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Larval Biology of Checkerspots

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7.1 Introduction

Butterflies have achieved prominent status in population and metapopulation biology. Accordingly, butterfly biologists should distinguish between events that influence internal dynamics of populations and those that influence interactions among populations. Interactions among populations are driven principally by decisions made by adult insects and by the consequences of those decisions, though highly mobile parasitoids can also be important (van Nouhuys and Hanski 2002b; chapter 8). Within-population dynamics could in theory be driven principally by variation in fecundity of adults or in mortality of any of the four life-history stages: eggs, larvae, pupae, and adults. In practice, as we show here, patterns of larval mortality are often of paramount importance in population dynamics. Negative effects on larvae are often related to spatial and temporal variation in the quality and availability of host plants. The numbers and proportions of individuals attacked by generalist and specialist predators and parasitoids vary greatly. When survival is exceptionally high, butterfly populations may exhibit explosive growth, whereas high larval mortality can lead to population extinctions. To understand the dynamics of a butterfly population, one needs to know the causes of variation in larval survival (Singer 1972, Dempster 1983; chapters 3, 4, and 8).

Because of their limited mobility, small butterfly larvae need to find the right host plant in the appropriate environmental conditions near the spot where they hatch from the egg. As the larvae grow, their capacity to move increases, but they are still limited to host plants in the area where they hatched. The presence of the larval host plant alone is not enough. For successful larval development, the host plant needs to grow under appropriate environmental conditions, which often means, in the case of checkerspots, a warm, dry microclimate. To successfully conserve a butterfly population, one needs to know which factors facilitate larval growth and survival (Singer 1972, J. A. Thomas 1984, 1991, 1995a, Ehrlich and Murphy 1987a, New et al. 1995).

As an introduction to checkerspot larval biology, we first describe three particular features of checkerspot caterpillars: group living, obligatory diapause, and unpalatability and aposematic coloration. We then present an overview of larval development in our two focal species, *Euphydryas editha* and *Melitaea cinxia*. In the rest of the chapter we focus on the following aspects of the checkerspot larval biology, emphasizing the comparison between *E. editha* and *M. cinxia*: geographic patterns in host plant use, variation in larval performance among and within host plant species, chemical defence of host plants, sources of larval mortality, the advantages of gregarious larval behavior and the role of group size in larval behavior and survival. Finally, we describe spatial and temporal variation in larval survival in *E. editha* and *M. cinxia* and discuss the consequences of such variation for population dynamics.

7.2 Three Particulars in Checkerspot Larval Biology

Egg Clusters and Gregarious Larval Behavior

Checkerspots lay their eggs in clusters (chapter 5; table 11.1), which make them somewhat exceptional among butterflies, as 90–95% of lepidopteran species lay their eggs singly (Stamp 1980, Hebert 1983). There is evidence that species that lay their eggs in clusters have greater population fluctuations and more outbreaks than species that lay their eggs singly (Nothnagle and Schultz 1987). Tendency for great fluctuations in numbers may also lead to increased vulnerability to local extinction, as suggested by high extinction rates of *M. cinxia* in the Åland Islands (Hanski et al. 1995b, Hanski 1999b; chapter 4) and of *E. editha* across its range (Parmesan 1996).

How long larvae remain in groups varies much among species (chapter 11). All checkerspot species live gregariously at least during the first one or two larval instars (Wahlberg 2000b), but it is not rare for the larvae to remain gregarious for several instars. In some species, such as *M. cinxia* (J. A. Thomas and Simcox 1982, Hanski et al. 1995a) and *Euphydryas aurinia* (Porter 1981, Warren 1994, Lewis and Hurford 1997), the conspicuousness of larval groups allows relatively reliable censuses during the larval stage (chapter 4). Because larval groups move slowly and only short distances from one host plant to another, tracking larval survival is possible in the field. Gregarious larvae spin webs on the host plants on which they live, and these webs can be fairly easy to find, even when larvae are small and would otherwise be cryptic. In species such as *Euphydryas phaeton* (Stamp 1982a) and *M. cinxia* in Finland (Kuussaari 1998), larvae diapause as groups and tend to remain gregarious until the last molt before pupating. Low mobility, web-building, and conspicuousness of larval groups also facilitate the study of some of the parasitoids that attack larvae and are important agents of mortality in many checkerspot populations (Ford and Ford 1930, Porter 1981, Lei and Hanski 1997; chapter 8).

Larval Diapause

A second key feature of checkerspot larval biology outside the tropics is the ability of larvae to diapause through extreme heat and cold and to facultatively reenter diapause several times, thereby extending their life spans to two or more years when conditions are adverse (Bowers 1978, Singer and Ehrlich 1979). In hot, dry climates, larvae typically enter diapause in late spring, remain in diapause during summer and early winter, break diapause some time between mid-winter and early spring, and then rapidly produce a single generation of adults. Larvae that break diapause in unusually adverse conditions (in years of drought or low host density) can reenter diapause after a small amount of feeding; they then attempt to complete their development in the following year. The nature of diapause is variable among populations as well as among species. For example, diapause is obligate in laboratory rearings of *M. cinxia* originating from low elevation sites in Finland and Andalucia (Spain) and from high elevation sites (1800 and 2000 m) in the French Alps. These sites close to the species' latitudinal and elevational limits have a single butterfly generation per year. In contrast, *M. cinxia* populations in the center of the species' range (low elevations in southern France, including the French Alps) have a variable number of generations per year and show facultative diapause in laboratory rearings (M. Singer, pers. obs.).

Unpalatability and Aposematic Coloration

Checkerspot larvae tend to be brightly colored (e.g., black with bright white, yellow, or orange stripes or spots; plate XI), which makes them highly conspicuous to visually searching predators. Birds and some invertebrate predators tend to avoid attacking the larvae. The fact that the majority of checkerspot butterflies use only host plants containing iridoid glycosides (Wahlberg 2001b; chapter 11) suggests that checkerspots use these compounds as a defense against predators. Detailed studies have shown that checkerspot larvae sequester iridoid glycosides and related iridoids produced by their host plants and use them for their own defense (Bowers 1988, 1991, Camara 1997b, Suomi et al. 2001). In both laboratory (Dyer and Bowers 1996, Theodoratus and Bowers 1999) and field experiments (Camara

1997b), generalist arthropods (insects and spiders) have been shown to be deterred by sequestered iridoid glycosides. Unpalatability of checkerspot larvae for birds has been shown using cage experiments. There is, however, much variation in the extent of unpalatability both among the species and populations using different host plants (Bowers 1980, 1990, 1991).

7.3 Overview of Larval Development

Euphydryas editha in California and *Melitaea cinxia* in the Åland Islands represent typical checkerspot butterflies, but they differ from each other in the details of their larval biology. The two species are contrasted in table 7.1.

Euphydryas editha

Euphydryas editha eggs are typically laid in batches of about 40 eggs, but the range is a few eggs to a couple hundred (Labine 1968, Singer et al. 1994, C. Boggs and M. Singer, unpubl. data). The eggs hatch synchronously after about two weeks, and the larvae often spin a web immediately upon hatching. The larvae live in the web for only several days in some populations of *E. editha bayensis*, but up to the entire prediapause development in many other populations (Moore 1989a, Hellmann 2002c).

Checkerspot larvae living in habitats where host plants tend to be ephemeral must be able to move from their natal plant to individuals of the same or other host species. For example, in *Euphydryas editha bayensis*, larvae search for food fairly widely if host senescence occurs. In this ecotype, prediapause development takes approximately three to five weeks and varies as a function of the abiotic conditions and host plant quality. Larvae diapause singly without a web on the ground, in plant litter, or under rocks. In this and other coastal ecotypes of *E. editha*, diapausing larvae may become aggregated simply because they share favorable overwintering sites. There can be important variation in body size among individuals at diapause because larvae vary in the timing and stage at which they enter diapause (third versus fourth instar; Singer 1971a).

Larval diapause is broken by winter rains on the coast and by snowmelt at higher elevations. Larvae feed for several weeks before finding pupation sites on the ground, under rocks or litter, or in pine cones, at the sixth or later instar (Singer 1971a, Singer et al. 1994). Postdiapause larvae forage singly and can move greater distances than prediapause larvae. The pace of growth and development of postdiapause larvae is strongly influenced by microclimate (figure 7.1) because larvae behaviorally thermoregulate by basking. To raise their body temperature to levels for optimal growth (30–35°C; Porter 1982; chapter 3), postdiapause larvae move among microclimates and cross slopes of different topographic exposure (Weiss et al. 1987, 1993). Working on *E. editha bayensis*, Weiss et al. (1987) found that postdiapause larvae disperse from a release site as much as 10 m per day, presumably in search of suitable foraging conditions. Dispersal involves a short-term trade-off against growth, but is compensated by the benefits of locating an area where body

Table 7.1. Comparison of larval life history in *Euphydryas editha* and *Melitaea cinxia*.

Trait	*Euphydryas editha*	*Melitaea cinxia*
Egg batch size	5–90	150–200
Web building and gregarious behavior	During first to second instar	From first until penultimate instar
Time of larval dispersion	In first and second instar	In last instar
Diapause	Solitarily in third or fourth instar	As a group in fourth or fifth instar
Flexibility of diapause	Reentering diapause possible	Reentering diapause not possible
Winter nest	No	Yes
Basking	Solitary basking in spring	Group basking in spring
Aposematism	Yes	Yes
Unpalatability	Yes	Probably

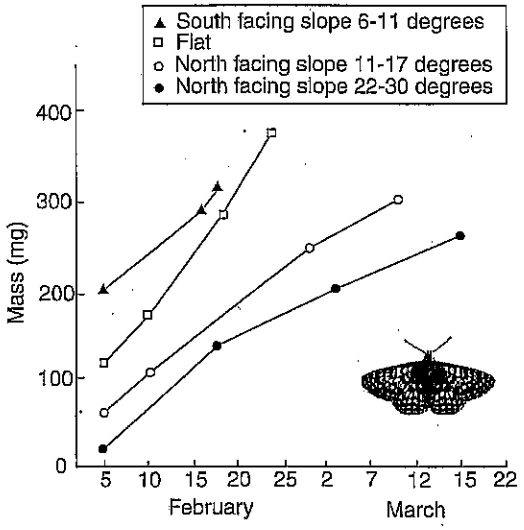


Figure 7.1. Mean postdiapause *Euphydryas editha* larval mass in the field on different slope exposures (Weiss et al. 1987).

temperature can be elevated to the optimal range for foraging and development.

Melitaea cinxia

In the Åland Islands, *M. cinxia* flies in June and lays large batches of eggs (typically 150–200) underneath the leaves of its host plants, *Plantago lanceolata* and *Veronica spicata* (Kuussaari et al. 1995, Kuussaari 1998; Plate IX). Larvae hatch after two to four weeks depending on the temperature. As soon as they have hatched in July, larvae spin a communal web on the host plant. Because of their restricted mobility, small larvae depend on the plant on which their mother laid the eggs. They feed gregariously in their web and grow slowly during the rest of the summer. The larvae prepare for diapause by spinning a dense winter nest (figure 2.5, plate IX), within which they molt for the last time before diapause and remain as a compact group over the winter. At this molt the color of the larvae changes from pale brown to black, and the head capsule becomes bright orange, giving the larvae the aposematic appearance that they will have after diapause and the deep black color that will assist in thermoregulation in the weak northern spring sunshine (Plates IX and XI). During early September, the larval groups are easy to find because the newly constructed winter nests are bright white and conspicuous on the green host plants.

