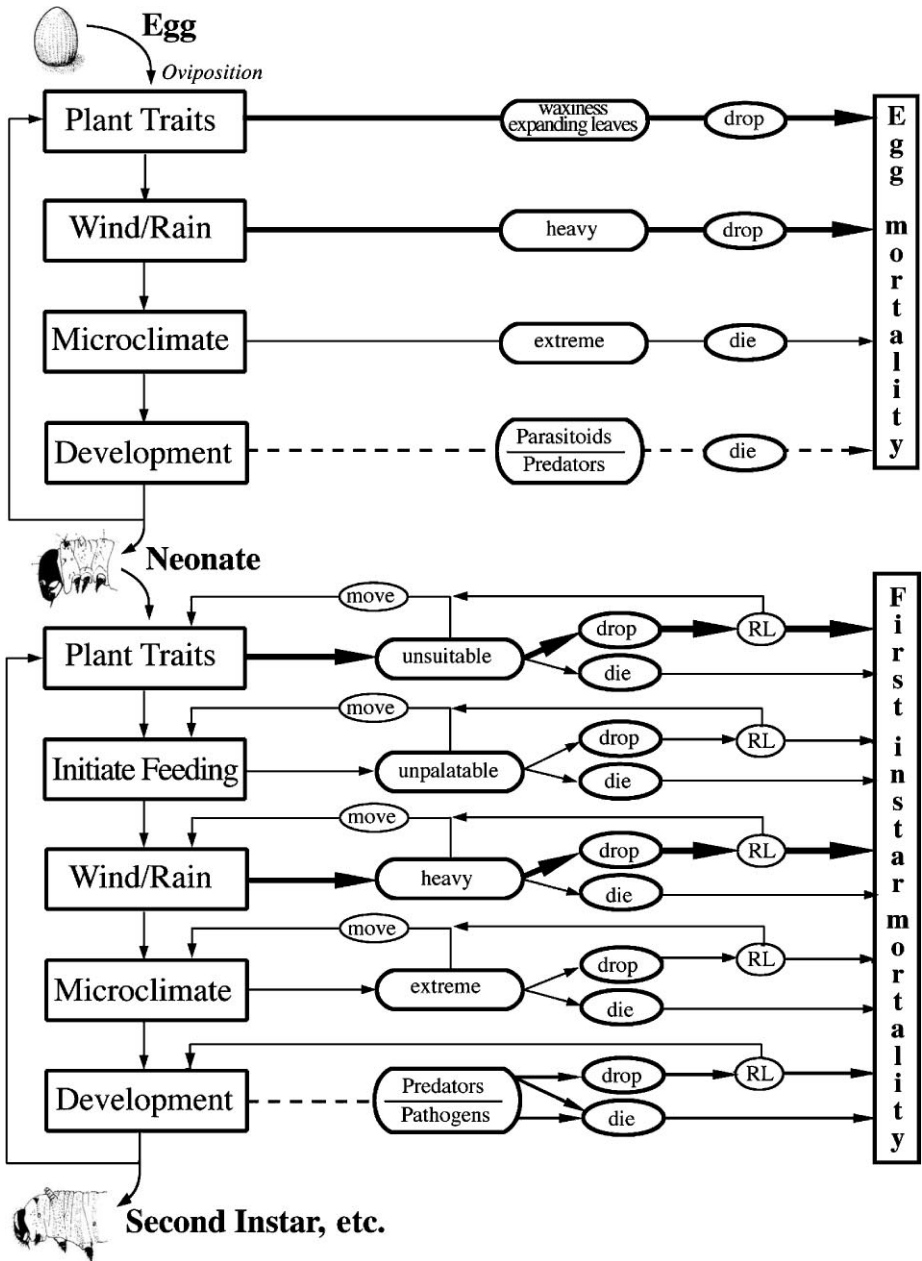


Figure 3 Conceptual model in flow diagram form detailing processes and interactions that take place from egg placement on or near a plant to establishment of a second instar larva. Life-tables only record mortality (extreme right-hand side) and cannot distinguish between suitability of plant (or plant part) and microclimate leading to increased movement (modified after 221). (RL = relocate plant)

almost all research has been on later instars. Thus, little is known about developmental changes in defenses apart from some of the obvious changes that some larvae undergo as they change from mimicry of bird droppings in early instars to a more general background crypsis in later instars (47, 66). Despite their small size and apparent vulnerability, neonates can defend themselves against natural enemies through the use of aposematic, cryptic, hiding, flight, and distributional defenses. For example, carboxylic acids and terpenes in the spines and neck glands situated ventrally in the prothorax, just in front of the first pair of legs of first instar larvae of the nymphalids *Dione junio* and *Abanante hylonome* repelled predatory ants, although later instars survived ant attacks better than first instars (181).

