



Immature Insects: Ecological Roles of Mobility

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Abstract: Immature insects' adaptations for finding the highest quality food and optimal environmental conditions are critical to maximizing a species' success. Optimal food and environmental conditions during immature development increase the insects' survival and shorten their development time; these conditions also result in earlier reproduction and more rapid growth of the insect population. Immature-stage mobility is important in finding suitable food and environment, building shelters, thermoregulating behavior, and evading, escaping, or defending against natural enemies. The immature stages can move distances ranging from a few centimeters to a few hundred meters; whereas adults that can fly can move distances of a few, hundreds, or even thousands of kilometers. Mobility gives immature insects greater access to available food. Neonate larvae often must move large distances to find their first meal or they perish. Air currents, stream flow, or phoresy can carry them farther than walking. Feeding habits of subsequent instars may change as they grow, and larvae may commute between feeding and resting (shelter) sites. An immature insect may feed at many locations during its development, and mature larvae wander in search of a pupation site. Larvae of >361 insect species in 59 families and 5 orders leave their feeding sites to find a pupation site. Among species with nonfeeding, short-lived adults, the immature stages may accumulate food reserves needed for egg production in the adult stage. Larvae select a safe site before entering larval or pupal diapause for overwintering or summer aestivation, and some larvae may remain mobile during diapause. Active pupae or nymphs may increase the chance of successful adult eclosion. In this article, we review the many important ecological roles of immature mobility.

The subject of immature-stage mobility is covered briefly in many reviews that deal with overall life history of a species, family, or order. A few reviews cover immature-stage mobility, but only for a single family or order (Davies 1976, Gaston et al. 1991, Stamp and Casey 1993, Costa and Pierce 1997, Zalucki et al. 2002, Bell et al. 2005, Gomes et al. 2006, Scharf and Ovidia 2006).

The immature stages can move distances ranging from a few centimeters to a few hundred meters; whereas adults that can fly can move distances of a few, hundreds, or even thousands of kilometers (Williams 1957, Schneider 1962; Johnson 1966, 1969; Stinner et al. 1983; Gatehouse 1997; Showers 1997). Neonate larvae can travel farther by way of air currents, stream flow, or phoresy than by walking. An immature insect may feed at many locations during its development, and mature larvae may wander in search of a pupation site. Among species with nonfeeding, short-lived adults, the mobility of the immature stages is important for accumulating food reserves needed for egg production in the adult stage (Chew and Robbins 1984, Wheeler 1996). Before entering larval or pupal diapause, larvae select a safe site for overwintering or summer aestivation, and some larvae may remain mobile during diapause. Pupae or nymphs that are mobile (active) increase the chance of successful adult eclosion.

In this article, we review the ecological roles of immature-stage mobility among several insect taxa. These include finding suitable food and environment, building shelters, thermoregulating behavior,

and evading, escaping, or defending against natural enemies.

Wind-Borne Dispersal

In at least 37 species in 9 families of Lepidoptera, the first or second instars drop from the host plant on a silk thread and are carried for a distance of up to a few hundred meters by wind (Table 1). In 17 out of the 37 species, the females are flightless, and this ballooning by young larvae is the primary means of dispersal. For two other species, *Euproctis chrysorrhoea* L., and *Dasychira plagiata* (Walker), the dispersal of immature stages is important because in the adult stage, the insects are heavy-bodied weak fliers. Positive phototaxis and negative geotaxis are important in positioning immature insects on their host plants so that they can catch the wind. Older larvae are too heavy to be transported by wind on a silk thread. In bagworm, *Thyridopteryx ephemeraeformis* (Haworth), ballooning may be more important in facilitating movement within a host plant than among hosts. In spruce budworm, *Choristoneura fumiferana* (Clemens), 97% of the larvae have silk threads no longer than 1.7 m, although some threads are as long as 17 m. The buoyant effect increases exponentially with length of silk. First instars of *C. fumiferana* disperse mainly within the crown of the host tree, whereas second instars disperse more readily between crowns (Regniere and Fletcher 1983). Raske and Bryant (1977) reported that 1% of *Coleophora fuscedinella* Zeller (not included in Table 1) ballooned. Immature stages of other species

Table 1. Lepidoptera Larva Reported to Balloon^a

Family	Species	Flightless
Cossidae	<i>Zeuzera coffeae</i> Nietner	N
	<i>Zeuzera pyrina</i> (L.)	N
	<i>Xyleutes ceramicus</i> (Walker)	N
Gelechiidae	<i>Pectinophora gossypiella</i> (Saunders)	N
Geometridae	<i>Alsophila pometaria</i> (Harris)	Y
	<i>Ectropis excursaria</i> (Guenée)	N
	<i>Erranis tiliaria</i> (Harris)	Y
	<i>Operophtera bruceata</i> (Hulst)	Y
	<i>Operophtera brumata</i> (L.)	Y
	<i>Paleacrita vernata</i> (Peck)	Y
Lymantridae	<i>Phigalia titea</i> Cramer	Y
	<i>Dasychira plagiata</i> (Walker)	N
	<i>Euproctis chrysorrhoea</i> L.	N
	<i>Lymantria dispar</i> (L.)	Y
	<i>Lymantria mathura</i> Moore	N
	<i>Orgyia antiqua</i> (L.)	Y
	<i>Orgyia definita</i> (Packard)	Y
	<i>Orgyia leucostiga</i> (Smith)	Y
	<i>Orgyia pseudotsugata</i> (McDunnough)	Y
	<i>Orgyia vetusta</i> Boisduval	Y
<i>Teia anartooides</i> Walker	Y	
Noctuidae		
	<i>Mythimna convecta</i> (Walker)	N
Ochsenheimeiriidae	<i>Ochsenheimeria vacuella</i> Fischer von Roslerstamm	N
Pyralidae	<i>Chilo partellus</i> (Swinhoe)	N
	<i>Chilo suppressalis</i> (Walker)	N
	<i>Ostrinia furnacalis</i> (Guenée)	N
	<i>Ostrinia nubilalis</i> (Hübner)	N
	<i>Scirpophaga incertulas</i> (Walker)	N
Psychidae	<i>Luffia ferchaultella</i> (Stephens)	Y
	<i>Metisa plana</i> (Walker)	Y
	<i>Oiketicus kirbyi</i> (Guilding)	Y
	<i>Thyridopteryx ephemeraeformis</i> (Haworth)	Y
Tortricidae	<i>Adoxophyes orana</i> (Fischer von Roslerstamm)	N
	<i>Choristoneura fumiferana</i> (Clemens)	N
	<i>Choristoneura parallela</i> (Robinson)	N
	<i>Choristoneura roseaana</i> (Harris)	N
	<i>Tortrix viridana</i> L.	N

^aFrom Bell et al. (2005) and Barbosa et al. (1989).

of Lepidoptera drop on a silk thread when disturbed, and ballooning may be of some importance for many other species.