The larvae become active during sunny days as soon as the snow has melted in late March or early April. The black larvae remain in tight aggregates and spend much time basking in the sun and spinning new webs as they move from one plant to another. The movements of the larval groups are often easy to follow based on the webs and defoliated host plants that they leave behind. During cold and cloudy weather the larvae tend to remain within the webs, where they are able to maintain a higher body temperature than outside (S. van Nouhuys, unpubl. data). The larvae also often stay in the webs overnight. During sunny weather the larvae usually feed and bask just outside the web. Postdiapause larvae molt into the penultimate instar inside a web, often synchronously as large clusters. As development proceeds, less time is spent basking and spinning webs, and the larvae tend to split into smaller subgroups (see section 7.6). In the last instar, larvae are much more mobile, and they tend to bask singly or in groups of only two or three larvae. Depending on the abundance of host plants, they may remain gregarious within an area of a few square meters, or they may become solitary and disperse long distances of >10 m. Larvae pupate within the vegetation close to the ground in early May.

7.4 Larval Host Plant Use and Performance

Checkerspot butterfly eggs are laid on plants belonging to 16 different families distributed throughout the Palaearctic, Nearctic, and Neotropics (chapter 2). All but two of the families are in the single subclass Asteridae, and members of all but two of these families produce iridoid glycosides as plant secondary compounds (Jensen et al. 1975, Higgins 1981, Tolman and Lewington 1997, Olmstead et al. 2000, Wahlberg 2001b). A checkerspot species may feed on many plant species in several families throughout its range, but individual populations are typically restricted to only one or to a couple of host genera, or to a single host species (Wahlberg 2001b; chapter 6). The plant on which an egg batch is laid depends on the phylogenetic history of the butterfly species, the evolutionary history of the particular population, the preference of the ovipositing female, and the array of available host plants (Singer 1984, Singer et al. 1992a; chapters 6 and 9). Once the eggs hatch, survival depends on the suitability of the host for larval development, environmental conditions (such as drought), natural enemies, and the tendency of the larvae to move among plants. Many of these factors can and usually do differ among host plant species, as well as among individuals of the same plant species.

While checkerspot larvae are all constrained somewhat by their mother's oviposition choice, the range of host plant use by larvae is usually less restricted than adult host plant range for oviposition. There is, however, great variation in the ability of larvae to move among plants (Warren 1987a, Tolman and Lewington 1997, Kuussaari 1998, Hellmann 2002c); therefore some species are more dependent on the host plant choice of ovipositing females than others. *Euphydryas editha* is an example of a checkerspot that can adjust to differences in host phenology by moving between host plant species within a generation. *Euphydryas phaeton* lays eggs on *Chelone glabra*, but postdiapause larvae are mobile and feed on a wide range of plant species (Bowers 1980). *Melitaea cinxia* larvae, on the other hand, move relatively little, and though they may be able to eat several plant species, they are restricted by adult oviposition preference. We use *E. editha* and *M. cinxia* to illustrate the pattern of host use within and among host plant species and then discuss the fitness consequences of the plants on which they feed. Because one of the characteristics that makes checkerspots a distinct group is their use of host plants that produce iridoids, we also summarize what is known about the ecological consequences of feeding on iridoid-producing plants.

Pattern of Host Plant Use in Euphydryas editha

Adults of *Euphydryas editha* oviposit on the leaves and flowers of hosts in nine genera: *Antirrhinum*, *Collinsia*, *Cordylanthus*, *Castilleja*, *Mimulus*, *Pedicularis*, *Penstemon*, *Plantago*, and *Veronica* (White and Singer 1974, Ehrlich and Murphy 1981b, Radtkey and Singer 1995, G. Pratt pers. comm.). Females often select just a subset of the plants available locally on which oviposition and larval development is possible. Populations with the same potential host resources often differ in the frequency with which they choose those resources and the order of their preference for them (chapter 6). For example, two populations on the eastern slopes of the Sierra Nevada, separated by only 150 km, are found in habitats where both *Collinsia parviflora* and *Penstemon rydbergii* are present (Singer and Parmesan 1993, Singer 1994). One population laid predominantly on *P. rydbergii*, while the other used *C. parviflora*, though in both habitats *C. parviflora* was the more abundant host. This divergence is explained both by genetic differences in female preference among the populations and genetic differences in the resistance of plants to oviposition among the sites (i.e., differences in plant chemistry as detected by ovipositing females).

If there is variation among populations in host use and host preference, an obvious question is whether females make the best choices for their offspring. Even in cases where larvae disperse from the natal host, we can ask whether females choose a suitable foraging arena for their young. To answer these questions requires knowledge of both oviposition choice and larval performance. We have explained above that oviposition (and oviposition choice) varies among populations; it turns out that *E. editha* larvae also vary in their ability to survive on the same host species across populations (Rausher 1982). In other words, knowing whether females make the right choices (i.e., whether they are adapted to their environment) is a local problem. Singer et al. (1994) studied the concordance of oviposition choice and larval performance in a series of *E. editha* populations, where larvae were assumed not to disperse from the natal host within 10 days of hatching. In eight populations where diet had been constant over a period of several years, individual females shared the same preference ranking of potential host plant species present in the habitat. The preference ranking was also adaptive. The rank order of plant species in the preference hierarchy of the adults, therefore, was the same as the rank order of those plants in their ability to support survival of experimentally placed neonate larvae. In contrast, two populations in which diet was observed to be undergoing rapid change (after anthropogenic disturbance) showed variation among females in the rank order of host preference, and the plant species preferred by most females was not the plant species that supported highest larval survival. This situation was temporary during the 1980s, and in both of these rapidly evolving populations, preference ranks were adaptive by the early 1990s. In one case this was achieved by rapid evolution of preference, such that the less preferred host became the more preferred (Singer et al. 1993). In the second case, the direction of natural selection on diet was reversed, and the host that had been less preferred but was more suitable became less suitable and remained less preferred (Singer et al. 1994, Singer and Thomas 1996). These results suggest that female *E. editha* tend to choose well for their larvae except in circumstances where anthropogenic influences have dramatically changed the relative suitabilities or availabilities of potential host plant species.

Depending on the degree to which larvae disperse from the natal host plant, the relationship between female oviposition choice and larval diet can be tightly or loosely coupled. In populations where larval groups stay together for most or all of the growing season and disperse little, larval diet and female oviposition choice are identical. As discussed above, however, larvae in some populations, particularly in coastal areas in California where plants are ephemeral, leave their natal host plant and explore neighboring areas for alternative plant resources. In these cases, larval diet and female oviposition choice can be distinctly different. *Euphydryas editha bayensis*, for example, often use multiple host species during larval development (Hellmann 2002c). Under conditions that accelerate host senescence, larvae survive best on *Castilleja* because they remain edible longer than the more common host species, *Plantago erecta* (Singer 1972, Hellmann 2002c; chapter 3). By moving, larvae can achieve the survivorship benefit regardless of the plant their mother chose as long as *Castilleja* are available in nearby areas (Hellmann 2002c). However, the likelihood that a larva will encounter a host species other than the one on which it was laid ultimately is determined by the neigborhood (not the individual plant) in which the female lays her eggs.

Pattern of Host Plant Use in Melitaea cinxia

Melitaea cinxia lays eggs on plants in the genera *Plantago* and *Veronica*, both of which are currently considered to be in the family Plantaginaceae (Judd et al. 1999, Olmstead et al. 2001). *Melitaea cinxia* has been recorded from six host species, with the most widely used one being *Plantago lanceolata* (table 7.2). *Melitaea cinxia* larvae are sporadically found feeding on related plant species (Tolman and Lewington 1997, Kuussaari 1998, Wahlberg 2001b), and, where host plants are scarce, postdiapause larvae have been occasionally observed feeding on unrelated species such as *Trifolium repens* and *Lotus corniculatus*. It is unlikely, however, that they could develop on these plants (Kuussaari et al. 1995, Kuussaari 1998).

Some populations appear to use all host species available for oviposition, while other populations exclude what appear to be suitable and abundant host plants, or at least do not use all available species in proportion to their abundances (Kuussaari et al. 2000). For example, on the island of Saaremaa in western Estonia, *M. cinxia* almost exclusively use *Veronica spicata*, even though *P. lanceolata* is equally or even more abundant. In Åland, *M. cinxia* uses *P. lanceolata* in the east where it alone is available, uses both *V. spicata* and *P. lanceolata* in the central parts of the main Åland Island, where both plants are present, but uses *V. spicata* with disproportionally greater frequency in the west where both plant species are present (Kuussaari et al. 2000; figure 7.2).

Table 7.2. Host plants used by *Melitaea cinxia* in Europe.

Host Plant	Predominance of Use[a]	Reference[b]
Plantago alpina	Primary	4
Plantago lanceolata	Primary and secondary	1, 6, 7
P. major	Occasional	1, 3
P. maritima	Occasional and primary	1, 3
P. media	Occasional	1, 3
Veronica[c] *incana*	Primary	2
V. longifolia	Occasional	1
V. serpyllifolia	Occasional	1
V. spicata	Primary and secondary	1
V. teucrium	Primary	5, 6
V. officinalis	Occasional	8
V. chamaedrys	Occasional	8
Centaurea sp.	Unknown	6

[a] The relative use of a particular plant where it is known.
[b] References: 1, Kuussaari (1998); 2, Wahlberg et al. (2001); 3, S. van Nouhuys (pers. obs.); 4, M. C. Singer (pers. obs.); 5, Weidemann (1988); 6, Tolman and Lewington (1997); 7, Higgins and Riley (1983); 8, M. Kuussaari and M. Nieminen (pers. obs.).
[c] The genus *Veronica* has been in the family Scrophulariaceae, but now it is considered Plantaginaceae (Olmstead et al. 2001).

