Appendix A: Monarch Biology and Ecology

Materials for this appendix were adapted from MonarchNet.org, MonarchJointVenture.org, MonarchLab.org, and MonarchParasites.org.

Monarch Life Cycle Biology:

Overview: All insects change in form as they grow; this process is called metamorphosis. Butterflies and moths undergo complete metamorphosis, in which there are four distinct stages: egg, larva (caterpillar) pupae (chrysalis) and adult. It takes monarchs about a month to go through the stages from egg to adult, and it is hormones circulating within the body that trigger the changes that occur during metamorphosis. Once adults, monarchs will live another 3-6 weeks in the summer. Monarchs that migrate live all winter, or about 6-9 months.

Monarch larvae are specialist herbivores, consuming only host plants in the milkweed family (Asclepiadacea). They utilize most of the over 100 North American species (Woodson 1954) in this family, breeding over a broad geographical and temporal range that covers much of the United States and southern Canada. Adults feed on nectar from blooming plants.

Monarchs have specific habitat needs: Milkweed provides monarchs with an effective chemical defense against many predators. Monarchs sequester cardenolides (also called cardiac glycosides) present in milkweed (Brower and Moffit 1974), rendering them poisonous to most vertebrates. However, many invertebrate predators, as well as some bacteria and viruses, may be unharmed by the toxins or able to overcome them. The extent to which milkweed protects monarchs from non-vertebrate predators is not completely understood, but a recent finding that wasps are less likely to prey on monarchs consuming milkweed with high levels of cardenolides suggests that this defense is at least somewhat effective against invertebrate predators (Rayor 2004).

Benefits gained by monarchs from cardenolides are not without cost. Milkweed plants vary greatly in cardenolide concentration, both individually and between species. Both the toxin and the sticky latex produced by the plants provide defenses against herbivores. Monarchs appear to be negatively affected by consuming plants with high cardenolide levels, and may actually starve to death when their mandibles are glued together by the latex or if their bodies become mired in a drop of latex formed when the plant is injured (Zalucki and Brower 1992; Malcolm and Zalucki 1996; Zalucki and Malcolm 1999;Zalucki et al. 2001). Larger larvae reduce this risk by chewing a notch at the base of the milkweed leaf midvein, cutting off the flow of sticky latex to the rest of the leaf and allowing more efficient eating (Fig. A.1).

Figure A.1: Larger caterpillars chew a notch at the base of the milkweed leaf midvein, cutting off the flow of sticky latex to the rest of the leaf, allowing more efficient eating (photo courtesy of Denny Brooks).

Like other plants, milkweed quality as a host for insects varies. Many insects are nitrogen limited (McNeil and Southwood 1978,Mattson 1980,Scriber 1984,Slansky and Scriber 1985,White 1993). They must consume large quantities of their host plants to accumulate enough nitrogen for growth and development, since animal tissue generally consists of 7-14% nitrogen by dry weight (dw) and plants consist of 0.03-7.0% nitrogen dw (Mattson 1980). Leaf nitrogen levels vary within a season, as plant tissue ages and as plants allocate more resources to reproductive tissue. In addition, plants grow in habitats with different levels of available soil nitrogen. Lavoie and Oberhauser (2004) studied the response of monarch larvae to plants manipulated through fertilizer treatments to contain varying leaf nitrogen levels, and found that they compensated for low nitrogen leaves by consuming more plant tissue per day. If increased consumption makes them more vulnerable to predation or plant defenses, this could result in decreased fitness levels.

The most important northern host plant is *Asclepias syriaca* (common milkweed, Fig. A.2), but a number of other species are used as well, such as *A. incarnata* (swamp milkweed). Central Plains host plants include the vine *Cynanchum leave* (sand or honey vine). A northeastern invasive plant in the same genus (*C. nigrum*) has spread west as far as Wisconsin. This species is attractive to ovipositing females, but monarch larvae do not survive on it (Haribal 1998). In the south, the most important host plants are probably *Asclepias oenotheroides* (zizotes milkweed), *A. viridis* (spider milkweed) and *A. asperula* (antelope horn milkweed), all fairly common throughout Texas and other southern US states.