The broad, flat body and long caudal setae of the crawler allow scale insects to be dispersed by the wind (Beardsley and Gonzalez 1975; Greathead 1989, 1997; Gullan and Kosztarab 1997). Positive phototaxis and negative geotaxis also are important in positioning immature Homoptera on their host plants so that they can catch the wind. Among armored scales, *Aonidiella aurantii* (Maskell) living on citrus trees are less likely to be dispersed by wind, whereas *Aulacaspis tegalensis* (Zehntner) living on sugarcane, a more temporary habitat, move to the tips of cane leaves where they are readily dislodged by the wind. Crawler density of *A. tegalensis* in the air increases as wind speed increases to 2.0 m/s, and crawlers may be caught in traps up to 1 km away. For first instars of the soft scale *Pulvinariella mesembryanthemi* (Vallot), calculated maximum dispersal distance was 190 km in 24 h at a wind speed of 8 km/h (Greathead 1997). Other soft scales have been found up to 4.8 km downwind [*Toumeyella numismaticus* (Pettit and McDaniel)] and 55 m from the source (*Coccus hesperidum*

L.) (Greathead 1997). Mealy bugs and scales in families Dactylopiidae, Eriococcidae, and Margarodidae also are dispersed by wind.

Stream Drift Dispersal

The taxa that exhibit stream drift, in the order of prevalence, include Ephemeroptera, the family Simuliidae in order Diptera, Trichoptera, Plecoptera, and the family Chironomidae in order Diptera (Waters 1972). Studies on stream drift have been summarized for Chironomidae (Davies 1976), Ephemeroptera (Elliott et al. 1988), Odonata (Corbet 1999), Plecoptera (Ernst and Stewart 1985, Stewart et al. 1988), Simuliidae (Crosskey 1990), and Trichoptera (Otto 1976). According to Waters (1972), the percentage of bottom fauna that drift range from 0.1 to 4%. For Plecoptera, daily downstream drift ranges from 5 to 50 m. For Ephemeroptera, maximum distance may be 100 m. Drift of simuliid larvae generally does not exceed a few hundred meters (Crosskey 1990). In contrast to the occurrence of caterpillar ballooning and scale transport by wind as first instars, stream drift can occur among all instars. For the Trichoptera *Rhyacophila nubila* Zetterstedt, the extent of drifting by instars was 2 > 3 > 4 > 1 > 5 (Fjellheim 1980). Instars 1 and 2 had a neutral phototaxis, but from second instar onward, larvae become increasingly nocturnal. Chaston (1972) reported a diel pattern for many species that have increased numbers drifting at night. Chironomids may drift when oxygen levels are low and settle again when oxygen levels are more favorable (Oliver 1971). For Plecoptera *Acroneuria abnormis* (Neuman), Walton et al. (1977) found that drift decreased with increasing substrate particle size, and water current velocity affected the drift only from gravel, the smallest particle size tested. Upstream movement is small (2–30% of downstream drift); for some species, it is greater near the banks than mid-stream (Bird and Hynes 1981).

Phoretic Dispersal

Phoresy allows immature insects that hatch from eggs at one location to be carried to many feeding sites. Some species of Meloidae and Rhipiphoridae lay their eggs on flowers; hatching larvae board hymenoptera adults visiting flowers and are transported to their nests, where they develop on host larvae (Clausen 1976). Hatching Eucharitidae larvae wait for adult ants on which they are carried back to the nest where they feed on ant larvae. Mantispidae lay eggs in spider habitats, and young larvae rear up on caudal suckers and sway back and forth with outstretched legs awaiting a passing spider (Redborg 1998). When the spider deposits its eggs, the mantispid larvae enter the egg sac before it is completed and feed on the spider eggs. Newly emerged female first instars of the gall-forming eriococcid, *Cystococcus echiniformis* Fuller, are phoretic on the winged males of the species (Gullan and Kosztarab 1997). A few species of blackflies (1.8%) are phoretic on mayfly nymphs or crab prawns, and change positions several times as they grow and complete larval and pupal stages on the carrier (Crosskey 1990). Hilsenhoff (1968) reported Chironomids to be phoretic on the larvae of Megaloptera and nymphs of Plecoptera.

Crawling and Tunneling

Females lay eggs on or near food, but newly hatched larvae often must still travel some distance to locate the food and begin feeding. When a host or plant part is unsuitable, exploration within and between plants is likely to continue (Zalucki et al. 2002). Variation in plant structure, leaf hairs and trichomes, leaf waxes, and leaf toughness contribute to suitability. Reavey (1992) found that the speed

of the neonate larvae of 42 Lepidoptera species varies from 0.7 to 267.8 cm/h. Grass feeders move faster than woody plant feeders downward, and herb feeders move upward and downward. For 12 of these species that were compared, the incidence of silking down was negatively correlated with larval weight.

Codling moth, *Cydia pomonella* L., females lay eggs on leaves, and the newly hatched larvae must search for an apple (Jackson 1982). Larvae move rapidly for a short time before slowing down. Larvae that do not find an apple after about 15 min crawl into a protected place and become motionless. Many of these larvae will find an apple later. Average velocities are 0.8 cm/min in the dark and 1.8 cm/min in the light. Larvae cannot move at 5 °C or above 45 °C; movement increases with temperature up to 30 °C and averages 4.7 cm/min at 30 °C.

In Eigenbrode and Shelton's study (1990), neonate *Plutella xylostella* (L.) moved 0.56 cm/min on suitable cabbage plants and 1.56 cm/min on less suitable cabbage plants. Early instar movement and spin down for *Heliocoverpa* (= *Heliothis*) *zea* (Boddie) are higher on mature soybean trifoliates than on terminals or expanding trifoliates (Terry et al. 1989). On whorl-stage corn, first-stage *Diatraea grandiosella* Dyar larvae moved from the site of egg hatch to immature leaves of inner whorl and fed for about 10 d (Davis et al. 1972). On tassel-stage corn, newly hatched larvae move to feed between the husk layers of the primary ears and ear shoots for 7–9 d and then feed on kernels and cob until they are 15–20 d old. After hatching, first-stage *Mythimna unipuncta* (Haworth) larvae aggregate in a tight mass concealed from view for 12–30 h on stubble before they move to oats or wheat to feed (Guppy 1961). Larvae feed during the early morning and move down to spend the rest of the day sheltered near the base of the plant. Almond moth, *Cadra cautella* (Walker), females lay eggs loosely on or near a commodity, and first instars must sometimes search for suitable food (Hagstrum and Subramanyam 2006). For example on peanuts, neonate larvae must find peanuts with cracked shells and enter through the cracks to feed on the peanut kernels.

Females of many soil-inhabiting Coleoptera, Diptera, and Lepidoptera whose larvae feed on plant roots (Table 2) lay eggs close to the host plant, but the neonate larvae must travel some distance by orienting to carbon dioxide, host volatiles, or both, to locate roots on which to feed (Johnson and Gregory 2006). Because corn rootworm eggs do not hatch until the next year, the new crop may be sown offset from that of the previous year (Villani and Wright 1990). Neonate larvae of *Diaprepes abbreviatus* (L.) drop from the citrus tree where eggs are laid to the soil and feed on the roots (Nigg et al. 2003). Lepidopteran larvae on plants (above ground) also may orient to host plant odors (Table 2). Odor cues may be more important for root-feeding insects than those that feed on plants above ground because visual cues cannot be used underground.