A Conceptual Model for Early Stage Survival and Behavior

No one factor can consistently account for the high level and variability of mortality in first instars. Because so many factors are potentially responsible (Figure 3), and these interact and are themselves variable, it is perhaps not surprising that mortality is high but variable. Thus, apart from weather effects, such as rainfall and high and low temperatures, the insect has to physically breach the plant's integument, along the way negotiating leaf hairs (e.g., 100), surface waxes (e.g., 70, 72, 73; see Leaf Waxes and Other Leaf Surface Chemicals), and a hard epicuticle (see below), all on a rapidly expanding leaf (3). Various experimental studies have shown that these factors may be crucial to survival (see below). Having penetrated the leaf surface, the larva will need to gain adequate nutrition (sugars, amino acids) while avoiding locally high levels of allelochemicals (200), as well as induced defenses (129). Constitutive allelochemicals may be locally high and contained within vacuoles, glands, and laticifers (44, 63, 65, 79). At this scale they may cause problems even for specialized herbivores (e.g., 244). Once the leaf integument is ruptured, a cascade of various plant responses is triggered that will influence larval abilities to continue feeding (e.g., 169). In many instances the larval behavioral response is to leave the plant module or entire plant by walking or ballooning (Figure 3; see Dispersal and Feeding Site Location of First Instars). Such losses may or may not result in death. Simply enumerating the losses does not tell us which mechanism may be responsible (Figure 3) or readily distinguish between direct mortality and movement.

If plant factors are crucial, the initial location of a larva on a plant may well influence its ability to establish itself. This has been found in some systems (22, 38, 115, 121, 122) but not others (1, 80). To this array of potential mortality factors we then overlay the third trophic level, which includes predators, parasitoids, and pathogens (Figure 3). Animals that wander more owing to unsuitable plant factors or microclimate may be exposed to a greater risk of predation from both sit-and-wait and active-search predators (111), as well as pathogens (10). Contact with predators will also influence movement of caterpillars (210). Given all these factors, it is not surprising that mortality is high and that the life-table paradigm does not enable this mortality to be readily disentangled (Figure 3) without detailed observation and experimentation.

We next review studies that have focused on the effect of external plant features and the internal characteristics that affect first instar development, physiology, behavior, and subsequent survival.

EXTERNAL PLANT FACTORS FACING A NEONATE

Because of their small size, physical aspects of the environment that may be unimportant to older instars can be critical to first instar larvae, particularly as neonates. Some of these aspects are addressed below.

Plant Architecture

Variation in plant modularity, size, and morphology affects neonate larvae (128, 142, 163). Whereas much variation may be accounted for by female oviposition choice, it is clear that plant structure has a direct impact on neonate behavior. Noctuid larvae on *Daphne laureola* preferred leaf whorls with shorter stems and lower-order branches because movement costs may be lower (6). The effects of variable plant architecture on neonate larvae may be controlled in part by larval foraging behaviors. In the social caterpillar, *Malacosoma disstria*, trail marking can facilitate sibling foraging through the production of more heavily marked trails by satiated larvae as they return from depleted feeding sites to bivouac sites (85).

Leaf Hairs and Trichomes

Leaf surface hairs and trichomes can affect neonate caterpillars in two ways. Nonglandular trichomes are mechanical defenses that impede the progress of caterpillars across the leaf, entrap larvae, or restrict access to the leaf surface (62). On a number of milkweeds monarch neonates have to graze down the leaf hairs to reach the surface (117, 159; Figure 1). Glandular trichomes, which secrete exudates, offer this mechanical defense but with the additional problem that the exudate may contain chemicals that are toxic to the insect (150) or mechanically hindering or sticky (225). Leaf area consumption of Siberian elm clones by neonate *Paleacrita vernata* was negatively related to the trichome density (61). Similarly, neonate *Spodoptera exigua* survival was significantly negatively correlated with glandular trichome density on 12 tomato accessions (75). On the glandular genotype of *Datura wrightii* neonate tobacco hornworm, *Manduca sexta*, larvae consumed less and grew slower. The difference was isolated to the presence of the glandular exudate, a complex mixture of sugar esters (225).