Fig. A.2: The most important host plant for monarchs in the eastern migratory population during the summer breeding season is common milkweed (*Asclepias syriaca*, photo courtesy of Karen Oberhauser).

Adult monarchs feed on nectar from blooming plants. Due to their large range and migratory life history, adults feed from many species of blooming plants.

Monarch eggs: While butterflies and moths do not care for their young after hatching, they do lay their eggs on the appropriate host plant, which will be food for the newly hatched caterpillars. For monarchs, that's milkweed! Monarch females usually lay a single egg on a milkweed plant, often on the bottom of a leaf near the top of the plant. Eggs are only about the size of a pinhead or pencil tip and are off-white or yellow, characterized by longitudinal ridges that run from the tip to the base.

As females lay their eggs, they secrete a small amount of glue to attach the eggs directly to the plant. It is difficult to tell just how many eggs female butterflies lay during their lives, but the average in the wild is probably 300 to 400. Captive monarch butterflies average about 700 eggs per female over 2 to 5 weeks of egg laying, with a record of 1179 eggs (Oberhauser 1997).

Each egg (Fig. A.3) is formed inside the female prior to fertilization, including the hard outer shell, called the chorion, which protects the developing larva inside. The shell is lined with a layer of wax, which helps keep the egg from drying out. The eggs have tiny funnel-shaped openings at one end, called micropyles. These holes penetrate all the way through the shell allowing sperm to enter, since eggs form their hard shell prior to fertilization. The raised areas on the egg shell are called ridges, they are also formed before the egg is laid. The dark head of the developing caterpillar can be seen near the top of the egg prior to emergence (Fig. A.4).

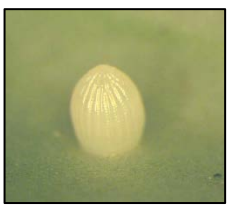


Fig. A.3: A monarch egg with visible ridges. Female monarchs always lay their eggs on milkweed plants, usually one at a time, though sometimes it's possible to find more than one egg on a plant (photo courtesy of Karen Oberhauser).

Fig. A.4: A monarch caterpillar ready to emerge from an egg (photo courtesy of Siah St. Clair).

Monarch eggs hatch about 4 days after they are laid, but the rate of development in this stage, like all other stages, is temperature dependent (ranging from 3-8 days), with individuals in warmer environments developing more rapidly (Zalucki 1982). The proteins that are an important constituent of eggs must either be derived from nutrients ingested during the larval stage or obtained from males during mating (Boggs and Gilbert 1979, Oberhauser 1997). While an individual monarch egg weighs only about 0.460 mg, about 1/1000 the adult mass, females often lay more than their own mass in eggs throughout their lives.

Monarch larvae have 5 instars: The word larva refers to the growth stage of all insects with complete metamorphosis. Larva is singular and larvae is plural. Caterpillar refers only to a butterfly or moth in this stage. Either word is correct, but most scientists say larva(e). It is during this stage that monarchs do all of their growing; in fact this is just about all that they do. These "eating machines" take few breaks even for resting. The entire larval stage in monarchs lasts from nine to fourteen days under normal summer temperatures.

Larvae, just like all other insects, have three distinct body parts: the head, thorax, and abdomen (Fig. A.5). The head has a pair of short antennae (these are not the tentacles), mouthparts (upper lip, mandibles, and lower lip), and six pairs of simple eyes, called ocelli. Even with all of these eyes, the caterpillar's vision is poor. The antennae help to guide the weak-eyed caterpillar as it moves around, and the maxillary palps (sensory organs), help direct food into its jaws. The spinneret produces silk, which the caterpillar uses to anchor itself when needed and to create the silk pad it uses to hang from when it pupates.