The unfed first instars of crawler scale insects that disperse by walking on the host plant rarely move between plants (Beardsley and Gonzalez 1975; Greathead 1989, 1997; Gullan and Kosztarab 1997). In the armored scale *Aonidiella aurantii*, wandering ranges from 174 to 206 min, and settling is influenced by the leaf or fruit color, crawler density, temperature, and dustiness of the leaves. Female *Phenacaspis pinifoliae* (Fitch) crawlers on Scots pine in Saskatchewan wandered four times farther than males. The walking speed of the soft scale *Pulvinariella mesembryanthemi*, crawlers is ~1 mm sec⁻¹; and they move upward on the plants to reach preferred younger leaves for feeding. Eggs of cuterebrid are laid in habitats frequented by their mammalian host and hatch rapidly in response to heat from the

Table 2. Species with Larvae using Chemical Cues to Locate Food^a

Order	Family	Species	Stimuli ^b
Root—			
Feeding			
Coleoptera	Elateridae	<i>Agriotes</i> spp.	CO ₂ , PV
	Scarabaeidae	<i>Costelytra zealandica</i> (White)	CO ₂ , UC
	Elateridae	<i>Ctenicera destructor</i> (Brown)	CO ₂
	Chrysomelidae	<i>Diabrotica undecimpunctata howardi</i> Barber	CO ₂
		<i>Diabrotica virgifera virgifera</i> LeConte	CO ₂ , UC
	Tenebrionidae	<i>Eleodes suturalis</i> (Say)	UC
	Carabidae	<i>Evarthrus sodalis</i> LeConte	CO ₂
	Curculionidae	<i>Hylastinus obscurus</i> (Marsham)	PV
		<i>Hylobius abietis</i> (L.)	PV
	Elateridae	<i>Hypolithus bicolor</i> Eschscholtz	CO ₂
		<i>Limonium californicus</i> (Mannerheim)	CO ₂
	Elateridae	<i>Limonium canus</i> LeConte	UC
	Scarabaeidae	<i>Melolontha melolontha</i> (L.)	CO ₂
	Curculionidae	<i>Otiorhynchus sulcatus</i> (F.)	CO ₂
		<i>Sitona lepidus</i> Gyllenhal	UC
<i>Sitona hispidulus</i> Fabricius		UC	
Diptera	Anthomyiidae	<i>Delia antiqua</i> (Meigen)	PV
		<i>Delia coarctata</i> (Fallen)	UC
		<i>Delia floralis</i> (Fallen)	PV
		<i>Delia radicum</i> (L.)	CO ₂ , PV
	Psilidae	<i>Psila rosae</i> F.	CO ₂ , PV
Lepidoptera	Pyalidae	<i>Elasmopalpus lignosellus</i> (Zeller)	CO ₂
Aboveground			
Lepidoptera	Bombycidae	<i>Bombyx mori</i> L.	PV
	Tortricidae	<i>Choristoneura fumiferana</i> (Clemens)	PV
		<i>Cydia pomonella</i> L.	PV
		<i>Papilio demoleus</i> L.	PV
	Papilionidae		

^aFrom Johnson and Gregory (2006) and Huang et al. (1990).

^bCO₂ = carbon dioxide, PV = plant volatile, UC = unidentified chemical.

host (Catts 1982). Wet newly hatched larvae stand erect on caudal pads and adhere to the host with sticky fluid from the egg. Neonate larvae of *Neodiprion swainei* Middleton move from current growth of the jack pine where the eggs are laid to the old foliage and feed in colonies of 40–70 individuals (Smirnof 1960).

Dispersal of Older Larvae or Nymphs

Mobility gives an immature insect greater access to available food. For example, instead of being restricted to a single leaf, caterpillars can eat many leaves. Dispersing their damage may make them less vulnerable to natural enemies. Costa and Pierce (1997) classified the types of foraging by species of gregarious lepidopteran larvae as patch restricted (119 species), nomadic (102 species), and central place (25 species). Patch-restricted foragers often build shelters and feed in the same place throughout their life; nomadic foragers generally do not build shelters and move around to feed at many locations; and central-place foragers build shelters but feed away from the shelters at many locations. Most gregarious caterpillars are found in 7 families, but 28 families have at least one species. Nomadic *Hemileuca oliviae* Cockerell are stationary as first instars, but travel an average of 1–3 m as second and third instars, 9 m as fourth instars, and 20 m as fifth instars (Hansen et al. 1984). The maximum larval movement occurs just before pupation.

Many British microlepidopteran larvae (17.6%, *n* = 200) change feeding habits as they develop from leaf mining to concealed external

feeders, where some of them can bear cases, spin webs, and tie or roll leaves (Gaston et al. 1991). These changes in feeding habits allow them to grow and become less susceptible to natural enemies. It may be necessary to leave leaf mines before leaves are shed in the fall in order to continue feeding on a plant in the spring. Larvae of the yellow horned moth, *Achlya flavicornis galbanus* Tutt, build larger ties on birch as they grow (Feichtinger and Reavey 1989). The distance between old and new ties ensures that feeding areas do not overlap. Larvae generally do not feed far from their ties, but they can find their ties again after feeding on leaves as many as 40 nodes away. Neonate *Plutella xylostella* larvae are leaf miners, whereas older larvae feed on the lower surface of a leaf (Talekar and Shelton 1993). Fourth instars of *Plutella xylostella* build a loosely woven cocoon where they have fed and pupate within. First to third instars of *Pieris brassicae* (L.) feed in tight aggregates on the underside of a leaf, but older larvae wander freely and singly over the plant (Willmer 1980). Some Plecoptera nymphs progress from herbivory-detritivores through omnivory to carnivory as they develop (Stewart et al. 1988).

Larvae of *Plutella xylostella* and *Autographa californica* (Speyer) drop from the plant when disturbed (Jones 1977). Larvae of *P. xylostella* move slowly, head wave frequently and turn often. This behavior is not altered by starvation and mature larvae can average 1.4 cm/10 sec. Fed or starved larvae of *A. californica* travel rapidly (~1 cm/10 sec for first instars to ~4 cm/10 sec for fifth instars), turn infrequently and head wave moderately. Well-fed larvae of *Pieris rapae* (L.) move slowly, head wave frequently, and turn often, but hunger causes faster, straighter movement without head waving. As starvation increases, larvae that are ready to pupate increase their speed more rapidly (1.5–3.15 cm/10 sec), stop head waving sooner, and straighten their path more quickly than those that are not ready to pupate.

On whorl-stage corn after 10 d of feeding, *Diatraea grandiosella* larvae leave immature whorl leaves and move down to bore into the stalk and tunnel (Davis et al. 1972). On tassel-stage corn, larvae after 15–20 d of feeding in the ear zone move to the stalk.

Early in the season before cotton bolls are available, female pink bollworm, *Pectinophora gossypiella* (Saunders), lay eggs on foliage, and the movement of first instars is impeded by leaf pubescence (Smith et al. 1975). Larvae feed when they encounter nectaries. Later in the season, eggs are laid on the bolls; the larvae attack one another because only one larva infests each boll and others must wander around the cotton plant seeking an uninfested boll (Brazzel and Martin 1955). On tomatoes, *Heliocoverpa zea* larvae travel 10/cm day; the distance is reduced after larvae begin feeding on the fruit, and the larvae move back to foliage before pupation (Snodderly and Lambdin 1982). *Mythimna unipuncta* second- to fifth-instars feed at night and rest under dead or yellowed leaves on the lower part of plants when not feeding (Guppy 1961). The sixth instars generally move to ground for shelter. Larvae of the stalk borer, *Papaipema nebris* Guenée, feed on grass before becoming fifth instars, but they then move to corn and tunnel into the stem to feed (Lasack and Pedigo 1986). Late instars of *Coleomegilla fuscedinella* move to the top of white birch trees to feed on growing shoots and new leaves (Raske and Bryant 1977).