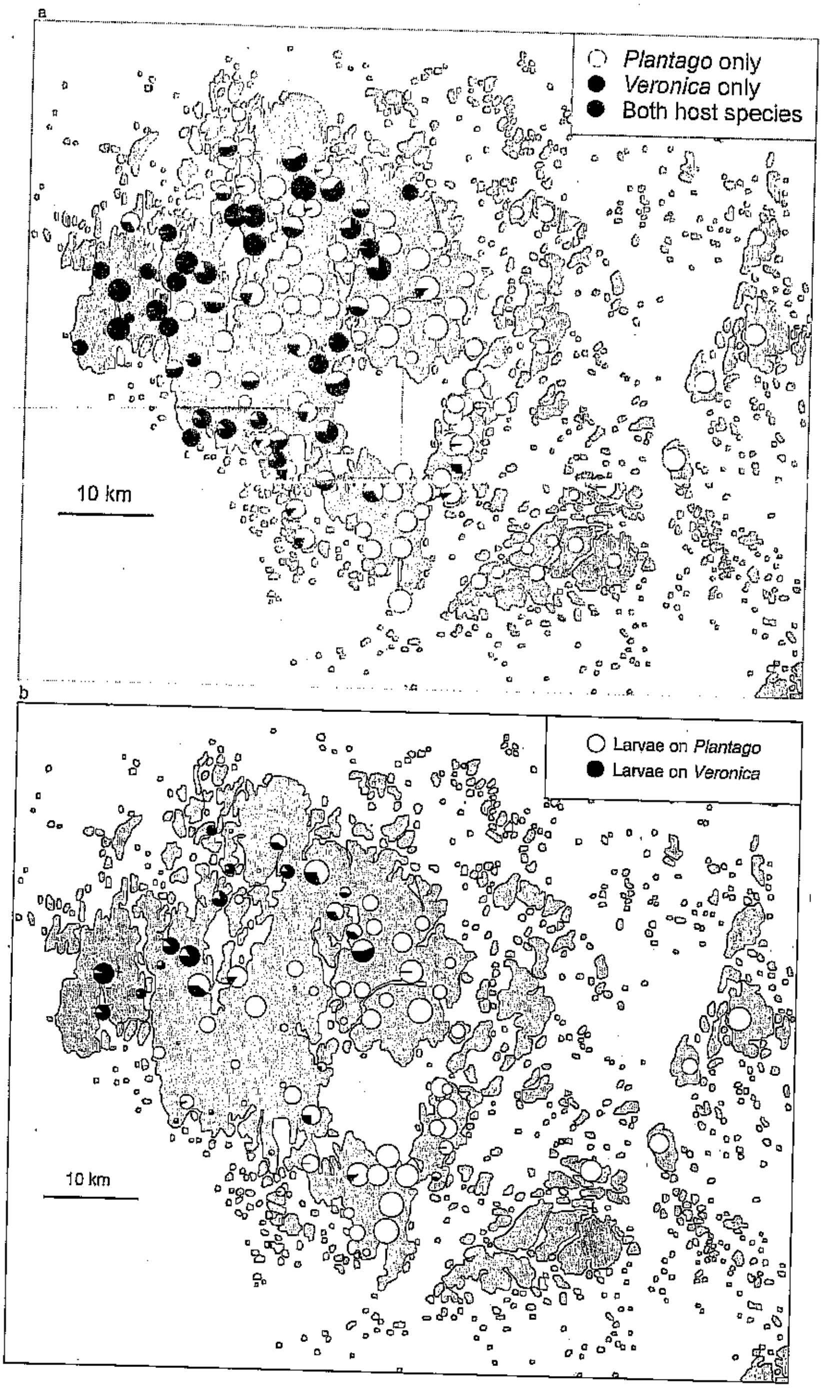
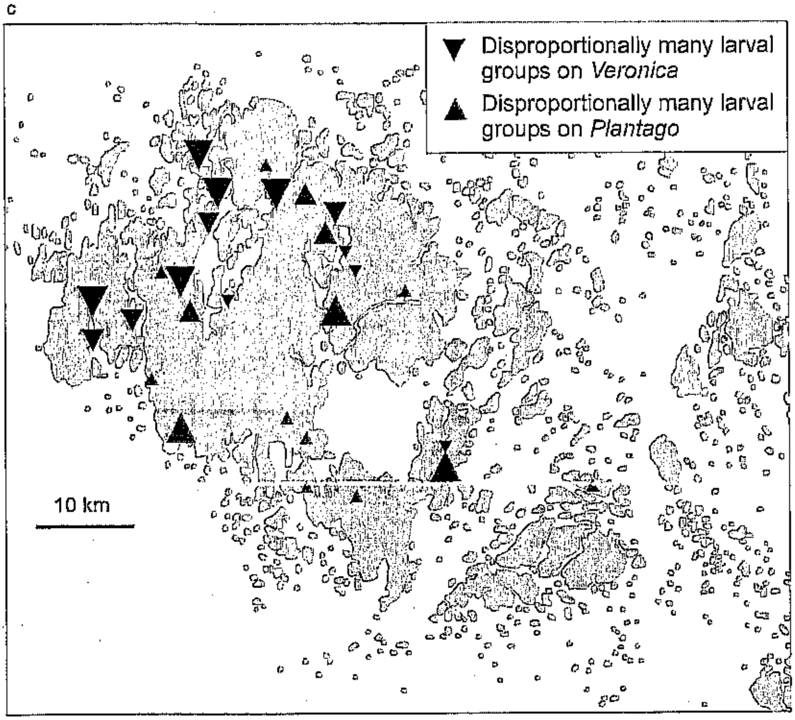


Figure 7.2. Map of *Melitaea cinxia* host plant use in the Åland Islands (modified from Kuussaari et al. 2000) (a) occurrence of the two host plant species, (b) observations of larval occurrence, (c) proportionality of larval host use.



It is clear that variation in host plant use in Åland is a consequence of both plant distribution and of variation in the oviposition preference of adult butterflies (Kuussaari et al. 2000, Hanski and Singer 2001; chapter 6). In contrast to *E. editha* (Ng 1988, Singer et al. 1988), there is no straightforward link between adult oviposition preference and the performance of *M. cinxia* larvae in the Åland Islands. There is a genetically determined southeast to northwest gradient in host plant preference in adult butterflies (Kuussaari et al. 2000; chapter 6), but there appears to be no corresponding variation in host plant suitability for larval development or local adaptation by larvae (van Nouhuys et al. 2003).

Records of survey data covering all of the populations in Åland over six years (1994 to 1999) show that in some years larval survival (number of larvae per group surviving until the spring) when feeding on *P. lanceolata* is high, whereas in other years survival on *V. spicata* is high. In spite of the large sample size (about 300 populations in each year), survival on the two host plants did not show an overall statistical difference (van Nouhuys et al. 2003; figure 7.3). This is the case even though parasitism by *Cotesia melitaearum* is more common among *M. cinxia* feeding on *V. spicata* than on *P. lanceolata* (van Nouhuys and Hanski 1999; chapter 8). In laboratory experiments the performance of larvae appears to depend on how the test plants are chosen, but there is some evidence that larvae grow larger and faster on *V. spicata*. In one laboratory experiment, van Nouhuys et al. (2003) compared the performance of larvae from two contrasting habitat patch types. Both patches contained a high density of *V. spicata* and *P. lanceolata*, but one was in an area where adult butterflies prefer *V. spicata* (site ID 21), and the other one was in an area where butterflies preferred *P. lanceolata* (site ID 1075). The progeny of butterflies from each population were compared on randomly selected suitable-looking host plants of each species from both populations. Larvae grew larger (ANOVA, $P = .001$) and groups were more likely to survive (logistic regression, $P = .02$) on *V. spicata* than on *P. lanceolata*, regardless of their origin. Larvae feeding on *P. lanceolata* from the habitat patch in which females laid eggs on *V. spicata* performed as well as larvae feeding on *P. lanceolata* from the

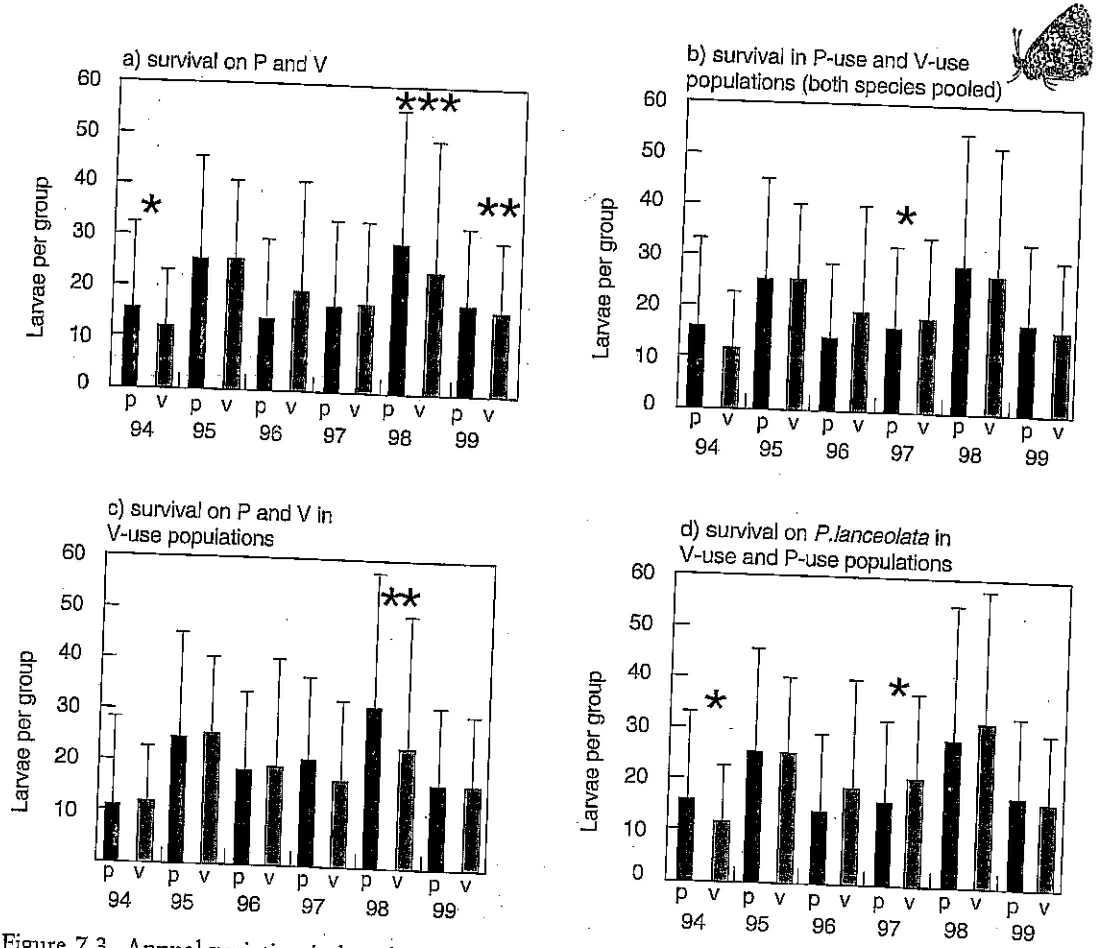


Figure 7.3. Annual variation in larval survival on *Plantago* (P) and *Veronica* (V) in the Åland Islands (van Nouhuys et al. 2003). The mean number (±1 SD) of *Melitaea cinxia* larvae surviving per nest from spring 1994 to spring 1999 (a) on each plant species (n = 1923); (b) in each host habitat patch type (both species pooled) (n = 1923); (c) on each plant in mixed-use habitat patches (n = 578); and (d) on *P. lanceolata* in *Plantago*-use and mixed-use habitat patches (n = 1545). Within-year differences between groups were tested as planned contrasts using analysis of variance. $^{*}p <$ .05, $^{**}p <$ .01, $^{***}p <$ .0001.

habitat patch in which it was used by ovipositing butterflies. These results (and similar corroborating experiments) indicate that the suitability of individual host plants does not vary spatially, nor are larvae locally adapted to the locally preferred host plant.

Melitaea cinxia larvae move among plants less than do *E. editha* larvae (see section 7.6). In Åland, most larvae only have access to a single plant species both because *V. spicata* is available in a small fraction of the habitat patches and because the plants grow in single-species clumps. But, in the uncommon mixed-habitat patches, larval groups may benefit by successfully moving to the alternate host species as *E. editha* do. This is because, although there is no great difference in host phenology and drought tolerance between the two host plant species, one or the other may senesce earlier, depending on spring and summer rain. For example, in 1995 larvae were placed on both host plants in one habitat patch before summer drought. Only those on *V. spicata* and those that were able to move to *V. spicata* survived (Kuussaari 1998).