A.

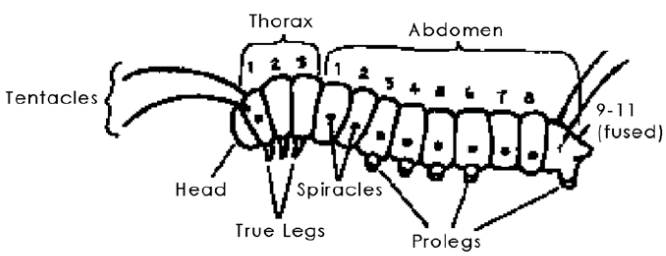


Fig. A.5: Monarch larva A. anatomy (Image from A Field Guide to Monarch Caterpillars), B. 5th instar larvae on milkweed (photo courtesy of Denny Brooks).

B.

Each thoracic segment has a pair of jointed, or true legs, while some of the abdominal segments have false legs, or prolegs (Fig. A.5). Monarchs have five pairs of prolegs. The prolegs have tiny hooks on them that hold the larva onto its silk mat or leaf. The fleshy tentacles at the front and rear ends of monarch larvae are not antennae, but they do function as sense organs.

Like other insects, monarchs obtain oxygen through holes in the sides of their thorax and abdomen called spiracles. The spiracles are connected to a network of long air tubes called tracheae, which carry oxygen throughout the body. Thus, unlike vertebrates, insect blood does not deliver oxygen to the rest of the body.

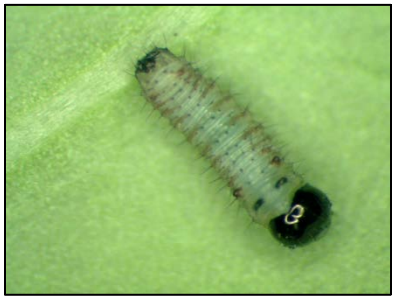
When a caterpillar first hatches, it will first eat its eggshell to recycle nutrients (Fig. A.6) and then begin consuming milkweed. As the caterpillar grows and becomes too large for its skin, it molts, or sheds its skin (Fig. A.7). The head capsule is the first part of the old skin to come off during the molting process. Then the old skin peels back from the front of the caterpillar. At first, the new skin is very soft, and provides little support or protection. This new skin soon hardens and molds itself to the caterpillar. The shed skin is often eaten before the caterpillar ingests more plant food. The intervals between molts are called instars. Monarchs have 5 instars.

Fig. A.6: A newly hatched monarch caterpillar (1st instar) consumes its eggshell (photo courtesy of Mary Holland).

Fig. A.7: A caterpillar that has just molted from a 2nd to a 3rd instar. Note the empty 'skin' behind the caterpillar on the milkweed leaf (photo courtesy of Janet Yeager).

Several physiological characteristics including tentacle length and stripes can help you distinguish between the 5 different monarch instars (Fig. A.8). Detailed instructions for distinguishing between different instars are given in Appendix B (A Field Guide to Monarch Caterpillars). In short, when first instar caterpillars hatch, they initially lack stripes, but they develop them during the first stage. Also, first instars only have small bumps for tentacles. Second instar caterpillars have stripes and have small knobs for front and back tentacles. Third instar caterpillars have short front and back tentacles but the front tentacles, if folded forward, barely reach the front of their heads. Fourth instar caterpillars have longer front and back tentacles, and if folded forward, these would reach to the front of their heads. Fifth instar caterpillars have long tentacles and if folded forward, the front tentacles would extend beyond the front of their heads. Since caterpillar size can increase dramatically even within the same instar (body length: 1st instar ranges from 2-6 mm, 2nd instar ranges from 6-9 mm, 3rd instar ranges from 10-14 mm, 4th instar ranges from 13-25 mm, 5th instar ranges from 25-45 mm), size is not a reliable indicator of instar stage (Fig. A.9).

A.



B.

C.

D.

E.