Once newly hatched gypsy moth, *Lymantria dispar* (L.), larvae find suitable foliage, they remain on it until they have molted into third instars (Campbell et al. 1975). Larvae begin wandering before reaching fourth instars; they locate daytime resting sites in the litter at the base of tree or at sheltered locations on the tree. Larvae

return to the foliage each night to feed. The movement of late instars to resting sites in the litter during the day often results in the larvae moving from one tree to another (Elkinton and Liebhold 1990). The first two instars of *Rhyacionia buoliana* (Schiff.) feed on needles from within webs (Pointing 1963). Third instars mine one or more buds and overwinter there. Larvae spin webs and molt before resuming feeding and migrating up in the tree crown. Web construction continues throughout feeding.

Upon hatching, first instars of *Neodiprion fulviceps* (Cresson) move immediately toward the apex of needles (Dahlsten 1966). Larvae move to adjacent fascicles, feed in groups of 30 or more per needle, and move back along a branch as foliage is destroyed. As the larvae mature, feeding groups become smaller until they are feeding singly or in pairs. According to Teras (1982), 40% of the fourth or fifth instars of *Neodiprion sertifer* (Geoffroy) knocked off of a pine tree climbed back up the tree within 1 h, and 70% within 2 h. Larvae of *Neodiprion lecontei* (Fitch) completely defoliate trees and migrate long distances to new foliage (Coppel and Benjamin 1965). When all of the jack pine foliage is destroyed, *Neodiprion swainei* larvae crawl down the tree trunk or drop to the ground (Smirnoff 1960). These larvae can infest trees that are 183 m or more from their original feeding site. Colonies on these trees are 2–3 times larger and consist of 120–170 individuals.

Walker and Merritt (1991) determined that fourth instars of the mosquito *Aedes triseriatus* (Say) spend 52.5% of their time feeding near the surface and 37.5% brushing while submerged. For larvae of *Culiseta longiareolata* (Macquart), surface hanging is the predominant activity, and it peaks before each ecdysis (Van Pletzen 1981). Browsing and gnawing is the most important feeding method, and it is the dominant activity of first instars during their first 8 h. They often remain submerged for periods up to 30 min. Similar behavior among young larvae has been reported for *Aedes vexans* (Meigen) (Van Pletzen 1981). The second most important activity by *C. longiareolata* is to use the mouth brushes to feed in eddies while moving slowly forward attached to the surface; the third is surface filter feeding. Larvae break away from the surface with two powerful lashes of the abdomen and sink passively to the bottom for browsing and gnawing. Ascent requires powerful swimming strokes of the abdomen. Surface hanging is the dominant activity of pupae although they can swim.

Onion maggot, *Delia antiqua* (Meigen), larvae feeding on onion seedlings consume more than one plant, and older larvae must locate new hosts (Villani and Wright 1990). Insects Wireworms and scarab grubs that overwinter as larvae must find host plants when they return to the soil surface in the spring. Source did not specify species of wireworms or scarab grubs. Larvae of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), leave over populated potato plants and travel up to ~76 m to locate a new host plant (Cass 1957). The distance traveled increases with instar, and fourth instars crawl ~48 cm/min on smooth and ~23 cm/min on rough, loose sandy loam soil.

European earwig, *Forficula auricularia* L., adults overwinter in a subterranean nest, lay eggs there before spring, and care for the eggs and young nymphs in their nest (Lamb 1975). Second instars leave the nest to forage for food at night and spend days in shelters. Neither nymphs nor adults of *Camnula pellucida* (Scudder) and *Melanoplus mexicanus mexicanus* (Saussure) can orient their movement toward a food supply (Riegert et al. 1954). Second instars of *C. pellucida* move ~1–4 m/h, and older nymphs move 6–11 m/h. Young nymphs and

adults move with the wind, and older nymphs move against wind. When winds are >16 km/h, grasshoppers remain in shelter. In 7 d, 10% of fifth instars can be ~91 to >274 m from release point, but 60% average <46 m from the release point.

Mobility of Immature Predators or Parasitoids

The coccinellid larvae, *Adalia bipunctata* (L.), *Adalia decempunctata* (L.), *Coccinella septempunctata* (L.), *Hippodamia quinquesignata* (Kirby), *Pharoscygnus numidicus* Pic., *Propylea quatuordecimpunctata* L., *Stethorus picipes* Casey, and *Stethorus punctillum* Weise recognize prey only after contact (Hodek 1967). Newly hatched first instars among the coccinellids *A. bipunctata*, *C. septempunctata*, and *P. quatuordecimpunctata*, are continuously active on bean plants searching for aphids (Banks 1957). Larvae crawl over bean leaves, frequently changing direction and following the leaf edge or vein when encountered. Larvae eventually move to top of the bean plant and then descend; they spend 76–85% of their time checking leaves. On tobacco, trichomes reduce the searching speed of the first instars of lacewing (*Chrysopa carnea* Stephens), coccinellids, [*Coleomegilla maculata* (DeGeer)] (Eley 1974), and *Hippodamia convergens* Guerin-Meneville (Belcher and Thurston 1982). When aphid colonies have been devoured, migrated, or been destroyed by pest management, syrphid larvae search for new aphid colonies (Schneider 1969). Hungry *Lasiopticus pyrastris* (L.) larvae use positive phototaxis or negative geotaxis to find prey.

Lacking the paralytic poisons of Hymenoptera, adult tachinids avoid contact with their hosts by depositing eggs in the hosts' habitat and depending on first instars to find hosts (Stireman et al. 2006). Tachinid larvae may ambush nocturnally feeding caterpillars on their host plant or burrow through soil or into galleries of concealed insects. Microtype eggs laid on host plants by Tachinidae may be ingested by hosts. Trichoptera species in the families Rhyacophilidae and Hydrobiosidae are predators that forage among rocks in streams for prey, and they do not build retreats except to pupate.

Mobility to Achieve Thermoregulation and Water Balance

By finding suitable environments and thermoregulating behavior, larvae minimize mortality, accelerate development, and reduce time required to reach the adult stage and reproduce. Second instars and older cabbage loopers, *Trichoplusia ni* (Hübner), move to shaded, cooler lower parts of cabbage plants when temperature is high and relative humidity is low, and they move up to economically important wrapper leaves and cabbage heads when temperatures are low and relative humidity is high (Hoy et al. 1989). *Colias eurytheme* (Boisduval) larvae remain inactive near ground at night and climb the plant in the morning to reach parts of the plant in their preferred temperature range, 15–30 °C (Sherman and Watt 1973). If the temperature becomes too high (≥ 30 °C), they move down toward the ground. At temperatures of 30–35 °C, all instars of *Malacosoma disstria* Hübner, and the first three instars of eastern tent caterpillars, *Malacosoma americanum* (F.) and western tent caterpillars, *Malacosoma californicum pluviale* (Dyar), become photonegative and move to cooler shaded areas (May 1979). *Hyphantria textor* (Harris) behaves similarly. The proportion of *Leptinotarsa decemlineata* larvae in the shade on the underside of leaves increases with air temperature >17 °C (Lactin and Holliday 1994). The nymphs of the migratory grasshopper, *Melanoplus sanguinipes* (F.), in a temperature gradient select the optimal temperature for feeding and development (Lactin and Johnson 1996). The *Aedes communis* (DeGeer) mosquito larvae

move around in subarctic pools to select preferred temperatures. Larvae of the antlion, *Myrmeleon immaculatus* DeGeer, move around in pits to select the coolest region (May 1979).