Leaf Waxes and Other Leaf Surface Chemicals

Although the simple presence or absence of surface waxes has been implicated as deterrents of larval feeding or establishment (127, 241), the type of leaf waxes, rather than leaf waxes per se, may be more critical to neonate larval establishment

and survival. On glossy-leaf varieties of cabbage, diamondback moth (*Plutella xylostella*) neonates spent more time walking, spinning silk, and taking test bites than on cabbages with normal wax bloom (70–72). This resulted in greater dispersal, lower establishment, and ultimately poorer survival on glossy leaf varieties (73, 74). Compounds found in higher levels in the glossy wax type over normal wax bloom included n-alkane-1-ols and alpha- and beta-amyrins (71). Similarly, increased walking rates and decreased feeding were found for neonate *P. rapae* caterpillars on glossy leaf varieties versus normal wax varieties of collard (215).

In addition to lipophilic waxes, leaf surface chemicals include many more hydrophilic primary and secondary metabolites, especially free amino acids and soluble carbohydrates (58). Whereas many of these chemicals influence oviposition choice by Lepidoptera, little is known about their direct or indirect effects on neonate behavior and performance (33, 69, 207).

Leaf Toughness and Hardness

The ability to locate leaf tissue that can be readily cut or torn by a neonate's mandibles and ingested is critical to its survival. The mechanical problems the larva has to overcome are toughness and hardness (156). Various penetrometer devices and cutting tests have been used (e.g., 35, 198) that indicate a deterrent effect of leaf structures to invertebrate herbivory (e.g., 35, 40, 83). Leaf toughness (due to cell walls) and hardness (due to localized amorphous silica) varies within and among plant modules (156; Figure 4) and affects wear and tear of mandibles (23). High hemicellulose content of corn partially explains resistance to fall armyworm (*Spodoptera frugiperda*) neonates (110).

Leaf Micro-Flora

The leaf phylloplane is home to a complex fauna of bacteria, fungi, and other microbes (13, 132). When such microbes are pathogenic to insect larvae, grazing on the leaf surface and thus ingesting the microbe is potentially dangerous to a caterpillar. Alternatively, plant pathogens may alter host quality (239). Although the evidence is scant, there is reason to believe that leaf micro-flora may be more of a threat to young than old caterpillars. In laboratory trials the time required for *B. thuringiensis* Cry1A(a) toxin to kill first instar fall-webworm caterpillars, *Hyphantria cunea*, was one third of the time required to kill second instar spruce budworm, *Choristoneura fumiferana* (191). How much of this difference is due to species differences, rather than instar differences, cannot be determined. Similarly, under field conditions, only first instar *D. plexippus* larvae were likely to become infested with the neogregarine parasite, *Ophryocystis elektroscirrha*, which is sufficient to lead to a detectable parasite load in the adult (146). However, neonates do have the ability to discriminate between potentially toxic diets. *Epiphyas postvittana* neonates were able to discriminate between diets containing *B. thuringiensis* toxins Cry1A(c) and Cry1Ba (105), and first instars of *S. frugiperda* had a clear preference for intact leaves of *Festuca arundinacea* over leaves infested with the

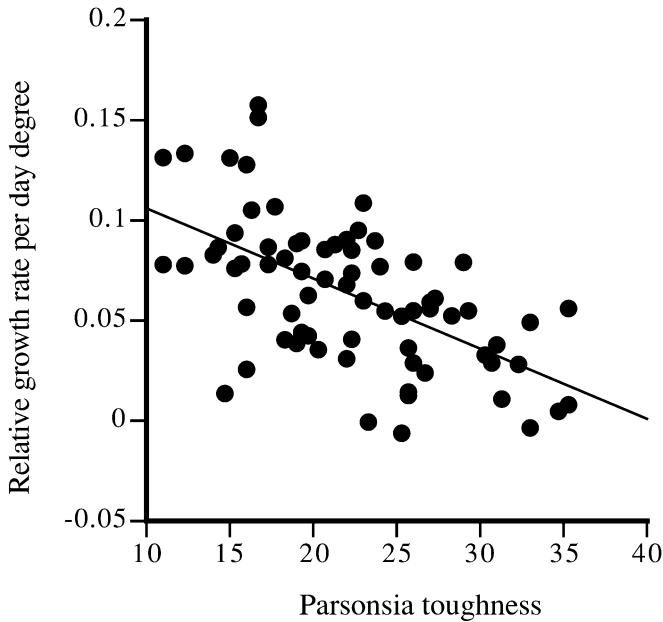


Figure 4 Relative growth rate of first instar *Euploea core* that had successfully established on a native host plant, *Parsonsia staminea* leaf, plotted against leaf toughness as measured using a penetrometer.

