LIFECYCLE OF LEPIDOPTERA

The typical life cycle follows a holometabolous, four-stage sequence—adult, egg, caterpillar (larva), and pupa—in which development during the pupal stage involves the metamorphosis from a caterpillar to an adult.

ADULT

Moths and butterflies are the sexually mature adult life stage of Lepidoptera. The adult serves three main functions in the life cycle: mating, dispersal, and oviposition. Many moths feed on nectar or a liquid sugar source for energy required for flight. Some species of macromoths do not have functional mouthparts and cannot feed. Consequently, they are relatively short-lived and will exhibit a short flight period.

Dispersal and flight activity Not all moths have wings, and not all moths with wings can fly. Typically, moths with wings have two pairs: a pair of forewings and a pair of hindwings. The forewings are attached to the second thoracic segment, the mesothorax. The hindwings are attached to the third thoracic segment, the metathorax. Individuals that do not have wings do not have flight muscles and typically are female. The absence of flight muscles is associated with a higher capacity for egg production. The males of species with flightless females have fully developed wings and can fly. Examples of species with wingless females are the lymantriids, *Orgyia antiqua* and *Orgyia pseudotsugata*, and the geometrids, *Erannis tiliaria*, *Operopthera bruceata*, *Operopthera danbyi*, and *Phigalia plumogeraria*.

The period for flight may be characteristic for a species. The daily rhythm and the seasonal pattern are the two temporal components to flight behavior. A minority of moth species, and nearly all butterfly and skipper species may fly during the day. Generally, moths fly during the night, but some of the night-flying species fly during the evening. No night-flying butterflies occur in the Pacific Northwest.

The time of season and the length of time for the flight period of a species may also exhibit a diagnostic pattern. Most species fly at certain times of the year and may be active for a period of 3 to 6 weeks, whereas a few species may have individuals in flight throughout much of the year. For instance, the arctiid *Lophocampa argentata* will be in flight during the last few days of July and the first 3 weeks of August, with a peak in flight around the end of the first week in August. The males of the geometrids *Operopthera bruceata* and *Operopthera danbyi* will be in flight only from the middle of November to the last week of December. The geometrid *Sabulodes aegrotata* has been observed in flight beginning the last week of January through the spring, summer, and fall, and up to the last week in November.

Mating and oviposition Typically, mating occurs soon after adults emerge from the pupae. The search for a mate is facilitated by volatile chemicals, called pheromones, which are emitted by a virgin female and act as a sex attractant. Males detect the pheromone molecules with their antennae and fly upwind to locate the chemical's female source. The act of mating may take many hours, but a female may begin laying fertile eggs immediately after mating. Pheromones are often species specific and help to isolate closely related species from each other.

Figure 3 Eggs of Lepidoptera. (A) *Phyllodesma americana,* (B) *Acronicta funeralis,* (C) *Coloradia pandora,* (D) *Phryganidia californica,* (E) *Spodoptera praefica.*

EGG

Females may lay eggs singly or in clusters, depending on the species. Most species attach their eggs to the vegetation that will serve as the foodplant for the caterpillar. For instance, *Phyllodesma americana* will attach a single egg to the leaf of various flowering trees that will then serve as food for the caterpillar. Some species, such as *Orgyia antiqua*, will deposit eggs on the silk surrounding the pupal skin. Other species scatter eggs on the soil surface. Egg production ranges from fewer than 100 eggs to more than 1,000 eggs per female.

CATERPILLAR (Larva)

Caterpillars are the active, feeding, immature stage of moths and butterflies. With few exceptions, caterpillars are herbivorous. Few species of caterpillars are predaceous, feeding on animals. Most caterpillars feed on foliage, but some feed on roots, seeds and flowers, and within branches and woody stems. Caterpillars of many species are monophagous or foodplant specialists, meaning they have restricted ranges of plants upon which they can feed. Specialist species may feed either on only one plant species, on only a few related plant species, or on many species within one genus of plant.

Many caterpillars are polyphagous, or generalist feeders. That is, the caterpillar can feed upon a wide range of plant species, typically covering five or six plant families, and still develop into a normal-sized adult in the usual period of time.

While caterpillars might be less obvious at first glance, they can be very abundant on certain plants at certain times of the year. Within a given environment caterpillars can be found in a variety of habitats and microhabitats. In general, they may be aquatic or terrestrial. They can be found in fruits, roots and stems as borers or miners; in foliage as miners; on the surface of foliage as skeletonizers or chewers; in galls; or in the nests of other insects, such as ants and bees.

Caterpillars develop in the egg and then emerge through the eggshell, which they sometimes eat. They increase in size each time they molt or shed their skins. The period between molts is termed an instar, and typically a caterpillar passes through five instars as it eats and grows (see Figure 7, page 17). In certain species a caterpillar that will develop into an adult female may develop through an additional instar and thus grow bigger than the male. However, based on external morphology, it is usually very difficult to distinguish between the sexes prior to pupation.