Fig. A.8: Monarch instars. A. first instar, B. second instar, C. third instar, D. fourth instar and E. fifth instar. (photos courtesy of Karen Oberhauser)

Fig. A.9: Two second instar caterpillars. Note the body size difference within the same instar stage (photo courtesy of Karen Oberhauser).

Monarch egg and larvae mortality is high: Monarch eggs and larvae have a slim chance of reaching adulthood; several studies have documented mortality rates of over 90% during the egg and larva stages (Borkin 1982, Zalucki and Kitching 1982, Oberhauser et al. 2001, Prysby and Oberhauser 2004). This mortality stems from both biotic and abiotic sources. Biotic factors that affect monarch survival include natural enemies such as predation (Fig. A.10), diseases and parasites, and interactions with their milkweed hosts. Parasitoid flies and wasps may also lay their eggs inside caterpillars or pupae, eventually killing the monarch and using the monarch's resources to fuel their own development. Abiotic factors include environmental conditions such as adverse weather and pesticides.

Fig. A.10: Arthropods (spiders, insects) are important predators of monarch eggs and caterpillars. Here, a true bug in the family Pentatomidae eats a 5th instar caterpillar (photo courtesy of Mary Holland).

Prysby (2004) documented overall impacts of natural enemies on monarch survival. By limiting predator access to monarch eggs and larvae with exclosures placed around naturally growing milkweed plants, she showed that both terrestrial and aerial predators represent significant sources of mortality. In addition, she found that monarch eggs were less likely to survive on plants on which ants had been observed, suggesting that ants are important predators.

This conclusion is supported by work in Texas by Calvert (1996,2004), who found that monarchs inside exclosures were much more likely to survive than those outside the structures. Calvert found that invasive fire ants currently kill most of the monarch eggs and larvae present in many areas in Texas, but thinks that pre-fire ant mortality may have been similarly high, since these invasive ants displaced native ants that also preyed on monarchs. In addition to predators, insect parasitoids are important sources of monarch mortality in some locations. Prybsy (2004) and the Monarch Larva Monitoring Project have both documented mortality rates of 10% to 90% in late instar monarchs due to tachinid fly (family Tachinidae) parasitoids, but these rates are variable from location to location and year to year.

Monarch eggs do not hatch in very dry conditions (Dunlap et al. 2000), and dry weather can kill milkweed. Very hot weather also causes mortality; several studies have shown that temperatures above approximately 35oC (95oF) can be lethal to all stages (Zalucki 1982, Malcolm et al. 1987, York and Oberhauser 2002). Likewise, extended periods in which temperatures are below freezing can kill monarchs, although this has been best studied in overwintering adults (Anderson and Brower 1993, 1996; Brower et al. 2004). Threats due to very hot or very cold temperatures are magnified during the breeding season, since monarchs are indirectly affected by conditions that affect milkweed health and survival. Freezing temperatures and extremely dry conditions are especially damaging to milkweed, and thus to monarchs.

Monarch pupae: During the pupa stage the transformation to the adult stage is completed in a process that takes about 9 to 15 days under normal summer temperatures. The ecology of monarch (or any other lepidopteran) pupae is unfortunately poorly-studied, at least partially due to the fact that it is extremely difficult to find monarch pupae in the wild. Their green color provides effective camouflage in a green world, and they appear to seek sheltered spots to undergo this transformation. Important questions on how larvae choose sites for pupation, how far they travel seeking these sites, what habitat characteristics are important in promoting pupal survival, and how much mortality from different sources occurs during this stage remain to be investigated.

Just before they pupate, monarch larvae spin a silk mat from which they hang upside down in a "J" shape (Fig. A.11). The silk comes from the spinneret on the bottom of the head. As it sheds its skin for the last time, the caterpillar stabs a stem into the silk pad to hang. This stem extends from its rear end and is called the cremaster.