endophytic fungus *Acremonium loliae* (102). This discrimination was lost by the fourth instar (103).

Microclimate

Local temperature and humidity can influence survival of first instar larvae either through effects on pharate larvae or on newly emerged neonates. Diapause is regulated in pharate gypsy moth, *Lymantria dispar*, by increased ecdysteroid titers that are maintained by exposure to cool temperatures (145). Ecdysteroids drop and diapause is broken by warm temperatures; thus, the timing of such microclimatic shifts in relation to bud-burst is an important determinant of neonate survivorship (81).

Light intensity, including UV wavelengths, is likely to influence neonate performance on plants through effects on plant primary and secondary metabolism and also through direct activation of some chemical defenses such as furanocoumarins and terpenes (17, 144). Manuwoto & Scriber (161) found that low light intensity resulted in increased feeding rates by the European corn borer, *Ostrinia nubilalis* on field corn. They concluded that this was more likely mediated nutritionally through higher leaf nitrogen concentrations than by lower concentrations of the chemical defense 2,4 dihydroxy-7-methoxy-1,4 benzoxazine-3-one (DIMBOA) (202, 204). Citral, a monoterpene aldehyde that occurs in several plant families, is

phototoxic to first instar cabbage looper larvae, *Trichoplusia ni*, in the presence of UVA light (95).

INTERNAL PLANT FACTORS THAT IMPACT NEONATES

Although plants appear to be sitting targets for their lepidopteran herbivores, it is now clear that they are extraordinarily variable in time and space for many different characteristics. From the lepidopteran neonate perspective, this internal variability centers primarily on their biochemical diversity and how this is targeted at herbivore host location, nutrition, deterrence, performance, and mortality.

Nutrition

Early instars generally have higher relative growth rates, consumption rates, metabolic rates, and assimilation efficiency, but lower net growth efficiency, than older instars (203). That is, younger instars tend to grow faster, consume more (with respect to body weight), and digest their food better, but they tend to convert digested food less efficiently. In feeding trials first instars are often more selective between plant genotypes than later instars (61). These differences may be driven by a combination of high surface area:volume ratios and absence of induced enzyme systems such as mixed function oxidases (27).

Nitrogen and leaf water content are important determinants of neonate performance (77, 166, 167, 172, 201, 203). For neonate *O. nubilalis*, high nitrogen concentrations in field corn grown under low light intensity were more important determinants of higher feeding rates than concentrations of the chemical defense 2,4 dihydroxy-7-methoxy-1,4 benzoxazine-3-one (DIMBOA) (161). Similarly, for first instar *S. frugiperda* larvae on susceptible and resistant corn, nutritional amino acids are more important determinants of corn susceptibility than toxins (110). Larvae of *Samea multiplicalis* that in early instars had experienced low dietary nitrogen or high temperatures sustained chronic impairment of their abilities to use food and grow (217).

Chemical Defenses

First instar caterpillars may be more susceptible to secondary plant chemicals than later instars. For example, Erickson (78) and Cohen (39) found no adverse effects of cardiac glycosides (toxins found in the latex of milkweed species) on larval growth and subsequent adult fecundity of *D. plexippus*, a milkweed specialist. However, their studies used fourth and fifth instar caterpillars. Using first instars, it has now been repeatedly demonstrated that cardiac glycosides do impose a physiological cost to feeding *D. plexippus* (243, 244, 245). Most plant/herbivore theories that deal with insect specialists assume that the specialist suffers no physiological cost in feeding on a host that is toxic to other animals (41, 81, 91, 113, 194). Although this may be true for the adults and/or later instars of many specialist herbivores, we urge workers to look at neonates to see if the assumptions hold.