Checkerspot Larvae and the Chemical Defense of Their Host Plants

Checkerspot butterflies are almost exclusively associated with plants that produce iridoids, mostly iridoid glycosides and seco-iridoids, which are noxious and thought to be produced by plants as defense against herbivory (Kooiman 1972, Bowers 1983b, 1988, Jensen 1991, Seigler 1998, Wahlberg 2001b). Iridoid glycosides deter many generalist herbivores (Bernays and DeLuca 1981, Puttick and Bowers 1988). Generalist herbivores that do feed on iridoid-producing plants or on an artificial diet containing iridoids do not often sequester the compounds (Bowers and Puttick 1986, Bernays 1988, Bernays and Cornelius 1988) but develop slowly or just to a small size (Bowers and Puttick 1988, Puttick and Bowers 1988; but see Stamp and Bowers 1994). For example, Puttick and Bowers (1988) found that survival and weight of the southern army worm, *Spodoptera eridania*, fed with an artificial diet without iridoid glycosides were greater than when their diet included the iridoid glycosides catalpol, loganin, or aucubin.

The situation is likely to be different in herbivores specialized in feeding on iridoid-producing plants, though there have been few experimental tests of the direct effects of iridoid glycosides on the larval growth in specialists. Camara (1997a) found no effect of iridoids on the weight of *Junonia coenia*. Harvey and van Nouhuys (unpubl. data) found that *Melitaea cinxia* larvae grew faster and in some cases became larger pupae when feeding on *P. lanceolata* with a high iridoid concentration than on *P. lanceolata* with a low iridoid glycoside concentration. Adult *M. cinxia* appear to oviposit more frequently on *P. lanceolata* containing higher than average concentrations of the iridoid glycoside aucubin in natural populations in Åland (Nieminen et al. 2003). However, the host plant *V. spicata*, which contains lower levels of the iridoids aucubin and catalpol than *P. lanceolata*, is used when available (Kuussaari et al. 2000) and is perhaps a more suitable host for larval development (van Nouhuys et al. 2003, M. Saastamoinen, unpubl. data). *Veronica spicata* does have other iridoids (Suomi et al., 2002) that could be converted to catapol and then sequestered.

For the most part, checkerspot larvae feeding on iridoid-producing plants are able to sequester iridoids and become distasteful or noxious themselves (Bowers 1980, 1981, 1990, Bowers and Puttick 1986, Stermitz et al. 1986, 1994, Franke et al. 1987, Gardner and Stermitz 1988, Belofsky et al. 1989, L'Empereur and Stermitz 1990a, Suomi et al. 2001). Additionally, iridoid glycosides function as oviposition stimulants for some specialist butterflies (Pereyra and Bowers 1988) and as feeding stimulants for at least some checkerspot butterflies (Bowers 1983b). It is generally thought that specialist herbivores benefit from the defensive chemistry of their hosts through reduced competition and inhibition of generalist natural enemies. However, some herbivores have primary natural enemies with narrow host ranges that are not hindered by the plant defensive chemicals sequestered by their hosts. It may even be that these specialist enemies avoid competition with generalist natural enemies, and perhaps direct predation, by using chemically defended hosts. Experimental studies on iridoid-producing plants, their herbivores, and the natural enemies of those herbivores, generally support these ideas (Bernays and DeLuca 1981, Bernays 1988, Puttick and Bowers 1988, Dyer 1995, Dyer and Bowers 1996, Camara 1997b, Theodoratus and Bowers 1999, Stamp 2001, Nishida 2002).

Most generalist predators appear to avoid larvae that ingest iridoids. Theodoratus and Bowers (1999) tested this by measuring the predation of iridoid-sequestering *Junonia coenia* larvae feeding on two different species of *Plantago* by lycosid spiders. They found in both laboratory and field experiments that the spiders ate more caterpillars feeding on *P. major*, which had a lower concentration of iridoid glycosides than on *P. lanceolata*. Similarly, *J. coenia* fed with diets of high iridoid glycoside concentration are rejected by at least three ant species (Dyer and Bowers 1996, Camara 1997b), predatory wasps, and stink bugs (Stamp 1992). Birds are similarly deterred by iridoid-containing larvae in cage experiments (Bowers 1980, 1991, Bowers and Farley 1990).

Specialist natural enemies of checkerspots cannot avoid iridoids, and, unlike generalist natural enemies, they must not be deterred by these compounds. The only known specialist enemies of checkerspot are internal larval parasitoids (chapter 8). These parasitoids must have mechanisms to detoxify plant defensive compounds. The effect of sequestered plant chemical defenses on parasitoids has been little studied. The plant secondary compound tomatine is detrimental to parasitoid wasps (Campbell and Duffy 1979), as is nicotine. Thorpe and Barbosa (1986) found that nicotine ingested by the moth larva *Manduca sexta* caused some mortality of immature *Cotesia* parasitoids, but it did not affect the overall size of surviving parasitoids. Barbosa et al. (1986) found that the negative effects of nicotine were greater for the generalist parasitoid *Hyposoter annulipes* than for the specialist *Cotesia congregata* (it is important to note that these two parasitoids use their host insect resources differently). In a laboratory study, Harvey and van Nouhuys (unpubl. data) found that the specialist parasitoid *Cotesia melitaearum* developed equally well in *M. cinxia* larvae feeding on high- and low-iridoid *P. lanceolata*. The parasitoid may be so well adapted to using a toxic host that there is no measurable cost, or the cost may be apparent only under some conditions (Nieminen et al. 2003; chapter 8).

If a specialist herbivore, which sequesters iridoids, and a generalist herbivore that does not concentrate iridoids, are presented to generalist predators, the specialist herbivore should be at an advantage (for reviews, see Bowers 1990, Camara 1997b). However, this pattern may not manifest if generalist herbivores have other means of defense. For example, Stamp and Bowers (1992) found that the specialist caterpillar *Junonia coenia* was more often killed by predatory stink bugs than a generalist caterpillar, *Pyrrharctia isabella*, while feeding on *P. lanceolata* because the generalist behaved more cryptically than the specialist.

The natural enemy community of checkerspots is a good model for the study of host specialization because so much is known about the ecology of the host butterflies and the host plant chemistry. Further comparative studies can be designed using host plant species and populations that vary naturally in iridoid concentrations and types and are used differently by herbivores (Kooiman 1972, Bowers and Puttick 1986, Bowers et al. 1992, Bowers and Stamp 1993, Camara 1997b, Darrow and Bowers 1999, Stamp and Bowers 2000b, Nieminen et al. 2003). Researchers can test for the effects of iridoids (or other potential chemical defenses) on insect communities by manipulating iridoid production through artificial selection in the laboratory (Marak et al. 2000) and by changing the iridoid content of artificial diet (Puttick and Bowers 1988, Lei and Camara 1999).

7.5 Larval Survival

Adult checkerspot butterflies produce 100–1500 eggs in their lifetime (chapter 5). The majority of the offspring perish before reaching adulthood, and the larval phase is often the riskiest stage for a holometabolous insect (Zalucki et al. 2002). Individuals that survive the foraging period typically have a high probability of surviving to reproduce. Because larval survival is often the key determinant of population size and distribution, understanding the sources and variation in larval mortality is essential to understanding and predicting butterfly population dynamics. We now turn to the factors that influence whether a larva survives to pupation. Because *E. editha* and *M. cinxia* feed on similar plant species in similar types of environments, they obviously share several mortality risks.

Sources of Larval Mortality

Larval mortality in checkerspots and in many other species generally stems from one of two sources: predation (including parasitism) and starvation (Haukioja 1993). Other factors such as larval desiccation, pathogens, cannibalism, and consumption by competitive herbivores also can cause larval death and are important in some lepidopteran populations (Gilbert and Singer 1975, Stamp and Casey 1993, Dwyer et al. 2000, Zalucki et al. 2002).

Predation and Parasitism

Potential larval predators include spiders, insect predators (e.g., stink bugs), parasitoids, and vertebrate predators (especially birds; see table 8.1). Vertebrate predation is often common during lepidopteran outbreaks (Crawford and Jennings 1989, Elkinton et al. 1996) and on species with normally high population density (Bowers et al. 1985, Alonso-Mejia et al. 1998), but it has not been frequently observed in checkerspots. Group feeding by larvae (see section 7.6) is an effective strategy against some predators, as is sequestration of defensive chemical compounds as discussed in section 7.4.

Laboratory experiments can assess whether a predator will consume a larva, and field monitoring of predator abundance indicates the potential for larval predation. But it is challenging to quantify larval mortality due to particular predators and parasitoids in the field. Luckily, parasitism is one source of mortality that is relatively easy to assess because some parasitoid species leave behind a signature of their presence. For this reason, and because parasitism is often heavy on checkerspots, the most thorough work on the predation of checkerspot larvae has focused on parasitism (chapter 8).

Natural enemies of *Euphydryas editha* larvae include spiders, predatory insects, and parasitoids (tables 8.1 and 8.2). The specialist hymenopteran parasitoids *Cotesia koebeli* and *Benjaminia fuscipenni* and the dipteran parasitoid *Siphosturmia melitaeae*, as well as several generalist parasitoids, attack *E. editha* (White 1973, 1986; table 8.3). However, there is no evidence that predation or parasitism explains a significant portion of larval mortality in this species (chapters 4 and 8). This may be because other forms of mortality, such as starvation, prevail, because defensive adaptations are relatively successful, or because predator populations are low where *E. editha* are found. Perhaps population fluctuations due to host plant availability make *E. editha* an unreliable host for specialist parasitoids.

True predation of *M. cinxia* larvae does occur, but it does not appear to account for a large part of larval mortality. Parasitism, in contrast, causes substantial larval death (tables 4.1, 8.1, and 8.3). Parasitism by the wasp *Cotesia melitaearum*, a checkerspot specialist, can be heavy in tightly clustered and high-density *M. cinxia* populations but not in regions where local populations are sparse and small. Thus *Cotesia melitaearum* is entirely lacking from a large fraction of *M. cinxia* populations (Lei and Hanski 1997, van Nouhuys and Hanski 2002a, 2002b). Parasitism by another specialist parasitoid, *Hyposoter horticola*, is less variable and typically causes about 30% mortality of postdiapause larvae (van Nouhuys and Hanski 2002b).

The prevalence of parasitism appears to be one difference between *E. editha* and *M. cinxia*. Further work is called for on parasitoid communities associated with *E. editha* to determine whether less-studied populations experience significant parasitism and under which conditions this might occur. For example, Moore (1989a) found up to 66% parasitism by the parasitoid *Cotesia koebeli* in one Sierra Nevada population of *E. editha*.