Fig. A.11: Pupation sequence (photos courtesy of Siah St. Clair)

While the process of complete metamorphosis looks like very distinct stages, continuous changes actually occur within the larva. The wings and other adult organs develop from tiny clusters of cells already present in the larva, and by the time the larva pupates, the major changes to the adult form have already begun. During the pupal stage this transformation is completed. Many moth caterpillars (but not all) spin a silken cocoon to protect them as pupae. Butterflies do not do this, and their pupa stage is often called a chrysalis. While it is fine to refer to the previous stage as either larva or caterpillar, it is not correct to call a butterfly pupa a cocoon, since it does not have a silken covering.

Just before the monarchs emerge, their black, orange, and white wing patterns are visible through the pupa covering. This is not because the pupa becomes transparent; it is because the pigmentation on the scales only develops at the very end of the pupa stage (Fig. A.12). This stage of development lasts eight to fifteen days under normal summer conditions.

Fig. A.12: Monarch pupae. A. early stage chrysalis/pupae and B. mature monarch chrysalis/pupae containing monarch close to emergence. Note that wings are visible through the chrysalis wall. (Photos courtesy of Siah St. Clair).

A.

B.

Adults: The primary job of the adult stage is to reproduce—to mate and lay the eggs that will become the next generation. Summer generation monarchs first mate (Fig. A.13) when they are 3 to 8 days old (Oberhauser and Hampton 1995), and females begin laying eggs immediately after their first mating. When adults mate, they remain together from one afternoon until early the next morning—often up to 16 hours! Both sexes can mate several times during their lives (e.g., Oberhauser 1989), and the ability of male monarchs to force unwilling females to copulate makes them unique among the Lepidoptera (Oberhauser 1989; Van Hook 1993; Frey et al. 1998). When females mate with more than one male, it is generally the last male that fertilizes their eggs (Solensky 2003, Oberhauser personal observation). Adults in summer generations live from two to five weeks.

Fig. A.13: Adult monarchs mating (photo courtesy of Wendy Caldwell)

Each year, the final generation of monarchs, adults that emerge in late summer and early fall, has an additional job. They migrate to overwintering grounds, either in central Mexico for eastern monarchs or in California for western monarchs. Here they spend the winter clustered in trees until weather and temperature conditions allow them to return to their breeding grounds. These adults can live up to nine months. Differences in lifespan between summer and overwintering monarchs is due to the fact that overwintering monarchs are not reproductive, and can thus funnel more energy into survival. In addition, the cool conditions in the overwintering sites slow their metabolism. Monarchs that overwinter do not lay eggs until spring (although they may mate before this).

Since there is a delay between adult emergence and egg-laying, and also because monarchs reproduce over a relatively long time period, maximizing reproductive success also requires being able to survive predators, environmental extremes and other sources of mortality. Adult survival during the breeding season is another under-studied area of monarch biology, despite its importance to monarch ecology. Full understanding of adult ecology during the breeding stage of their lives will require measuring the effects of nectar availability and quality, the distances that females will fly to find milkweed host plants, the degree to which breeding monarchs remain in one area or move, and the effects of abiotic conditions on adult survival (Oberhauser 2004).

Male and female monarchs can be distinguished easily (Fig. A.14). Males have a black spot on a vein on each hind wing that is not present on the female. These spots are made of specialized scales which produce a chemical used during courtship in many species of butterflies and moths, although such a chemical does not seem to be important in monarch courtship. The ends of the abdomens are also shaped differently in males and females (Fig. A.15), and females often look darker than males and have wider veins on their wings (Fig. A.14).

Fig. A.14: Adult monarch A. male (photo courtesy of Nicole Hamilton) and B. female (photo courtesy of Candy Sarikonda). Note that males have a spot on each hindwing and that black veins on female wings are wider.

A.

B.

Fig. A.15. Adult monarch A. male and B. female abdomens (photos courtesy of Bruce Leventhal).

A.

B.