Below the upper threshold temperature (28 °C for first instars, 36 °C for second and third instars, and 38 °C for fourth to sixth instars), *Choristoneura fumiferana* larvae select microhabitat based on humidity rather than temperature (Wellington 1949). Within leaf rolls, silk cases and larval aggregations create humidity levels that are so high that water loss is minimal (Willmer 1980). *Pleuroptya ruralis* Scopoli in leaf rolls, *Inachis io* L. in aggregates, and first to third instars of *P. brassicae* in aggregates do not need to compensate for water loss, but older *P. brassicae* larvae wandering over whole plant surface do. Grubs of the Japanese beetle, *Popillia japonica* Newman, move as deep as 29 cm to stay below the frost line (Hartzell and McKenna 1939). Larval sawflies, *Perga dorsalis* Leach, increase convective cooling by raising their abdomens and evaporative cooling by spreading fluid over their bodies (May 1979).

Malacosoma americanum, among the earliest of spring caterpillars, must compensate for temperatures barely above their developmental threshold (Joos et al. 1988). When not feeding, they bask in aggregates in or on tents (Knapp and Casey 1986), where temperature is always at least 4 °C above air temperature (Joos et al. 1988). The basking behavior of *Euphydryas aurinia* (Rottemburg) larvae can raise body temperatures up to their optimum, 35 °C (Porter 1982). By ascending the stems of blue gamma grass and assuming a head-down resting position, larvae of *H. oliviae* can significantly lower body temperature (Capinera et al. 1980). Larvae track the sun, maintaining the stem between them and the incident sunlight.

Casey (1976) reported that the behaviors of two desert caterpillars, the whitelined sphinx, *Hyles lineata* (F.) and the tobacco hornworm, *Manduca sexta* (L.), regulate their body temperature. Larvae of *H. lineata* descend to ground shortly after sunrise and ascend again at midday. Early in the morning, they orient perpendicular to the sun, and orientation later in the day depends upon temperature. When air temperature was 28 °C, roughly half of larvae oriented parallel to the ground, but when air temperature was 36 °C, most oriented perpendicular to the rays of the sun. Larvae of *M. sexta* remain day and night on the underside of jimsonweed leaves. During the morning, larvae were on the periphery of plants, and some oriented perpendicular to the rays of the sun. Mid-morning, many moved from outer parts of the plant to the interior where they were shaded from the sun.

Danaus plexippus (L.) caterpillars spend ~64% of the daylight period basking in the sun; ~44% are inactive while ~53% are feeding (Rawlins and Lederhouse 1981). Almost 90% of the inactive period is in direct sun with broadside orientation to the sun. Larval behavior raises body temperatures by 3–8 °C. Kukul et al.'s study (1988) of larvae of the high arctic caterpillar, *Gynaephora groenlandica* (Wocke), found that they spent 59.4% of time basking, 14.9% moving, and 20.0% feeding. Body temperatures were 30.5 °C while basking, 26.7 °C while moving, and 23.9 °C while feeding.

Evasion of Natural Enemies

Many species of lepidopteran larvae evade natural enemies by remaining on the underside of leaves, foraging at night, commuting to feeding sites, moving away from unfinished leaves, or snipping off unfinished leaves (Heinrich 1979). Heinrich and Collins (1983) list 13 species of Sphingidae, 3 species of Saturniidae, 8 species of Notodontidae, and 5 species of Noctuidae that hide feeding damage

by eating the whole leaf, trimming leaves, or chewing off partially eaten leaves. They also list 13 species of Lepidoptera from 7 families that are unpalatable, have spines or warning coloration, and do not hide their feeding damage.

Larvae of *Pieris rapae* have significantly different foraging behavior on broccoli than on radish (Mauricio and Bowers 1990). The distance traveled by late instars on broccoli during one day is ~23–83 cm. Larvae of this species spent ~9% of the time feeding, ~10% moving, and ~90% being stationary; larvae were exposed to sun during ~75% of the observations. *Euphydryas phaeton* (Drury) larvae in one day traveled ~25 to 50 cm (Mauricio and Bowers 1990). Larvae of this species spent ~14% of the time feeding, ~18% moving, and ~82% being stationary; larvae were exposed to the sun during ~92% of the observations. A larva of *E. phaeton* would rarely eat >50% of a single leaf. The average total number of leaves fed upon by a larva during observations was 55; ~84% of the leaves showed <25% of the leaf area consumed by a larva.

In a study by Sih (1986), the larvae of the mosquito *Culex pipiens* L. responded to the predator *Notonecta undulata* Say by moving less and moving to edge of container. Larvae of *C. pipiens* also responded to a chemical or chemicals produced by *N. undulata* predation.

Shelter-building

Immature insects build shelters to protect against unfavorable environmental conditions and natural enemies. Most Trichoptera spin silk to build portable tubular cases (Integripalpia), domes (Spicipalpia), or retreats (Integripalpia) (Wiggins 2004). As tube-building caddisflies grow, material is added to the front to enlarge the case and trimmed from rear with mandibles to keep length manageable. Retreat-making caddisfly larvae build silk nets to remove food from flowing water. Except for the predaceous species, all chironomids larvae build silk cases on or within the substrate (Oliver 1971). Among the Lepidoptera, species of Psychidae and Tineidae also build portable case shelters.

Larvae of many gregarious species of Lepidoptera build tents, or roll, cut, fold and tie portions of their food plant to build shelters (Costa and Pierce 1997). Silk shelter building has been reported for 15 species of central-place foragers and 44 species of patch-restricted foragers. Leaf and silk shelters have been reported for 4 species of central-place foragers and 28 species of patch-restricted foragers. Young larvae of only one nomadic forager were reported to build a leaf and silk shelter.

Many Lepidoptera can be recognized as belonging to the families Thyrididae, Gelechiidae, Pyralidae, Tortricidae, Lasiocampidae, Oecophoridae, Nymphalidae, Hesperidae by their shelters alone (Greeney and Jones 2003). Greeney (2009) revised the classification and keys for Hesperidae shelters.

Antlions build inverted funnel pits for shelter and to catch prey (Tuculescu et al. 1975). Digging activity always proceeds by backward movement just below the soil (doodling) with periodic flicking of particles with the head that may last from a few minutes to several hours. Pit construction begins with circular movement that creates a circular groove. The final diameter of the pit is larger than the initial circle. The larva moves backward around the initial circle, flicking soil particles up to 20 cm; as the groove deepens, the bottom steadily shifts toward the center of the circle. The larva frequently stops circling movement and criss-crosses several times through the central cone to remove portions of it. Larvae enlarge the pit at intervals and will do some reconstruction of the pit after it has been

disturbed by prey capture (Griffiths 1986). Starved, disturbed larvae are more likely to abandon the pit and move to a new location than are well-fed larvae. Larvae can move up to 2 m every 5–70 d to build a new pit (Farji-Brener 2003). Starved larvae travel farther than fed larvae (Scharf and Ovadia 2006). Pit location is influenced by shade, soil temperature, soil particle size, rain, and soil moisture.