Plant defenses are likely to have major effects on outbreaks of generalist herbivores. Roth et al. (195) found that performance of neonate gypsy moth larvae varied significantly among host plant species and was negatively affected by leaf phenolics but not by ascorbic acid (154). The spatial patchiness of resistant tree stands has been implicated in gypsy moth outbreaks (148).

Other polyphagous Lepidoptera are less affected by plant allelochemicals than oligophagous species. Neolignan extracts from magnoliaceous hosts of *troilus* group swallowtail butterflies reduced survivorship of first instar *Papilio palamedes* and *P. troilus* that have restricted diet breadths. However, neonates of the polyphagous *P. glaucus* were not affected by the neolignans, and magnolol had no effect on neonates of another polyphagous lepidopteran *H. cunea* (180). Sesquiterpene lactones in tulip tree and simple phenolics in quaking aspen are likely to be responsible for marked differences between neonate survivorship in two sibling species of *Papilio*, *P. glaucus* and *P. canadensis* (153). Instead of an effect on survivorship, the aspen phenolic glycoside, tremulacin, prolonged the duration of the first instar in gypsy moths (152). Plant lectins proved to be highly toxic to neonate *O. nubialis* larvae and resulted in slower growth rates of survivors (49).

SEQUESTERED METALS Plants that grow in soils with high concentrations of heavy metals can accumulate the metals and influence herbivore performance. Leaves of *Streptanthus polygaloides*, which hyperaccumulated nickel, were acutely toxic (96% mortality after 10 days) to neonates of the polyphagous noctuid *S. exigua* (26). Sublethal effects also occurred and the heavy metals may interact with secondary metabolites (26).

CONSTITUTIVE DEFENSE EXPRESSION The impact of constitutive plant defense on neonates is variable and dependent on the particular insect/plant system. When fed tobacco or *Arabidopsis* plants genetically modified to express high levels of proteinase inhibitors, first instar larvae of the polyphagous *Spodoptera littoralis* showed increased mortality and decreased larval weights (53). Different flavonoid profiles have been implicated in susceptibility and resistance of sugar cane varieties to neonates of the pyralid *Eldana saccharina* (196). Douglas fir leaf terpenes had little effect on neonate *L. dispar* larvae fed artificial diet, but leaf phenolics alone, or in combination with terpenes, reduced both growth and survivorship in neonates (126). Similarly, peppermint monoterpenes had little effect on neonates of the variegated cutworm, *Peridroma saucia* (108).

In a test of the predictions of optimal defense theory (81, 194), Manuwoto & Scriber (162) tested the effects of tannins on neonate larvae of the forb-feeding southern armyworm, *Spodoptera eridania*, and the tree-feeding promethea silkmoth, *Callosamia promethea*. In contrast to prediction of a generalized reduction in food digestibility, only *S. eridania* showed suppressed growth rates that were similar across all concentrations of both hydrolyzable and condensed tannins. Moreover, the negative impact on *S. eridania* was not due to reduction of food digestibility, but to reduced consumption rates and decreased conversion efficiency (161).

INDUCED DEFENSE EXPRESSION Induced plant chemical defenses are generally thought to reduce the costs of constitutive expression in plants and target generalist herbivores (129). However, induced nitrogen-based defenses can also be effective against specialist herbivores. Neonate *M. sexta* were smaller and ate less on *Nicotiana sylvestris* plants in which alkaloid content was induced by leaf damage (12) and also grew more slowly and had higher mortalities on *Nicotiana attenuata* plants that were induced with the volatile signal methyl jasmonate (224). In earlier experiments *M. sexta* also grew more slowly on damaged tomato plants than on controls, and damaged plants had higher concentrations of proteinase inhibitor, but larval growth rates were not affected directly by extracted proteinase inhibitors (240).

RESINS AND LATEX Resins and latex carried in laticifers occur in more than 20,000 plant species (147). Latex is an aqueous suspension of particles in living cells and acts like an inducible defense that is mobilized instantly to damage sites (44, 63, 65). By virtue of their small size, neonate Lepidoptera are especially vulnerable to the mechanical, repellent, and toxic effects of latex, so larvae have evolved many different ways to try to circumvent latex expression (64, 243). These include vein pinching, trenching, or channeling, vein severing, mid rib severing, and partial petiole severance by larvae according to the size of their mouthparts and leaf morphology (37, 63–65, 243).