The body of an adult butterfly is divided into the same major parts as the larva: head, thorax, and abdomen. There are four main structures on the adult head: eyes,antennae, palpi, and proboscis. A butterfly's relatively enormous compound eyes are made up of thousands of ommatidia, each of which senses light and images. The two antennae and the two palpi, which are densely covered with scales, sense molecules in the air and gives butterflies a sense of smell. The straw-like proboscis is the butterfly's tongue, through which it sucks nectar and water for nourishment. When not in use, the butterfly curls up its proboscis (Fig. A.16).

Fig. A.16: Monarch proboscis A. curled (photo courtesy of Sonia Altizer) and B. extended to drink nectar (Photo courtesy of Candy Sarikonda).

A.

B.

The thorax is made up of three segments, each of which has a pair of legs attached to it. The second and third segments also have a pair of wings attached to them. The legs end in tarsi (singular, tarsus), which grip vegetation and flowers when the butterfly lands on a plant. Organs on the back of the tarsi "taste" sweet liquids. Monarchs and other nymphalid butterflies look like they only have four legs because the two front legs are tiny and curl up next to the thorax.

Monarch Annual Migration:

Overview: In North American, monarchs exhibit two migration patterns. Monarchs east of the Rocky Mountain range overwinter in central Mexico and migrate north and east in the spring, with subsequent generations eventually reaching Canada. In the fall, monarchs again migrate south to central Mexico. West of the Rocky Mountains, monarchs overwinter in tree groves along the Pacific coast in California. In the spring, monarchs expand their range north, south and east, returning to California groves in the fall.

Both populations of monarchs produce several generations per year, with only one overwintering generation. East of the Rockies, the overwintering generation mates and migrates north in the spring, populating the southern region of the US. Successive generations populate regions to the north and east until a 4^{th} generation emerges as far north as Canada. This fourth generation emerges in the late summer and cues such as shorter day lengths affect the hormonal and physiological state of the fourth generation. Monarchs in this generation enter a state of reproductive diapause (they do not mate) and instead migrate south to central Mexico, a distance of up to 3,000 miles! While migrating, monarchs build fat stores by feeding on nectar. In the spring, this same fourth generation breaks out of reproductive diapause, mates and migrates north. West of the Rocky Mountains, monarchs also have several generations per year, with one generation that overwinters along the Pacific Coast, and then disperses in the spring. Successive generations populate areas to the east, north and south.

While the Rocky Mountains act as a natural barrier between the Eastern and Western populations, there is some evidence that monarchs may cross between populations though these events are rare. For example, some monarchs tagged in Arizona have been found in Mexico.

Fall migration ecology

Unlike most temperate insects, monarch butterflies cannot survive extended periods of freezing temperatures, so North American monarchs fly south to spend the winter at roosting sites. In the spring, these overwintering monarchs fly north toward their breeding range. The monarch is the only butterfly to make such a long, two-way migration, flying up to 4830 kilometers in the fall to reach its winter destination (Urquhart and Urquhart 1978). Monarchs east of the Rocky Mountains generally fly to overwintering sites in the mountains of central Mexico, while monarchs west of the Rocky Mountains typically overwinter along the California coast, although recent observations by Pyle (1999) suggest that some western monarchs move south and southeast out of the inland northwest and Great Basin, entering Mexico from Arizona. The magnitude and destination of this movement is not understood. Another unanswered question about the western North American monarch population is the degree to which it is truly migratory, or whether it undergoes an annual range expansion and contraction in California. Wenner and Harris (1993) suggest that many monarchs are year-round residents of California whose offspring are able to spread to surrounding states during the mild summer weather but are forced to return to California or perish when the inhospitable northern winters return. This issue is still being debated.

Stable isotope studies (Wassenaar and Hobson 1998) and recoveries of tagged butterflies (Urquhart and Urquhart 1978, Monarch Watch 2004 and OR Taylor personal communication) suggest that the majority of monarchs that migrate to Mexico originate in the Midwest. However, these studies also show that the overwintering populations are comprised of monarchs coming from a wide geographic area that covers much of the range shown in Fig. A.17. Unfortunately, similar studies revealing the origins of monarchs overwintering in California have not been conducted.