Most caterpillars feed and develop as solitary individuals, but a few species aggregate. Some aggregating caterpillars construct nests. For instance, the caterpillars of *Lophocampa argentata* aggregate on branches of Douglas-fir but do not construct nests. The caterpillars of *Hyphantria cunea* and *Malacosoma californicum* live in large colonies in silk nests they spin among the twigs and branches of trees.

Caterpillar growth rates are strongly influenced by temperature and the nutritional quality of foodplants. Generally, the cooler the temperature, the slower the growth rate. The nutritional value of vegetation depends on its protein (nitrogen), water, and allelochemical content. Most plants

contain between 1% and 7% nitrogen by weight, and the higher the content, the more nutritious it is. The same holds for water content. The closer water content is to the higher end of the plant's normal range, the more nutritious it is. Allelochemicals are plant-derived chemicals—terpenes, alkaloids, phenolics, and various proteins—that can stimulate or deter feeding. Some are toxic to caterpillars and some are not. Some that are not toxic to caterpillars, are toxic to one or more of their predators. In turn, some unaffected caterpillars have developed mechanisms whereby they store toxins as a defense against their predators. Many of the poisonous caterpillars are aposematic, meaning they are brightly colored, with the colors serving to warn away would-be predators. Two examples are the brightly colored caterpillars of the cinnabar moth, *Tyria jacobaeae*, and the monarch butterfly, *Danaus plexippus*.

PUPA

Metamorphosis occurs inside the pupa. A butterfly pupa is called a "chrysalis." A moth pupa, called a "cocoon," may be covered in silk, or naked, and can be encased in rolled foliage or in the soil. Once a caterpillar has attained a critical size, it changes behavior and stops feeding and begins searching for or creating a site to pupate. Pupation can be quick, lasting 2 to 3 weeks, or prolonged, lasting more than one year. The pupa is the overwintering life stage in many species. Typically, overwintering pupae are in diapause, a state within which development of the adult is arrested or slowed down to a low rate. The adult will not mature and emerge from a pupa in diapause unless the pupa is first exposed to a period of cold, followed by a period of increased warmth.

Overwintering A majority of the species of Lepidoptera in the Pacific Northwest overwinter either in the pupal or egg stage. Only a few of the common species in the Pacific Northwest overwinter as caterpillars, including the arctiids *Gnophaela vermiculata*, *Lophocampa argentata*, and *Pyrrharctia isabella*; the geometrid *Neoalcis californiaria*; and the dioptid *Phryganidia californica*. Species with overwintering caterpillars tend to occur in regions with a mild winter. Some species, such as the mourning cloak butterfly, *Nymphalis antiopa*, overwinter in the adult stage.

Figure 4 Pupae of Lepidoptera. The pupa of a butterfly (A) is known as a chrysalis. The chrysalis of *Danaus plexippus* hangs head down; the chrysalis of *Papilio zelicaon* is recumbent, head up, and held by a silken belt. The pupa of a moth (B) may be naked (no silk), or variously enveloped in silk (cocoon). The noctuid pupa lacks silk, and could be found in leaf litter on the ground, buried in the soil in a small cell, or in a rolled leaf. The cocoon of *Nola minna* is attached to a twig of its foodplant.

Figure 5 Parasitoids of Lepidoptera. (A) A female *Cotesia yakutatensis* laying eggs in an early instar of *Autographa californica*; (B) larvae of *Cotesia yakutatensis* emerging from the host caterpillar; (C) pupae within a silken mass, spun by the parasitoid larvae, around the shriveled remains of the host caterpillar.

Natural Enemies Lepidoptera have many natural enemies including predators and pathogens. Predators of many types devour Lepidoptera, often in great quantities. These predators include rodents, reptiles, bats, birds, spiders, nematodes, beetles, true bugs, and parasitoids. Pathogens cause fatal diseases in Lepidoptera. The more important pathogens are viruses, bacteria, protozoa, microsporidia, and fungi.

Lepidoptera are equipped with physical and physiological defense mechanisms against such natural enemies, including stinging hairs on caterpillars, as in *Hemileuca eglanterina*, camouflage, or crypsis, evidenced in the white, gray, and black tones in the forewings and hindwings of adults such as *Semiothisa* and *Itame*. Behavioral protective features include flashing bright colors or eyespots, which startle predators and are evidenced in the hindwings of the noctuid *Catocala ophelia*, the sphingid *Paonias excaecatus*, and the saturniid *Antheraea polyphemus*.

Figure 6 Parasitoids of Lepidoptera. (A) A pair of tachinid eggs on *Papilio bairdii*; (B) larvae of an ectoparasitic wasp on the caterpillar of *Drepanulatrix* sp.; (C) a trio of tachinid maggots (note swollen areas) inside the caterpillar of *Trichoplusia ni* (note dark spots where respiratory funnels of the parasitoid larvae have pierced the caterpillar's exoskeleton); (D) solitary pupa of a parasitoid that had fed on the hemolymph and internal organs of *Papilio zelicaon*; (E) quartet of pupae attached to the exoskeleton of *Nadata gibbosa*; (F) a multitude of pupae of *Copidosoma* sp. inside the cadaver of *Euxoa sp*.