Changes in Host Quality and Interactions

For folivores, leaf age and its correlate, leaf quality, are critical factors that affect establishment, growth, and survival of neonates. The factors that change in a leaf as it ages depend on the plant species, but generally leaf toughness and digestibility-reducing allelochemicals increase and nitrogen and water content decrease, whereas other secondary chemicals may increase, decrease, or remain constant (21, 203). Inability of neonate larvae to find leaves suitable for establishment can lead to high mortality, even if the same leaves are suitable for older instars (38). Mortality of first instar *L. dispar* caterpillars ranged from 0–84% on foliage of Douglas fir, increasing as leaf age increased (173). In deciduous trees synchrony between egg hatch and bud burst can be critical; a delay of egg hatch only a few days after bud burst caused a significant decrease in growth rate of neonate forest tent caterpillar, *Malacosoma disstria*, on trembling aspen (183). Changes in host quality following bud-burst are so rapid in white spruce that first instar *Zeiraphera canadensis* are unable to utilize the most vigorous apical shoots, and their foraging occurs in different parts of the tree than later instars (31). Even apparently minor differences in leaf quality can affect first instar larval growth rate. The relative growth rate of neonate *Euploea core corinna* caterpillars was significantly negatively correlated to increasing leaf toughness (as measured by a penetrometer) on a native host plant, *Parsonsia straminea*, despite all leaves being suitable for larval establishment (Figure 4) (unpublished results from “Larval Growth Experiment 1” in 37).

The effects of plant chemical defenses on neonates can interact with other factors such as temperature, predators, and larval age (135, 211, 237, 238). Yang et al. (242a) found that chlorogenic acid reduced the negative impact of tomatine on the growth rate of first and second instar *M. sexta* larvae and that the magnitude of the allelochemical effects was increased at cooler temperatures. They found developmental differences in larval responses to the allelochemicals where chlorogenic acid shortened first instar duration, but the effect on the second instar was dependent upon temperature and the presence of tomatine.

NEONATE BEHAVIOR AND PHYSIOLOGY

First instar caterpillars are not simply small versions of later instars. Behavior and physiology can be markedly different in younger instars, and unless otherwise known, it should not be assumed that because you know the biology of a fifth instar, you know the biology of a first instar.

Dispersal and Feeding Site Location of First Instars

Location of a suitable feeding site is a critical part of the life of a neonate caterpillar (90; Figure 3). With the exception of some leaf-mining species (e.g., Gracillariidae, Nepticulidae), where the neonates tunnel directly into the host leaf below the egg (164, 179) or eggs are laid directly into the leaf (168), most neonate caterpillars have a prefeeding movement phase, be it local leaf exploration or longer distance dispersal (18, 199). Such dispersal commonly leads to the selection of newly expanding leaves by neonates for their first meal (e.g., 125).

Longer distance dispersal in many neonate caterpillars is commonly achieved by ballooning, a process in which the neonate lowers itself on a strand of silk and is carried by the wind (43). This behavior is recorded for several lepidopteran families, including Cossidae, Geometridae, Lymantriidae, Noctuidae, Psychidae, and Pyralidae (43). As caterpillars age, ballooning becomes impossible because of their increased weight, and dispersal must be by walking.

The percentage of the first instar population that disperses by ballooning is variable, from 15–26% in *L. dispar* (60, 246; but see 148) to 93% in common armyworm, *Mythimna convecta* (171). Ballooning may occur regardless of host quality (48), or as a result of low host quality (30, 107, 139). The distance traveled by ballooning caterpillars is dependent on wind velocity, height of release point, size of caterpillar, size of silk strand, and presence of barriers (155, 171, 218, 246).

In addition to full ballooning, neonates may move within a host by lowering themselves on silk threads (223). The mortality of ballooning larvae is not well documented and is often assumed to be large (e.g., 107). Where eggs are laid on nonhost plants, or if neonates disperse away from a poor quality host, then mortality may increase proportionally with the distance to a new host (9) and can be influenced by abiotic factors such as soil and ambient temperature (219).