Starvation

A shortage of food can occur where host plant density is low or larval density is high or when host plants wither before caterpillars have finished development. All these factors appear to play a role in the mortality of checkerspot larvae, which feed on more or less ephemeral or patchily distributed host plants. The degree to which larvae are affected by food shortage can be mediated by larval mobility. Relatively immobile larvae are unable to locate new host individuals when their natal host plant becomes unsuitable or is consumed. Mobile larvae, in contrast, are able to leave an unsuitable host individual and locate another one (Dethier 1959; section 7.6). Whether larvae suffer higher rates of mortality while dispersing than if they had remained in place depends on the distribution of potential food plants and the vulnerability of larvae to predation en route.

Starvation is an important source of larval mortality in *E. editha* (Singer 1972, White and Singer 1974). Coastal populations of *E. editha* forage on host plants that undergo annual senescence before the onset of summer drought (chapter 3). In years when senescence occurs before most larvae have grown enough to enter summer diapause, larval mortality rates are high, in excess of 90% (Singer 1972, Hellmann 2002c). Hence, the relationship between timing of host senescence and egg hatching is important, and variation among years in this relationship leads to variation in the number of larvae that survive to diapause and ultimately to adulthood. This single factor explains a large amount of the population fluctuations in one well-studied population at Jasper Ridge, California, and similar considerations likely apply to other coastal populations (McLaughlin et al. 2002a; chapter 3). In montane populations of *E. editha*, larval mortality from starvation is also an important factor. In a metapopulation at Rabbit Meadow, 2350 m above sea level, there is often competition among larvae and subsequent starvation when large numbers of larvae defoliate an individual host (C. D. Thomas et al. 1996, Boughton 1999a). Frost events in montane areas also cause massive larval starvation when hosts are killed (Singer and Thomas 1996).

Because different plant species often senesce at different times, host use plays a role in determining rates of larval mortality in *E. editha*. In the San Francisco Bay Area, for example, larvae feed on two host species: one that senesces relatively early, *Plantago erecta*, and another one that senesces up to two weeks later, *Castilleja* (Weiss et al. 1988; chapter 3). The montane metapopulation at Rabbit Meadow also uses two hosts that differ in the same manner; *Collinsia torreyi* causes larval mortality due to early senescence, and *Pedicularis semibarbata* does not. Thus, larval mortality in any single habitat and year depends both on weather (because it influences host senescence) and on the fraction of larvae that forage on each of the two hosts (figure 7.4). In years when the longer lasting host persists long enough to sustain *E. e. bayensis* larvae while the other one does not, habitats with high abundance of *Castilleja* are likely to have greater larval survivorship than habitats where that host is sparse (Hellmann 2002c). Studies also suggest that population extinction rates vary with host plant use in *E. editha*; populations that forage on *Pedicularis* have a greater tendency to persist (M. Singer and C. Parmesan, unpubl. data).

Melitaea cinxia larvae also suffer from starvation. Large-scale starvation of prediapause larval groups is caused by occasional late summer droughts, which result in temporal withering or complete drying out of host plants over large areas in the Åland Islands (chapter 4). Although droughts affect entire landscapes rather than single habitat patches, typically there is variation in the severity of drought among different parts of Åland (figure

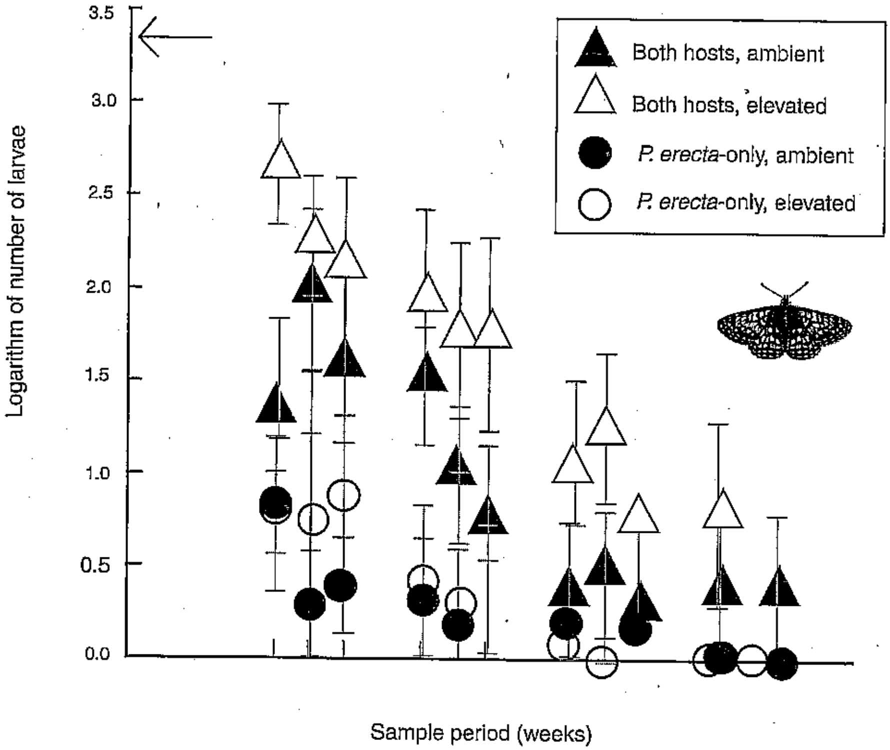


Figure 7.4. Host plant-dependent survival in *Euphydryas editha* (Hellmann 2002a). Prediapause larvae were grown on plots of plants containing either one (*Plantago erecta*) or two (*Plantago erecta* and *Castilleja exserta*) host plants under two temperature treatments in the greenhouse. Host plant availability treatments reflect distributional differences of the two hosts in the field. Temperature treatments represent different microclimatic conditions as would occur in nature across slopes of different exposure or across years as determined by weather. The number of larvae in the treatment with both host plants over time was significantly higher than in the treatment with only the common host (area under the abundance curve). Further, the survival of larvae is higher when both hosts are present under elevated temperatures than under ambient temperature. This result suggests that access to the less common but long-lasting host, *Castilleja*, confers a significant survival advantage to larvae foraging on senescing host plant material, and this advantage is greatest when temperature is high.

4.14). On one hand, drought may cause a cluster of local extinctions when all the larval groups in several habitat patches run out of food (Hanski 1999b). On the other hand, there is variation in habitat quality among the habitat patches, and during droughts larval survival may be relatively high in patches with soil that retains moisture well. Even within local populations, a fraction of larvae survive because microhabitat and soil type can vary at a small spatial scale.

Melitaea cinxia larvae can starve when egg batches are laid on plants growing in areas of low host-plant density. The larvae run out of food after defoliating the single or few host-plants in the close neighborhood and are not sufficiently mobile to find more food. In spring 1994, postdiapause larval survival was followed closely in all the larval groups that survived the previous winter in 20 local populations of *M. cinxia* in different parts of Åland. Nearly half (47%) of the larval groups were located in areas of such low host-plant density that shortage of food was likely to decrease larval growth (table 7.3; M. Kuussaari, unpubl. data). Clear signs of starvation (i.e., an entire larval group starved, some larvae starved or were found feeding on nonhost plants such as *Trifolium repens*) were observed in 38% of the larval groups in low host-plant density areas, whereas no signs of starvation were observed in areas of higher host plant density (table 7.3). Both postdiapause larval survival and growth rate were positively correlated with host plant density ($P < .01$).

Comparison with Other Life Stages

We have suggested that processes critical to the population ecology of checkerspot butterflies occur during the larval stage. In particular, variation in larval mortality due to weather, host plant use, predation, and parasitism causes fluctuations in population size. There are also important risks that limit survival of eggs, pupae, and adults and thus are important contrasts to the risks discussed above for larvae. Eggs can be preyed upon or fail to hatch. Eggs of *M. cinxia* are eaten by ants and by ladybird and lacewing larvae (table 8.1). The fraction of eggs consumed is a little-studied issue in both *E. editha* (Moore 1989a) and *M. cinxia* (chapter 4), but the fitness consequences of such predation may be high because entire larval groups are lost. Additionally, eggs can fail to hatch due to inbreeding depression (Haikola et al. 2001; chapter 10) or unsuitable abiotic conditions, such as heavy showers (chapter 4).

The extent of pupal mortality is even less well known, but it is clear that the sources and magnitude of this mortality factor vary greatly among species and populations. For example, the mortality of *E. editha* pupae placed in the field varied from 53% to 89% among habitat types and years (White 1986). Predation, cold weather, and parasitoids (table 8.3) are the likely causes of pupal mortality. A fraction (13%) of *M. cinxia* pupae placed in the field in one year was lost to parasitism (Lei et al. 1997).

Extreme weather events including frost and high winds have been known to kill adult *E. editha* butterflies, and even entire populations (Singer and Thomas 1996, C. D. Thomas et al. 1996, Hellmann 2002b). Females may be at particular risk of predation while ovipositing (Moore 1987); experimental manipulations in the San Francisco area showed that *E. editha* populations tend not to suffer heavy losses of adults (Ehrlich et al. 1975). In 1964, every captured butterfly was removed from the populations (area C: $n = 123$; area H: $n = 1353$), but abundance in 1965 was not obviously affected (Hellmann et al. 2003). There have been practically no observations of adult predation on *M. cinxia* apart from infrequent predation by dragonflies (I. Hanski pers. comm.), but extreme weather undoubtedly decreases adult longevity and limits reproductive success.

Table 7.3. Host plant density and the occurrence of postdiapause starvation in 20 local populations of *Melitaea cinxia* in the spring 1994 (M. Kuussaari, unpubl. data).

Host Plant Density[a]	No. of Larval Groups	Entire Group Starved	Some Larvae Starved	Feeding on Nonhost Plants	Some Signs of Starvation	%
High	14	0	0	0	0	0
Moderate	22	0	0	0	0	0
Low	32	5	3	4	12	39

[a] *Plantago lanceolata* density: low < 20, moderate = 20–35; high > 35 *Plantago* rosettes/m².

7.6 Role of Group Size in Larval Behavior and Survival

Advantages of Cluster Laying and Gregarious Behavior

We have already emphasized that laying eggs in clusters and gregarious larval behavior, at least during the first larval instar, are common traits among checkerspot butterflies (Stamp 1980, Wahlberg and Zimmermann 2000). Some advantages of these traits have been studied in checkerspots, including *Euphydryas aurinia* (Porter 1981, 1982), *E. editha* (M. Singer, unpubl. data), *E. phaeton* (Stamp 1981a, 1982a), *M. cinxia* (Lei and Hanski 1997, Kuussaari 1998, van Nouhuys and Hanski 1999), *Chlosyne lacinia* (Clark and Faeth 1997a, 1998), and *C. janais* (Denno and Benrey 1997). Increased larval growth rate and survival with increasing group size, especially during the first larval instars, have been demonstrated in several species of checkerspots (Clark and Faeth 1997a, Denno and Benrey 1997, Kuussaari 1998), as well as of other Lepidoptera (Lawrence 1990, Fitzgerald 1993).

Most hypotheses proposed to explain the evolution of egg clustering and gregarious larval behavior in Lepidoptera focus on the benefits of gregarious behavior for larval survival and growth rate (Clark and Faeth 1997a, Denno and Benrey 1997). These hypotheses are usually based on either increased foraging efficiency or enhanced defense against natural enemies with increasing group size, mechanisms that are not mutually exclusive. Other potential explanations for egg clustering include avoidance of egg desiccation (Stamp 1980, Clark and Faeth 1997a) and increased fecundity when females are time limited as opposed to egg limited (Courtney 1984, Parker and Courtney 1984). As noted by Bryant et al. (2000), there are so many potential causes and consequences of group living that it may be common for several different factors to affect the costs and benefits of gregariousness in a particular case.