Tiger beetle larvae initially enlarge the cavity in which the egg was laid and prey on passing insects from this burrow (Pearson 1988). The burrow is enlarged following each molt. However, occasionally when disturbed by a natural enemy or flooding, they leave the burrow, use their legs to scuttle across the ground and relocate their burrow.

Escaping Natural Enemies. All instars of green cloverworm, *Hypona* (= *Plathypena*) *scabra* (F.), flip violently from the leaf on which they are feeding when they contact another insect—even another green cloverworm (Yeargan and Braman 1986). Some of the older larvae may respond by snapping the front part of their body at a predator or crawling away from the predator along the leaf margin. Some older instars that do not exhibit dropping behavior are captured by the predator, but those that drop immediately always escape. The first three instars drop on a silk thread and later ascend to resume feeding. Other instars do not drop on silk thread and fall to lower part of the plant or to the ground. The braconid parasitoid *Diolcogaster facetosa* (Weed) recognizes the silk thread even when it does not see the host larvae on foliage, and it slides down the thread to parasitize the larva. This recognition of the thread is important because young green cloverworm larvae often rest between bouts of feeding by hanging from threads beneath leaves. The silk thread of first instars is too fragile to hold both host and parasitoid, and parasitoids are often unsuccessful. All six instars of the geometrid, *Ectropis excursaria* (Guenée) drop from the leaf when disturbed and may hang suspended by a silken thread (Mariath 1984).

Young larvae of *Diprion frutetorum* (F.), *Diprion similis* (Herting), and *Neodiprion sertifer* immediately retreat to the needle base when disturbed (Coppel and Benjamin 1965). Older larvae show defense displays or drop from needles. A droplet of oral exudate that is capable of rapidly incapacitating a parasitoid accompanies displays. When disturbed, females of the scale *Leptococcus eugeniae* (Miller and Denno) fall from the host plant and float like snowflakes (Gullan and Kosztarab 1997).

The fourth instars of the mosquito *Aedes triseriatus* respond to stimulus by diving and generally remain motionless, often under a leaf (Walker and Merritt 1991). *Aedes aegypti* (L.) respond to shadows or vibration by swimming to the bottom and recover by floating upward (Mellanby 1958). *Anopheles maculipennis* Meigen and *Culex molestus* Forskal sink passively when alarmed and swim actively to surface upon recovery. Repeated stimulation produces satiation, but a different kind of stimulus produces a complete response. Phototaxis can override geotaxis. Chill coma occurs at temperatures several degrees cooler than alarm reaction.

Fighting Natural Enemies

Aggressive behaviors against adult parasitoids include biting, head or tail flicking, and head rearing (Gross 1993). Lepidoptera larvae commonly bite off appendages of parasitoids; head jerking or flicking are common defensive behaviors of caterpillars and sawflies. As larvae grow, the response to natural enemies shifts from escape to fighting. Defensive behavior of caterpillars toward the predator *Podisus maculiventris* (Say) reduces the predator's ability to subdue

Table 3. Species of Larvae Reported to Leave Feeding Sites to Find Pupation Sites

Order	Family	Species	Source
Coleoptera			
	Bruchidae	<i>Caryedon albonotatum</i> (Pic)	Southgate 1979
		<i>Caryedon cassia</i> (Gyllendal)	Southgate 1979
	Carabidae	<i>Calosoma sycophanta</i> (L.)	Baker 1972
	Chrysomelidae	<i>Calligrapha sclari</i> (LeConte)	Baker 1972
		<i>Chrysomela scripta</i> F.	Baker 1972
		<i>Colaspis pini</i> Barber	Baker 1972
		<i>Monocesta coryli</i> (Say)	Baker 1972
		<i>Pyrrhalta cavicollis</i> (LeConte)	Baker 1972
		<i>Pyrrhalta lutella</i> (Mueller)	Baker 1972
		<i>Zengophora scutellaris</i> Suffrian	Baker 1972
	Coccinellidae	<i>Coleomegilla maculata lengi</i> Timberlake	Lucas et al. 2000
		<i>Laricobius erichsonii</i> Rosenhauer	Baker 1972
	Curculionidae	<i>Brachyrhinus sulcatus</i> (F.)	Baker 1972
		<i>Conotrachelus naso</i> LeConte	Baker 1972
		<i>Hylobius radialis</i> Buchanan	Baker 1972
		<i>Polydrusus impressifrons</i> Gyllendal	Baker 1972
		<i>Rhynchophorus cruentatus</i> F.	Baker 1972
		<i>Curculio caryae</i> (Horn)	Harrison et al. 1993
		<i>Hypera postica</i> (Gyllendal)	Harcourt and Guppy 1975
	Dermestidae	<i>Dermestes frischii</i> Kugelann	Campbell 1989
		<i>Dermestes lardarius</i> L.	Campbell 1989
		<i>Dermestes maculatus</i> DeGeer	Campbell 1989
	Laemophloeidae	<i>Cryptolestes ferrugineus</i> (Stephens)	Smith 1972
	Nitidulidae	<i>Carpophilus hemipterus</i> (L.)	Campbell 1989
		<i>Carpophilus mutilatus</i> Erichson	Campbell 1989
		<i>Glischrochilus quadrisignatus</i> (Say)	Campbell 1989
		<i>Stelidota geminata</i> (Say)	Campbell 1989
	Tenebrionidae	<i>Tribolium castaneum</i> (Herbst)	Toews et al. 2005
Diptera			
	Calliphoridae	<i>Calliphora erythrocephala</i> (Meigen)	Denlinger and Zdarek 1994
		<i>Calliphora vicina</i> (Robineau-Devoidy)	Gomes et al. 2006
		<i>Calliphora vomitoria</i> L.	Gomes et al. 2006
		<i>Chrysomya megacephala</i> (F.)	Gomes et al. 2006
		<i>Chrysomya albiceps</i> (Wiedemann)	Gomes et al. 2006
		<i>Chrysomya rufifacies</i> (Macquart)	Gomes et al. 2006
		<i>Cochliomyia americana</i> Cushing and Patton	Travis et al. 1940
		<i>Cochliomyia macellaria</i> (F.)	Gomes et al. 2006
		<i>Lucilia caesar</i> L.	Gomes et al. 2006
		<i>Lucilia cuprina</i> (Wiedemann)	Gomes et al. 2006
		<i>Phaenicia sericata</i> (Meigen)	Gomes et al. 2006
		<i>Phormia regina</i> (Meigen)	Gomes et al. 2006
	Ceratopogonidae	<i>Culicoides furens</i> Poey	Kettle 1962
		<i>Culicoides melleus</i> (Coquillett)	Linley and Adams 1972
		<i>Culicoides nubeculosus</i> Meigen	Kettle 1962
		<i>Culicoides tristriatulus</i> Hoffman	Kettle 1962
	Cuterebridae	<i>Cuterebra latifrons</i> Coquillett	Catts 1982
	Drosophilidae	<i>Drosophila melanogaster</i> Meigen	Sokolowski 1985
	Glossinidae	<i>Glossina morsitans</i> Westwood	Denlinger and Zdarek 1994
	Muscidae	<i>Haematobia irritans</i> (L.)	Hoelscher et al. 1967
		<i>Musca autumnalis</i> DeGeer	Jones 1969
		<i>Musca domestica</i> L.	Barber 1919, Hewitt 1914
		<i>Muscina stabulans</i> (Fallen)	Gomes et al. 2006
		<i>Stomoxys calcitrans</i> (L.)	McPheron and Broce 1996
	Sarcophagidae	<i>Sarcophaga argyostoma</i> (Robineau-Desvoidy)	Denlinger and Zdarek 1994
		<i>Sarcophaga bullata</i> (Parker)	Denlinger and Zdarek 1994
		<i>Sarcophaga crassipalpis</i> Macquart	Denlinger and Zdarek 1994
		<i>Sarcophaga peregrina</i> Robineau-Desvoidy	Denlinger and Zdarek 1994
	Tephritidae	<i>Anastrepha fraterculus</i> (Wiedemann)	Aluja et al 2005, Hodgson et al. 1998
		<i>Anastrepha ludens</i> (Loew)	Aluja et al 2005, Hodgson et al. 1998