If eggs are laid away from the host plant, or on parts of the host plant unsuitable for larval establishment, then movement to locate a feeding site is critical. Potato tuber moth, *Phthorimaea operculella*, lay their eggs predominantly in the soil, and neonates need to locate their host plant. In this species success in locating a host appears to be dependent on the host species, with 80% of neonates locating potato, but only 50% locating other potential hosts (227). In intercropping situations, up to a third of *Chilo partellus* eggs may be laid on nonhosts, requiring the neonates to locate a host (9). Lightbrown apple moth, *Epiphyas postvittana*, is a polyphagous leafroller pest of many fruit crops in New Zealand, and the highly mobile neonate larvae showed clear host selection behavior among 15 host and 11 nonhost plant species, whereas ovipositing females did not discriminate (90).

Generally, once a neonate is on a suitable host it will settle and establish a feeding site. If the host or plant part is unsuitable, then exploration within and between plants is likely to continue (32, 90, 115, 131, 219, 227). Studying neonate settling, or lack of it, has been used on several occasions in screening for host resistance in genotypes of commercial crops. Examples include *C. partellus* on maize (7, 8, 34, 136, 137), *P. xylostella* on cabbage (11, 71, 72), *S. frugiperda* on corn (242), *P. operculella* on potato (158), and *Diatraea saccharalis* on sugar cane (236). Neonates will also continue moving if the host plant contains toxins, such as those derived from *B. thuringiensis*. In the laboratory, first instar *E. postvittana* larvae eventually left artificial diet containing *B. thuringiensis* toxins and accumulated on control diet, which did not contain toxins (105). In the field, on whole cotton plants, neonate *H. virescens* dispersed more frequently from transgenic *B. thuringiensis* cotton plants than from nontransformed plants (182).

The actual mechanisms by which neonates locate suitable hosts, or parts of hosts, are generally not well studied, but are presumed to be similar to later larval stages (see reviews in 21, 211). Neonate *E. postvittana* may use both visual (104) and chemical cues (106) in orientation, whereas codling moth neonates orient anemotactically to apple fruit, particularly those already infested with conspecifics (140, 141). Plant physical features may also be involved in orientation, with neonate *O. nubilalis* larvae cueing in on leaf-axils (42).

Feeding Behavior

Feeding behavior can change markedly between early and late instars. At the extreme are examples where no feeding occurs in the first instar (e.g., 87). Size and physical ability to consume certain diets may influence changes in feeding behavior in certain lepidopterans, for example wood-borers. Larvae of some *Aenetus* species are arboreal wood-borers as late stage larvae, but as early instars live in leaf litter as fungus/detritus feeders (96, 222). Similarly, for the last two years of their three-year larval cycle the larvae of the giant wood moth, *Endoxyla cinerea*, are borers of hardwood *Eucalyptus*, but for the first part of their life cycle it is thought that they may feed on fine roots and root hairs (175).

The early instars of most lycaenid larvae are phytophagous, and later instars engage in mutualisms with ants or even become predatory (2, 184, 220). These mutualisms may drive specialized neonate feeding behavior on high-nitrogen plants, engaged in nitrogen-fixing mutualisms, because the larval secretions attractive to ants are protein rich (185).

Even when the host is not a woody plant, the ability to bore into a stem appears to influence the feeding behavior of caterpillars. The corn borers *O. nubilalis*, *E. saccharina*, and *C. partellus* all feed on maize leaf sheaths or tassels until approximately the third instar, when they bore into the stem of the host (42, 127, 136). Even at this stage, stalk wall toughness and waxes on the stalks are considered limiting factors to the entry of sorghum by *E. saccharina* (127).

In addition to changing from external feeders to internal borers, many caterpillars change from being leaf miners as early stage larvae to being external feeders as late stage larvae. Gaston et al. (94) reviewed the literature on British microlepidoptera and found that 200 out of 1137 species had marked changes in their feeding habits as they grew. Most common of those 200 were species that were leaf miners or concealed feeders as early instars and became external feeders, case-bearers, or leaf-tying and leaf-rolling caterpillars as late instars.

For 42 species of British Lepidoptera, life history was strongly correlated with egg and larval size (193). Species that overwinter as eggs produce the largest eggs and largest neonates. However, neonate body size was not correlated with speed of movement or tolerance of starvation. Instead, egg size and survival were related to larval food type, with woody plant feeders producing larger eggs and larvae than herb feeders; larval survivorship decreased in the food order: lichens > grass > woody/herbs.