The benefits of increasing group size vary during butterfly development from egg to pupae. Large clusters of eggs may avoid desiccation better than smaller clusters or single eggs, as was experimentally shown in the laboratory for *Chlosyne lacinia* (Clark and Faeth 1998). Decreasing group size increased egg desiccation also in a field experiment on *M. cinxia* (Kuussaari 1998). In the latter experiment eggs were placed under the leaves of host plants in small mesh baskets that excluded egg predators. Invertebrate predators like lacewing (Chrysopidae) and lady beetle (Coccinellidae) larvae have been observed to cause substantial egg mortality in *M. cinxia* populations locally, but it is not known whether the rate of egg predation is associated with egg cluster size. Parasitism and predation of *E. phaeton* eggs in one study was not affected by cluster size nor by the number of clusters per plant (Stamp 1981b). Similarly, parasitism of *M. cinxia* by *Hyposoter horticola*, which acts as an egg parasitoid because it lays eggs in host larvae that have not yet hatched, also appears to be unrelated to egg cluster size (van Nouhuys and Ehrnsten 2004).

Facilitation of feeding due to larval aggregation is likely to be most pronounced during the first larval instar, when the small larvae establish their first feeding site (Shiga 1976, Fitzgerald 1993, Clark and Faeth 1997a). At this stage, the physical plant defenses, such as trichomes, are most difficult to overcome (Young and Moffett 1979, Zalucki et al. 2002). Another critical ability likely to improve with increasing group size is building of the feeding web. Web building is best developed in species that have large or medium-sized egg clusters, whereas it can be nonexistent in species with small egg clusters. Constructing substantial webs may be advantageous when larval groups are large because the per capita energetic cost of building the web may be less for larvae in large than in small groups. This aspect of larval biology has not been studied.

Web building also varies significantly within species living under different conditions. For example, *M. cinxia* in low-elevation southern France and the Russian steppe appear to overwinter in small groups with little or no webbing (S. van Nouhuys and M. Singer, pers. obs.), while *M. cinxia* in Åland and the high Alps diapause as family groups in dense webs. Both weather and natural enemies are likely to be important selective forces. The defensive function of webs has not been well studied, but generalist predators are most likely hindered by a dense web, as are at least some parasitoids. Tachinid flies attempting to oviposit in *E. maturna* postdiapause larvae can only do so through holes in the web (Wahlberg 1998); however, specialist parasitoids of *M. cinxia* and *E. phaeton* readily move within the web to parasitize early instar larvae (Stamp 1982b, S. van Nouhuys pers. obs.). Webs actually stimulate the search behavior of *C. melitaearum*, which parasitizes *M. cinxia* (S. van Nouhuys unpubl. data).

Group living may have a substantial effect on growth rate, especially after winter diapause, when black larvae may bask in tight clusters and increase their body temperature close to developmental optimum during cold but sunny spring days (Porter 1982, Casey et al. 1988, Stamp and Bowers 1990, Casey 1993, Kuussaari 1998, Bryant et al. 2000). Rapid development is critical in populations in areas with a short growing season. Additionally, increased growth rate due to gregarious behavior may help the larvae escape specialist parasitoids, as the larvae may manage to pupate before their parasitoids emerge (Porter 1983). The gregarious basking of *M. cinxia* larvae during warm springs allows them to increase their development rate so that the majority of them pupate before the spring generation of the parasitoid *C. melitaearum* become adults. The parasitoid cocoons, which are white, immobile, and often in the shade, cannot control their own development rate. Consequently, during cool spring seasons the host and the parasitoid are developmentally better synchronized, and a larger fraction of larvae are available for parasitism, increasing parasitoid population size substantially (S. van Nouhuys and G. C. Lei unpubl. data).

Larval aggregations may avoid predation and parasitism more successfully than solitary larvae by various kinds of active defenses, such as head jerking (Stamp 1982b, 1984) and regurgitation (Stamp 1984, Peterson et al. 1987). Head-jerking behavior can knock attacking parasitoids off the larvae, an effect that is enhanced when many larvae jerk their heads simultaneously (Stamp 1982b).

Although active defenses may be enhanced in large groups, large groups may also attract more predators than small groups. In *M. cinxia*, parasitism by *Cotesia melitaearum* increases with increasing group size (Lei and Hanski 1997, van Nouhuys and Hanski 1999). Increased resource competition among larvae is another potential disadvantage of large group size. Gregarious larvae are more often distasteful and conspicuously colored than solitary larvae (Stamp 1980, Guilford 1988), which has led to the suggestion that gregarious larvae avoid predation, especially by birds, through aposematism (Bowers 1980, 1981, 1993, Stamp 1980). The strength of the warning signals of aposematic species may be amplified by group size (Bowers 1993, Fitzgerald 1993).

Because species putatively most closely related to the checkerspots also sometimes lay their eggs in clusters (Kallimini and Nymphalini: Harvey 1991; chapter 2), egg clustering may well be ancestral in checkerspots. The interesting question, therefore, is not why checkerspots lay their eggs in clusters, but rather why there are different degrees of larval gregariousness within the checkerspots. In the following sections we take a closer look at variation in group size and its effect on larval survival, as well as gregarious behavior and larval mobility, mostly based on data on larval behavior and development in the highly gregarious *M. cinxia* and in the less gregarious *E. editha* larvae.

Variation in Group Size

In *M. cinxia* in the Åland Islands the average egg cluster size is about 170 eggs, but it can vary from < 50 to > 350 eggs (figure 7.5). In the field, small egg batches may result from various disturbances to ovipositing females. For instance, an attack by ants (Wahlberg 1995; chapter 8) or other predators such as dragonflies or a sudden change in weather (M. Kuussaari pers. obs.) may cause the female to terminate oviposition. Especially large larval groups may result from fusion of groups when more than one egg batch has been laid on the same host plant. This happens even in relatively low-density populations of *M. cinxia* because some host plant individuals tend to be especially attractive to egg-laying females (Singer and Lee 2000) and because ovipositing butterflies are attracted to conspecific eggs (M. Singer and L. Ramakrishan unpubl. data). Multiple egg batches per plant is demonstrated by a survey of naturally occurring egg batches on 4295 randomly selected *P. lanceolata* plants in 5 *M. cinxia* populations. Of the 39 plants that had egg batches, 34 plants had 1, 4 plants had 2, and 1 plant had 3 batches of eggs. Thus, multiple egg batches on one plant were observed more often than predicted by chance (M. Kuussaari unpubl. data).

Nonrandom accumulation of egg batches on some host plant individuals is also well known in other checkerspot species, such as *E. aurinia* (Porter 1981) and *E. phaeton* (Stamp 1981a). In a Sierra Nevada population of *E. editha*, Moore (1989a) found up to 19 clusters of eggs on a single *Pedicularis semibarbata* individual. Most of the host plants receiving eggs received more than one egg cluster during the butterfly flight season. Studies by Rausher et al. (1981) suggest that eggs are contagiously distributed on *Pedicularis* in *E. editha* because females are more likely to alight and lay eggs on large, isolated plants.

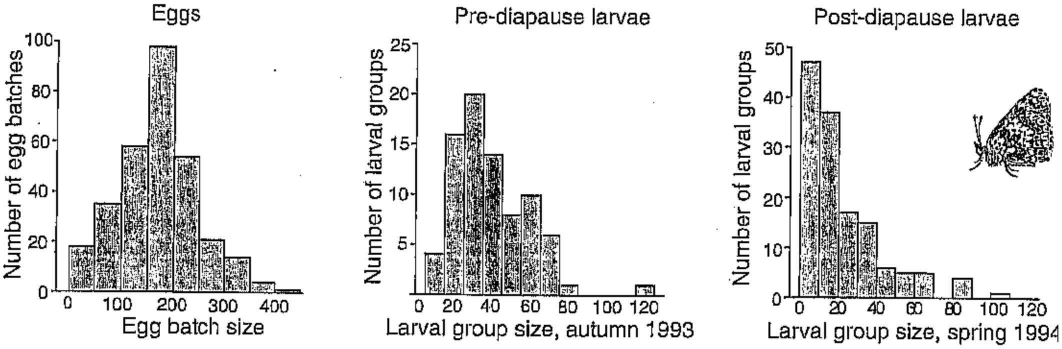


Figure 7.5. Distribution of *Melitaea cinxia* group size at the egg stage and before and after winter diapause (modified from Kuussaari 1998).

When the number of larvae per plant is high, the advantage of being on a populated plant must decline (Rausher et al. 1981, C. D. Thomas et al. 1996). In populations where hosts senesce, competition among larvae on the same plant may be limited because host plant quality, not host plant depletion, determines the need for dispersal (Singer and Ehrlich 1979). In such populations, larval competition may occur as the number of nonsenescent hosts declines, but this competition is a function of the number of larvae in a foraging area and not the number of groups on an individual plant. In all checkerspots, optimal group size may differ on different host plant species or in different foraging environments as a function of plant size, timing of senescence (Moore 1989a), and the availability of alternative host plants.

Group Size and Larval Survival

Variation in group size among populations of *Euphydryas editha* stems from genetic variation in egg cluster size and is associated with the species of host plant used (M. Singer, unpubl. data). For example, populations on *Pedicularis semibarbata* have mean egg cluster sizes of 50–90, those on *Collinsia tinctoria* 20–30, and those on *Collinsia torreyi* only 5–7. At Rabbit Meadow in the western slopes of the Sierra Nevada mountains, where *Collinsia torreyi* has been recently colonized by *E. editha* from *Pedicularis semibarbata*, the mean cluster sizes were larger on *Collinsia* than on *Pedicularis* (52 and 48 eggs on average, respectively; Moore 1989a). A similar difference was observed among captive insects split into two groups, with each group offered only one host species (Singer 1986a). In an experiment, newly hatched larvae were placed in groups of 1, 5, 20, and 50 on *Pedicularis* and *Collinsia* at Rabbit Meadow over 4 different years. In one year group size had little effect, but in the other years larval survival was highest in groups of 5 on *Collinsia* and in groups of 20–50 on *Pedicularis*. Single larvae had close to zero survival on *Pedicularis*, but 60% survival on *Collinsia*. Natural selection on group size, therefore, was different on the two hosts in a direction that would explain the evolved differences between geographically separate populations specialized on these hosts. In the final year of the study, a tanglefoot (predator exclusion) treatment was added to the group size experiment on *Pedicularis* (it was not feasible to exclude predators from *Collinsia*). The effect of group size on survival totally disappeared; hence, it appears that there was an interaction among fitness, group size, and host use that was predator mediated.