prey (Marston et al. 1978). Velvetbean caterpillar, *Anticarsia gemmatalis* Hübner, and *Plathypena scabra* swing their bodies back and forth in a rapid whipping motion that usually causes them to drop from the plant. Larvae of corn earworm, cabbage looper, and the soybean looper, *Pseudoplusia includens* (Walker), attempt to bite the proboscis of a predator and roll violently. This frequently results in corn earworms breaking away from predators and sometimes results in their falling off the plant. The loopers are less aggressive and rarely break away or fall off the plant. At the slightest disturbance, first instars of *Mythimna unipuncta* drop from the plant on a silk thread and hang motionless (Guppy 1961). The last five instars are not as easily disturbed; when touched, they often rear the head and thorax, lashing toward the intruder before moving away. On the ground, they curl up when disturbed.

Pupation Site Selection

Larvae of >361 species in 59 families and 5 orders leave their feeding sites to find a pupation site (Table 3), often in the soil or litter covering the soil. Leaving feeding habitat can increase the predation on the wandering larvae, but reduce the mortality of pupae from predators or parasitoids at the feeding site. By burrowing into the soil, larvae may find a more suitable environment than that at the feeding site; however, larvae of some species just find a cooler, drier place in the food. Most species of blowfly larvae move <1m, but some may move >30 m (Norris 1965). At least 8 species of Calliphoridae (in addition to those in Table 3) leave their feeding sites to find pupation sites (Gomes et al. 2006). Housefly larvae generally move ~61 cm and pupate at a depth of ~23 cm, but they may move as far 5 m to find a favorable environment. When choosing pupation sites, mature *Stomoxys calcitrans* (L.) larvae move as far as ~9 m responding to moisture, temperature, light, pH and osmolality (McPheron and Broce 1996).

Larvae of *Culicoides melleus* (Coquillett) move farther up the bank before pupation (Linley and Adams 1972). Wandering time ranged from <10 min for *Anastrepha* spp. larvae (Aluja et al. 2005) to <1 h for tsetse fly, *Glossina morsitans* Westwood, larvae, and >1 wk for *Sarcophaga* spp. larvae (Denlinger and Zdarek 1994). Cuterebrid larvae drop from their hosts and burrow 8–25 cm into soil or debris to pupate (Catts 1982). Larvae of tachinids leave their host and pupate in the soil (Stireman et al. 2006). Sokolowski

Table 3. (continued)

Order	Family	Species	Source
		<i>Anastrepha obliqua</i> (Macquart)	Aluja et al 2005, Hodgson et al. 1998
		<i>Anastrepha striata</i> Schiner	Hodgson et al. 1998
		<i>Anastrepha suspensa</i> (Loew)	Hennessey 1997
Hymenoptera			
	Argidae	<i>Arge pectoralis</i> (Leach)	Baker 1972
	Cephiidae	<i>Cephus cinctus</i> Norton	Holmes 1975
	Cimbicidae	<i>Cimbex americana</i> Leach	Baker 1972
	Diprionidae	<i>Neodiprion fulviceps</i> complex	Stark and Dahlsten 1961
		<i>Neodiprion gillettei</i> (Rohwer)	Dunbar and Wagner 1992
	Pamphiliidae	<i>Acantholyda erythrocephala</i> (L.)	Baker 1972
		<i>Acantholyda zappei</i> (Rohwer)	Baker 1972
		<i>Neurotoma fasciata</i> (Norton)	Baker 1972
	Tenthredinidae	<i>Perga dorsalis</i> Leach	May 1979
		<i>Pikonema alaskensis</i> (Rohwer)	Baker 1972
		<i>Pristiphora erichsonii</i> (Hartig)	Baker 1972
	Xyelidae	<i>Pleroneura brunneicornis</i> Rohwer	Baker 1972
Lepidoptera			
	Coleophoridae	<i>Coleophora fuscedinella</i> Zeller	Raske and Bryant 1977
	Gelechiidae	<i>Pectinophora gossypiella</i> (Saunders)	Rice and Reynolds 1971
		<i>Phthorimaea operculella</i> Zeller	Ono 1983
	Geometridae	<i>Ectropis excursaria</i> (Guenée)	Mariath 1984
	Lymantriidae	<i>Lymantria dispar</i> (L.)	Campbell et al. 1975
	Noctuidae	<i>Agrotis ipsilon</i> (Hufnagel)	Showers 1997
		<i>Anticarsia gemmatalis</i> Hübner	Lee and Johnson 1990
		<i>Heliocoverpa</i> (= <i>Heliothis</i>) <i>zea</i> (Boddie)	Fitt 1989
		<i>Plathypena scabra</i> (F.)	Bechinski and Pedigo 1983
		<i>Mythimna unipuncta</i> (Haworth)	Guppy 1961
	Papilionidae	<i>Battus philenor</i> (L.)	Wagner 2005
		<i>Papilio glaucus</i> L.	Wagner 2005
		<i>Papilio polyxenes</i> F.	Wagner 2005
	Pieridae	<i>Pieris brassicae</i> (L.)	Willmer 1980
		<i>Pieris rapae</i> (L.)	Harcourt 1961
	Plutellidae	<i>Homadaula anisocentra</i> Meyrick	Hart et al. 1986
	Pyrilidae	<i>Cadra cautella</i> (Walker)	Hagstrum and Subramanyam 2006
		<i>Ephestia elutella</i> (Hübner)	Richards and Waloff 1946
		<i>Homoeosoma electellum</i> (Hulst)	Riemann et al. 1986
		<i>Plodia interpunctella</i> (Hübner)	Tsuji 1996
	Sphingidae	<i>Manduca sexta</i> (L.)	Dominick and Truman 1984
	Tortricidae	<i>Croesia semipurpurana</i> (Kearfott)	Beckwith 1963
Thysanoptera			
	Thripidae	<i>Frankliniella parvula</i> Hood	Lewis 1973
		<i>Kakothrips pisivorus</i> (Westwood)	Lewis 1973
		<i>Odontothrips loti</i> (Haliday)	Lewis 1973
		<i>Thrips angusticeps</i> Uzel	Lewis 1973

(1985) reported that for *Drosophila melanogaster* Meigen, larval descendants of pupae collected from grapes in a vineyard had a shorter foraging path and pupated nearer the surface than those collected from soil in the vineyard.