Social Behavior

For some 5–10% of Lepidoptera, across a diverse taxonomic array, eggs and the caterpillars are aggregated (112, 208). Sometimes such aggregations continue through all larval stages, e.g., *Ochrogaster* spp. and *Panacela* spp. (43), but often the aggregation breaks up by the third or fourth instar when larvae feed singly or in small groups. Aggregation is considered to confer numerous advantages, including increased foraging efficiency, defense against natural enemies, and improved thermoregulation (36, 57, 84, 186 and references therein). For most Lepidoptera the role of aggregation in enhancing feeding facilitation is most evident in first instars (84, 85, 120).

Feeding Physiology and Enzyme Systems

Dietary exposure to plant allelochemicals can induce physiological responses in neonates that determine the feeding behavior of later instars. Neonate *P. rapae* exposed to deterrents from nasturtium did not reject nasturtium leaves as second instars, but neonates not exposed to the deterrents rejected nasturtium leaves (116). Larvae of *S. multiplicalis* that fed on food plant low in dietary nitrogen in their

first two instars took longer to complete development and had an extra instar regardless of later experience of dietary nitrogen. Larvae on lower dietary nitrogen compensated by faster feeding, but displayed a lower growth rate (217).

Low constitutive expression of chemical defenses in plants may result in the induction of increased enzyme activity in the gut of neonates. De Leo et al. (53) found that there was increased production of proteolytic enzymes when larvae were fed tobacco plants engineered for low expression of proteinase inhibitor in comparison with larvae fed plants engineered for high expression. The authors suggested that the increased levels and diversity of proteolytic enzymes result in enhanced larval performance. Alternatively, higher levels of allelochemicals may induce enzyme production. In the case of neonate gypsy moth larvae, consumption of phenolic glycosides induced esterase enzyme activity, and their survival rates were positively correlated with enzyme activity (154). In a test of luna moth, *Actias luna*, larval performance on leaves of 11 tree species, neonate exposure, and subsequent survival led to induction of detoxification enzymes in fifth instar larvae, especially quinone reductase and glutathione transferase in larvae fed leaves containing juglone and related quinones (151). However, when Lindroth & Hemming (152) tested the response of gypsy moth neonates to tremulacin in aspen, they found that high esterase levels were not induced by tremulacin and were not sufficient to detoxify the high levels of this phenolic glycoside found naturally.

Induction of detoxification enzymes in neonate larvae was suggested as a plausible explanation for the increased tolerance of *H. zea* neonates to 2-tridecanone in the trichomes of *Lycopersicon hirsutum* after they had been exposed to 2-tridecanone as eggs (130).

CONCLUDING REMARKS

Although rarely acknowledged directly, it appears that many studies of caterpillars focus on older instars instead of first instars simply because the older and larger caterpillars are easier to handle and observe. Only rarely (e.g., 210) are specific reasons given why one instar is chosen over another. However, first instars are not simply smaller versions of their older siblings. Researchers should work on the instar that is most appropriate to their question, not the one most convenient to handle.

A major ongoing debate in population ecology has surrounded the causative factors underlying the abundance of phytophagous insects (for review see 45, 46, 55, 214, 216). In many cases these studies identify the early life stages as the period during which the greatest losses take place. This mortality is due to a complex interaction between the substrate (plant) on which the neonate finds itself, its behavioral and physiological ability to overcome an array of plant factors, as well as weather effects and interactions with the same and next trophic level, all acting contemporaneously and intensely over a narrow window of time (Figure 3). Not surprisingly, mortality is high but variable. This variability means we can go from average levels of abundance to outbreaks of later instars quickly. It is insufficient

to simply construct life-tables for these stages. Experimental manipulations are needed to better define the causes of mortality and quantify their effects (e.g., 138, 243). Direct observation of neonate Lepidoptera, although difficult and tedious, will go a long way to demystifying the folklore that surrounds the ecology of this critical life stage.

Entomologists, insect population ecologists, and evolutionary biologists need to come to grips with the causes of the variance in survival of the neonate stage. Techniques to do this are available (see e.g., 20, 37, 68, 160, 244, 245), and there is no excuse for continuing to say it is too difficult. The need for this kind of research was highlighted recently by the debate sparked over the risk posed to monarch butterflies by the pollen of transgenic maize. Instead of rising to the challenge of undertaking careful field experiments on intact plants, many still retreated to meaningless bioassays based on freeze-dried pollen sprayed in a water suspension onto milkweed leaf disks or artificial diet in the comfort of a laboratory.

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