A striking feature of *M. cinxia* is the consistently positive effect of group size on survival throughout development from egg stage to the last caterpillar instar, which has been demonstrated by experimentally varying group size (figure 7.6). Figure 7.5 shows natural group size variation in *M. cinxia* just before and immediately after winter diapause. Groups with < 25 larvae have only a small chance of surviving over the winter. The likely reason is that small groups are unable to build a high-quality winter nest, which is necessary for successful overwintering (Nieminen et al. 2001). The quality of winter nests of experimentally inbred *M. cinxia* larvae was scored significantly lower (with thin silk and holes in the nest) than the quality of winter nests in control groups (dense silk, no holes; Nieminen et al. 2001). Consequently, winter mortality of the inbred groups was higher than mortality in the con-

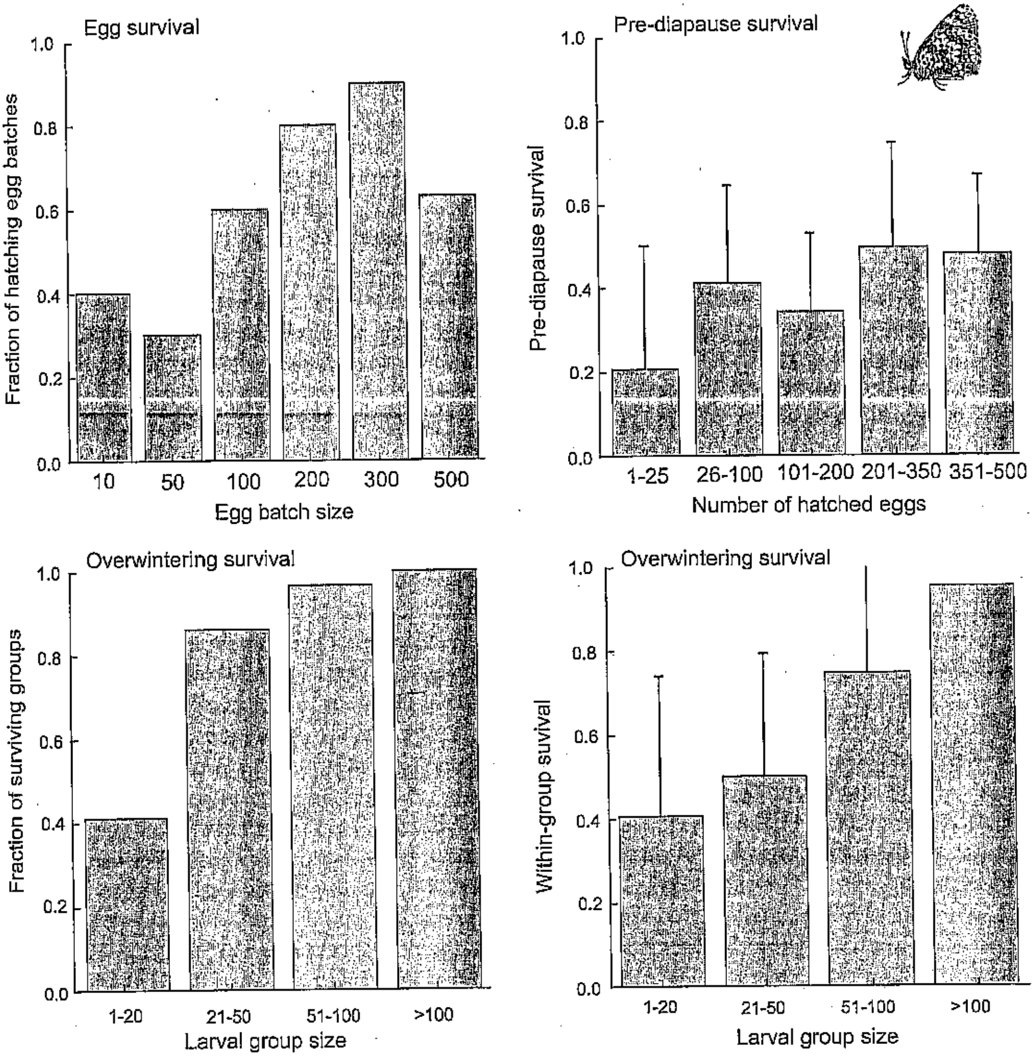


Figure 7.6. Effect of group size on survival in *Melitaea cinxia* in an experiment in which group size was manipulated (modified from Kuussaari 1998).

trol groups (Nieminen et al. 2001). Results from larval survival studies suggest that during the prediapause larval development of *M. cinxia*, the benefits of large group size are greater than the costs, even though the risk of parasitism (Lei and Hanski 1997) and the quantity of host plant tissue needed for development (Kuussaari 1998) increase with increasing group size. Because larval groups typically face a high level of prediapause mortality, large initial group size is a good strategy for preparing a high-quality winter nest necessary for successful overwintering. In this context it may not be accidental that attraction of females to conspecific eggs was documented in Finnish *M. cinxia* that spin winter nests, but not in *M. cinxia* from southern France that do not spin winter nests. The response to conspecific eggs differed significantly between *M. cinxia* from the two regions (M. Singer and L. Ramakrishan unpubl. data).

After diapause, large group size could be expected to have negative effects by increasing resource competition among larvae with growing food demands, but in practice, negative effects have seldom been observed. On the contrary, field studies conducted before the dispersion of larvae in the final instar suggest that both growth and survival increase with group size during postdiapause larval development in *M. cinxia* (Kuussaari 1998). This could be partly because larvae overwintering in large groups probably started out the spring with more energy reserves than larvae who had overwintered in small groups. Growth rate in large groups was also enhanced by group basking. The temperature in the aggregations of black larvae tended to be about 20°C above ambient temperature (30.6°C on average in larval groups in sunny weather) during early spring (Kuussaari 1998). When host plant availability is limited, larval groups tend to split into smaller subgroups and to move longer distances, thereby decreasing resource competition among siblings. Because a large portion of the plant consumption by larvae (>80%) occurs during the last instar when larval survival is difficult to monitor, it is not known to what extent the larvae suffer mortality caused by large group size at this stage.

Larval Dispersion and Movement Distances

After egg hatching, larval group size gradually declines because of larval mortality, group splitting, and larval dispersal. There is much variation both within and among checkerspot species in the timing of larval dispersal. Among the five species of checkerspots in southern Finland, *Melitaea athalia* larvae disperse soon after their first or occasionally after their second molt in July or August (Warren 1987a, Wahlberg 1997b, S. van Nouhuys pers. obs.), whereas the other four species remain in groups until diapause. *Euphydryas maturna* and *Melitaea diamina* disperse immediately after diapause (Wahlberg 1997a, 1998), but larvae of *E. aurinia* and *M. cinxia* remain in conspicuous groups and exhibit a similar basking behavior during cool spring days. *Euphydryas aurinia* larvae disperse after their first molt in the spring, but *M. cinxia* larvae tend to remain together for still another larval instar before dispersing in the final instar just before pupation. The reasons for these differences in the level of gregarious behavior among closely related species remain an interesting question for further research.

Variation among species in the benefits of increasing group size may be associated with the timing of larval dispersal. In a comparative study by N. Wahlberg (unpubl. data), the growth of the larvae of *Melitaea deione*, a species in which larvae disperse soon after hatching, was not affected by group size. In contrast, the larvae of *Melitaea parthenoides* grew faster in larger groups and remained gregarious until diapause in the field. It is interesting to note that *M. athalia* larvae, which disperse early, are cryptic and solitary and, unlike *M. cinxia*, respond to disturbance by dropping from the plant (S. van Nouhuys pers. obs.).

Prediapause larvae of *E. editha* tend to disperse individually. The distances that individual larvae are able to disperse are likely to increase with age, and the cost of dispersal probably decreases with age. Although groups do not appear to migrate as units, new groups can be formed in *E. editha* late in the season as the majority of hosts become unsuitable (senesce). In *E. editha bayensis*, groups can be found on long-lasting *Castilleja* individuals, although eggs were not laid on these plants; such groups probably represent a mixture of larvae from different egg batches (J. Hellmann pers. obs.). These late-forming groups have been occasionally observed to form loose webs. Competition among siblings and nonsiblings and the appearance of larval groups may also occur as the number of suitable host plants declines due to host depletion (C. D. Thomas et al. 1996).

After diapause, *E. editha* larvae often disperse great distances relative to their size, up to 10 m/day. Postdiapause larvae in coastal populations eat as they move, feeding almost exclusively on *P. erecta* (because *Castilleja* has not yet germinated) and consuming entire plants as they disperse. Weiss et al. (1987, 1988) studied the movement and growth of postdiapause larvae of *E. editha bayensis* and found that the position of larvae in the landscape significantly affected the accumulation of body weight. As mentioned before, postdiapause larvae bask in the sun to elevate their body temperature and to increase their rate of growth. Whether larvae are found on cool, north-facing or warm, south-facing slopes significantly affects the amount of sunlight they receive and hence the rate at which they grow (chapter 3). Weiss and colleagues found that larvae in low-insolation environments grew to pupation two weeks slower than larvae in high-insolation environments. Given temporal constraints on the feeding time of prediapause larvae (section 7.5 and chapter 3), it should be advantageous for prediapause larvae to move to sites where they can grow fast.

The movement capacity of the first two instars of *M. cinxia* is extremely limited. At this stage the larval group just expands its web and moves only on the host plant individual that it occupies. The mobility of the larvae increases as they grow but remains limited to a maximum of 1–2 m before winter diapause (Kuussaari 1998). The distances moved by prediapause larval groups get longer with increasing group size, but most groups move < 0.5 m before diapause (figure 7.7). In the spring, the movement distances increase with group size and developmental stage (figure 7.7) and decrease with increasing host plant abundance. Before the ultimate larval instar, the average distances moved even by large larval groups tend to be less than 1 m. However, large groups in areas of low host plant availability may move up to 6 m in search of food. Finally, last instar caterpillars are substantially more mobile, and although entire groups rarely move more than a few meters as a group, single larvae have been observed at distances more than 10 m from any known larval group. The maximum distance that a final instar *M. cinxia* caterpillar has been observed to move is 16 m, but no studies have been conducted specifically to quantify movement abilities of full-grown larvae.

Unlike *E. editha bayensis*, *M. cinxia* larvae are quite systematic in their foraging. When feeding on *Plantago lanceolata*, the primary host plant in the Åland Islands, the larvae usually do not leave a plant until it is completely defoliated. After defoliation of one host plant, they move as a group to a neighboring plant. If drought causes host desiccation, *M. cinxia* larvae stay in their web and wait for rain. In contrast, when prediapause *E. editha* larvae are faced with a senescent host, they keep searching until they starve or find a new host if they are not large enough to enter diapause. This difference reflects the difference between a north temperate and a Mediterranean climate and between a perennial and an annual host. An *E. editha* larva feeding on an annual host at the end of California spring cannot wait for rain to reinvigorate its food supply. Its only chance is to quickly find a patch where hosts are still edible.

In the spring, an average postdiapause larval group of *M. cinxia* consumes about 90 *Plantago* individuals (rosettes), and the largest larval groups defoliate up to 400 plants (M. Kuussaari unpubl. data). When movements of larval groups were intensively monitored in low-density *M. cinxia* populations in spring 1994, it was possible to measure the defoliated areas (area within which >90% of host plants were consumed) after the larvae had pupated. Typically, all host plants were completely devoured within distinct areas, while in the surroundings there were practically no signs of larval feeding. The average area defoliated was 3.5 m^2, and the maximum was 15 m^2 defoliated by the largest groups of larvae.