Mature larvae of *Manduca sexta* wander for 10–30 h before burrowing into the soil and building an underground chamber for pupation (Dominick and Truman 1984). Many mature larvae of mimosa webworm, *Homadaula anisocentra* Meyrick, in urban areas move as far as 15–24 m from an infested tree before pupating; those that find a heated structure are more likely to survive cold winters (Hart et al. 1986). Larvae of *Ectropis excursaria* move to soil near the food plant to pupate (Mariath 1984). Lee and Johnson (1990) found pupae of *Anticarsia gemmatalis* <2 cm below the soil surface, but not

on soybean plants. Mature fifth instars of the *Cydia pomonella* leave apples through the entrance tunnel or a new tunnel and move to the tree trunk in search of a pupation site (Jumean et al. 2009). Aggregation pheromone from freshly spun cocoons attracts additional larvae and aggregation protects them better from parasitization. Potato tuberworm larvae, *Phthorimaea operculella* Zeller, prefer a dry, enclosed, dark place in that order (Ono 1983). Wandering of sunflower moth larvae, *Homoeosoma electellum* (Hulst), before pupation is closely correlated with the purging of the gut; daytime wandering may have originated as a defense against predation (Riemann et al. 1986). Most *Lymantria dispar* larvae pupate in locations used earlier as daytime resting sites, but some may be many feet away from the closest living tree (Campbell et al. 1975). Developmental times of checkerspot butterfly, *Euphydryas editha* (Boisduval), pupae depend on the location selected by larvae (Weiss et al. 1987). Larvae can disperse >10 m d⁻¹; they disperse farther on cooler slopes and stop dispersing when the temperature is suitable (30–35 °C). In addition to the 20 species in Table 3, Baker (1972) and Wagner (2005) report that >230 species of Lepidoptera (25 additional families) leave their feeding sites to find a pupation sites. Of these species, 68% are from 5 families (23 Geometridae, 22 Lycaenidae, 30 Noctuidae, 56 Notodontidae, and 41 Sphingidae). Some additional species pupating in leaf shelters end up on the ground when leaves fall.

Cocoons of sawflies are spun by larvae deep in mineral soil (*Neodiprion lecontei*), in needles and litter above soil (*Neodiprion nanulus nanulus* Schedl), and shallowly at sod roots [*Neodiprion abbotii* (Leach)] (Coppel and Benjamin 1965). Mature larvae of the *Neodiprion fulviceps* complex leave the pine tree to pupate; 73% of pupae are found within 91 cm of the tree trunk; and 90% are found within the shade produced by the tree (Stark and Dahlsten 1961). From 18 to 39%

of larvae tend to burrow in loose soil, particularly where shade and litter are absent. Female larvae are more active and disperse farther from the tree to pupate than do male larvae.

After completing development inside the stems of wheat or grasses, a larva of the wheat stem sawfly, *Cephus cinctus* (Norton), tunnels down inside the stem to below ground level and cuts the stem at about ground level by making a groove around the inside of stem with its mandibles (Holmes 1975). The stem above the groove falls to the ground; the larva plugs the open end of the occupied below-ground stem with frass and forms a cocoon in which it spends the winter and pupates the next spring.

Baker (1972) reported that 14 species of Diprionidae and 15 species of Tenthredinidae (in addition to those listed in Table 3) leave

their feeding sites to find pupation sites. For most terebrantia, fully fed second-stage Thysanoptera move to soil or litter beneath the food plant to enter the resting stage (Lewis 1973).

Mature larvae of the stored-product insects *Cadra cautella* (Hagstrum and Subramanyam 2006), *Plodia interpunctella* (Hübner) (Tsuji 1996), *Cryptolestes ferrugineus* (Stephens) (Smith 1972), and *Tribolium castaneum* (Herbst) (Toews et al. 2005) wander in search of a pupation site. Mature nitidulid third instars leave the fruit and burrow into the soil before pupating (Campbell 1989). Several species of *Dermestes* larvae leave the food source to search for a pupation site and bore into nonfood materials before pupating (Campbell 1989). Fourth instars of pecan weevils, *Curculio caryae* (Horn), leave nuts that have fallen to ground and burrow 5–30 cm deep into soil to pupate, but they remain there as larvae for the remainder of the year before pupating. Adults eclosing from pupae remain in the soil for another year. Some bruchid larvae feed on more than one seed within a pod, and larvae of the genus *Caryedon* spp. leave the pods to pupate 5 cm deep in soil (Southgate 1979). About 90% of the coccinellids larvae, *Coleomegilla maculata*, leave the potato plant to pupate, probably to reduce risk of predation (Lucas et al. 2000). In Canada, pupation of *Hypera postica* (Gyllenhal) occurs on foliage, but in western parts of the United States, pupation occurs in litter (Harcourt and Guppy 1975). Leaving feeding sites to pupate can be important in maintaining pest populations because they are not killed when commodities are harvested and processed.


Diapausing larvae often find an aestivation or overwintering site for larvae or pupae. Studies on temperate ($n = 317$) and tropical ($n = 73$) insect species show that many diapause in the larval (32 and 36%) or pupal (30 and 21%) stages (Denlinger 1986). Diapausing *Trogoderma granarium* Everts larvae leave food in response to accumulated fecal odors, locate a hiding place, and later infest fresh commodities stored in warehouses (Stanic and Shulov 1972).

Adult Ecllosion Site Selection

The pupae of the mosquito, *Culiseta longiareolata*, attach to the water surface by their horns, which allows adults to emerge from the water (Van Pletzen 1981). Chironomids in the subfamily Tanypodinae and two genera in the family Podonominae have free-living pupae that swim to the surface so adults can emerge (Oliver 1971). All others are sedentary. Just before adult emergence, the sedentary pupae move to the surface with the aid of air that has accumulated within the pupal skin around the thorax of the adult. Plecoptera nymphs crawl out of the water to objects or plants before adult's eclosion (Stewart et al. 1988). The Ephemeroptera, Neuroptera family Corydalidae, and Odonata nymphs or larvae also leave the water before adult eclosion (Baker 1972). Pupae of the Lepidoptera *Prionoxystus robiniae* (Peck) in the family Cossidae and *Sylvora acerni* Clemens in the family Aegeriidae wriggle partway out of their tunnels in trees before the adults eclosion.

Conclusions

Optimal food and environmental conditions during immature stages increase their survival and shorten their development time; this results in earlier reproduction and more rapid insect population growth. The immature insects' adaptations for finding the highest quality food and optimal environmental conditions are critical to maximizing the success of a species. First instars often must move a long distance to find their first meal or perish. Feeding habits of subsequent instars may change as they grow. Immature stages may

accumulate nutrients necessary for egg production by adults. Commuting between feeding and resting sites, and evasive, escape or defensive behaviors may minimize attack by natural enemies. Shelter construction and behavioral regulation of temperature and water balance may be important in maintaining a suitable environment, and immature stages are generally responsible for finding a good pupation site. The pupation site may also be the site for aestivation or overwintering. Behavior of larvae or nymphs may be important in facilitating adult eclosion. Therefore, the mobility of immature stages plays many important ecological roles. 

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