7.7 Spatial and Temporal Variation in Survival and Population Dynamics

The suitability and availability of food for checkerspot larvae is often closely tied to climate and weather

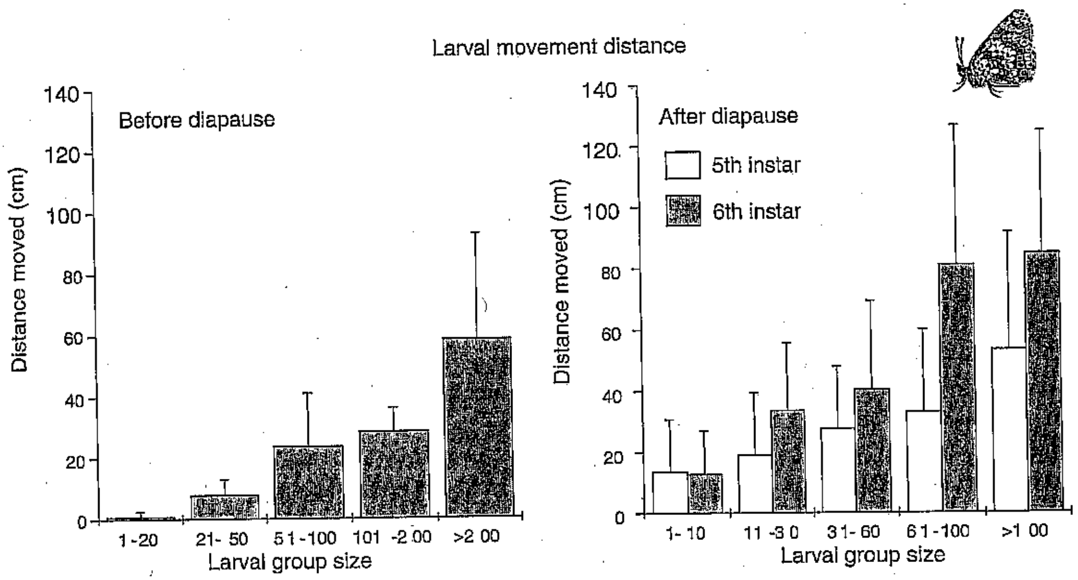


Figure 7.7. Pre- and postdiapause larval movement distances in *Melitaea cinxia* as a function of group size (modified from Kuussaari 1998).

and may vary widely within and among habitats and among years. Habitat alteration due to grazing, logging, and other human-caused environmental disturbances also influences the quality of foraging habitat for larvae over space and time and contributes to variation in population size among sites and over time (Singer et al. 1993, Hanski et al. 1995b, Singer and Thomas 1996, Weiss 1999). Also, populations of natural enemies are not constant over space and time (Lei and Hanski 1997, van Nouhuys and Tay 2001). Spatial and temporal variation in all these factors creates a mosaic of risks to larvae.

The primary source of variation in larval mortality within a habitat patch is variation in the weather that a patch experiences across years. A secondary source of variation is a factor that mediates the effect of climate: topography (important to *E. editha*) or within-patch heterogeneity (important to *M. cinxia*). In the case of coastal *E. editha* populations, for example, years with exceptionally low or high seasonal rainfall lead to population declines, presumably by affecting the phenology of prediapause larvae and their host plants (Ehrlich et al. 1980, Dobkin et al. 1987, McLaughlin et al. 2002a). Such extremes do not affect larvae equally, however. The distribution of postdiapause larvae in the year after an extreme year suggests that larvae on cool slopes fare better than larvae on warm slopes. Cool slopes offer a climatic refuge, presumably by maintaining suitable phenological overlap between developing larvae and senescing host plants (Singer 1972, Weiss et al. 1988, 1993; chapter 3).

Annual variation in weather also affects the survivorship of *M. cinxia* larvae. Summer drought decreases group size at diapause, and survival over the winter decreases with increasing severity of winter weather. Both summer drought and winter weather have an influence on the average group size in the following spring. Large groups survive to diapause and survive over the winter better than small groups. In addition to group size, survival appears to depend on the host plant distribution, soil water retention, and small-scale topography. There is no large-scale topographic variation (hills or mountains) in Åland, but small-scale topography, such as small slopes, rocks, and ant hills influence the effect of drought on plants, as does soil quality and host plant distribution. Larvae on a withering plant a short distance from suitable alternative host plants have a greater chance of persisting through drought conditions than larvae on isolated withered host plants or those surrounded by other withered plants.

Sources of larval mortality also vary among populations. Drought events, for example, are typically widespread (Ehrlich et al. 1980), but the intensity of drought varies across space so that conditions are more severe at some sites than at others. Differences in habitat quality among sites lead to systematic differences in larval mortality. For example, sites may differ in the total abundance or mixture of larval host plants, affecting the ability of larvae to move among hosts, the amount of time that larvae are able to forage before diapause (coastal *E. editha*), or the total number of larvae that reach adulthood (*M. cinxia* in Åland). For *M. cinxia*, mortality rates are significantly lower at sites lacking the parasitoid *C. melitaearum* than at sites where parasitoids are present at high density (Lei and Hanski 1997), and this parasitoid is more successful when it attacks larval groups on one of the two host plant species (*Veronica spicata*; van Nouhuys and Hanski 1999). However, *C. melitaearum* is not present in most populations, and although in some years larval survival is higher in habitat patches dominated by one host plant species or the other, on average *M. cinxia* survive equally well on both host plants (van Nouhuys et al. 2003; figure 7.3).

Habitat management influences larval survival. Although cattle grazing is the primary factor maintaining meadows open and suitable for *M. cinxia* in the long term, its short-term effects on larval survival and population persistence are negative. Larval groups on meadows occupied by grazing mammals are frequently trampled or eaten by sheep, cattle, and horses (M. Kuussaari and M. Nieminen pers. obs.). As a consequence, active grazing increases the risk of local population extinction and decreases the probability of colonization of currently empty habitat patches (Hanski et al. 1995b). Cattle grazing has similarly both positive and negative effects for *E. editha*. Near coastal populations it tends to decrease cover of invasive plants (Weiss 1999; chapter 12), but grazing presumably also causes some mortality due to incidental trampling. The initial introduction of cattle, of course, was ultimately responsible for the expansion of invasive plants in the first place in North America. In some locations, *E. editha* have even shifted their host use in response to habitat changes caused by grazing (Singer et al. 1993a). If cattle are removed, or if land management for cattle production is stopped, these populations could risk extinction from food shortage.

Density-dependent Larval Survival and Population Dynamics

We have shown that variable weather and topography cause variation in larval survival and that weather largely drives population fluctuations in checkerspot butterflies. This is not to say, however, that larval density would never influence checkerspot larval survival and population dynamics. Negative density dependence has been shown to affect local dynamics of *M. cinxia* (Hanski 1999b), and food limitation for large numbers of larvae has been observed in some populations of *E. editha* (White 1974, Boughton 1999). As we discussed in section 7.6, at the level of individual larval groups, "density" (number of larvae per group) has a generally positive effect, with the caveat that there is local adaptation in group size related to the size (and possibly other qualities) of the host plant primarily used in the population.

Increasing density is likely to increase mortality by two primary mechanisms, first by increasing competition for food and second by increasing predation or parasitism due to aggregation, or increase in population sizes of natural enemies. Both mechanisms are known to occur in *M. cinxia* populations in the Åland Islands. As shown by the results in table 7.3, food shortage causes starvation of *M. cinxia* larvae even in low-density populations of the butterfly, and higher larval density inevitably increases competition for food. The specialist parasitoid *Cotesia melitaearum* rarely persists in low-density *M. cinxia* populations and rarely significantly influences the population dynamics of the butterfly. However, in large and tightly clustered *M. cinxia* populations, *C. melitaearum* populations have been large, and the proportion of larvae parasitized has been high, causing both steep declines in local abundance and even local extinctions of the host butterfly (Lei and Hanski 1997, van Nouhuys and Hanski 2002b).

The role of larval density for *M. cinxia* population dynamics was studied experimentally in 22 local populations in Åland during two generations in 1993–94. In half of the populations local larval density was increased by relocating larval groups. In the remaining populations the larvae were also relocated but retaining the original local density (M. Kuussaari unpubl. data). The population sizes were compared in the next generation. As predicted, population growth rate was lower in the populations in which local density was experimentally increased than in the control populations, probably as a direct consequence of increased competition for food.

The results of the above experiment demonstrate that defoliation of host plants by *M. cinxia* can affect population dynamics. However, such extreme situations have been rare during the past 10 years of intensive research in Åland. The only case of a complete large-scale defoliation of practically all host plants in a habitat patch was observed in spring 1994, when the largest local population of *M. cinxia* in Åland was comprised of more than 100 larval groups. The habitat patch was a dry, sandy meadow of 2500 m^2 with abundant *P. lanceolata* covering more than half the area. A large proportion of the host plants in that meadow became defoliated two or more times during the spring, and the larvae had to wait for plant regrowth before being able to complete their development and pupate. Even though substantial larval mortality due to starvation probably occurred, a large proportion of the larvae were eventually able to pupate because of the relatively quick regrowth of *P. lanceolata* after defoliation. Consequently, a similar density of larval groups was observed in the same population in the next larval generation in autumn 1994. The population crashed, however, before the next adult generation, probably because of the very high parasitism rate by *C. melitaearum* in the spring 1995 (G. Lei pers. comm.).

Models of the well-studied *E. editha bayensis* populations at Jasper Ridge during their long decline to extinction (chapter 3) suggest a small role for density-dependent factors (McLaughlin et al. 2002a). Strong density dependence is unlikely to occur in *E. editha* except when populations are at exceptionally high levels, though the role of parasitoids in *E. editha* deserves further study.

7.8 Conclusion: The Checkerspot Larva as a Gambler

Checkerspots spend most of their lives as larvae. We began by remarking that negative events happen to these larvae and that the nature and frequency of these events are often key factors in butterfly population dynamics. However, we should not give the impression that larvae are powerless in the face of this onslaught. At several points in their lives they make active decisions that have dramatic consequences for the survival of themselves or their offspring. Checkerspot larvae are wonderful gamblers, and, because the fecundity of adults is so high, they play for high stakes. Certainly *M. cinxia* does. Larvae in Finland have an obligatory diapause, but they can decide whether to enter diapause at the beginning of the fourth or the fifth instar. This decision must be made before the end of the third instar. Once made, it is irrevocable, but, because these gregarious larvae do not investigate their surroundings, the decision must be made with little knowledge about food availability. We have watched a group of more than 100 larvae starve en masse because they chose to feed rather than diapause in fifth instar only to find, once they started to forage, that their host was totally defoliated with no others in reach. *Euphydryas editha bayensis* larvae likewise are gamblers. A female larva growing in the cool San Francisco Bay springtime has the option of pupating early and becoming an adult with relatively low fecundity and high likelihood of offspring survival. Alternatively, it could remain longer in the larval stage and become a highly fecund adult with high probability of offspring mortality from host senescence. Surprisingly, *E. editha bayensis* larvae take the second option (chapter 3), thereby driving the subspecies to the limits of its ecological tolerance and generating the highly stochastic population dynamics that are its trademark. These two examples illustrate how larvae are not mere passive feeding machines crawling around, eating their food, and waiting for events to happen to them. They assimilate and use information to make complex decisions that influence not only the events that happen to them but those that descend upon their offspring. However, the availability of information on which to base these decisions is often poor.