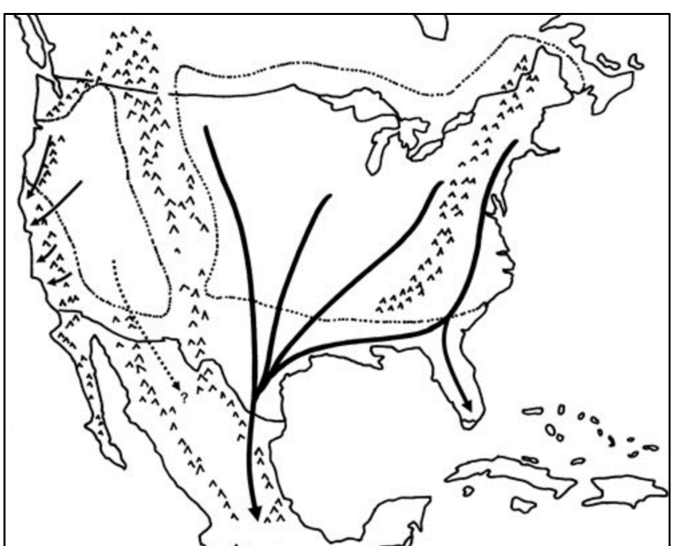


Fig. A.17: Monarch fall migration patterns east and west of the Rocky Mountains (drawing courtesy of Sonia Altizer and Michelle Solensky).

Australian monarchs also exhibit seasonal movement, moving from inland to coastal areas in a north to northeasterly direction during the fall and winter (James 1993). However, because the most spectacular monarch migrations (in terms of distance and numbers of migrants) occur in the eastern North American population, much of the research on monarch migration has focused on this population. These insects, weighing about half a gram, fly from their summer breeding range that covers more than 100 million ha, to winter roosts that cover less than 20 ha. Since the discovery of these winter roosts in Mexico by the scientific community in 1975 (Urquhart 1976), researchers have struggled to understand the cues that cause monarchs to begin their migration, the mechanisms they use to orient and find the overwintering sites and the patterns of fall and spring flight.

Initiation of migration: While non-migratory monarchs become reproductive within a few days of eclosion, late summer and early fall monarchs emerge in reproductive diapause, a state of suspended reproductive development. Diapause is controlled by neural and hormonal changes (Barker and Herman 1976, Herman 1981) triggered by environmental factors that signal the onset of unfavorable conditions, in this case winter. Goehring and Oberhauser (2002) found that decreasing daylength, fluctuating temperatures and senescing host plants each caused an increase in the proportion of monarchs that emerged in reproductive diapause, but the strongest response occurred among monarchs exposed to all three cues. Making use of more than one cue to assess current and near future habitat suitability could be a more optimal strategy for organisms in unpredictable environments.

Perez and Taylor (2004) tested the common assumption that reproductive diapause and migratory behavior in monarchs are coupled by exposing fall migrants to summer daylengths and temperatures. These butterflies exhibited reproductive behavior, but continued to show migratory flight directionality. They argue that while reproductive diapause can be readily reversed in fall migrants, migratory behavior is resistant to changes in environmental conditions. This finding is supported by Borland et al. (2004) and data from the Monarch Larva Monitoring Project (2004); many monarchs appear to become reproductive when they reach the southern US during their fall migration. The importance of this late reproduction to overall monarch population dynamics, and the environmental triggers that promote it, is still undetermined, but it suggests that an increase in the availability of milkweed in gardens and parks may trigger reproduction (Goehring and Oberhauser 2004).

Orientation and migration pathways: Insect orientation in general is poorly understood, and monarchs are no exception. The ability of monarchs that are spread over 100 million ha to converge in a very small area in the mountains of central Mexico is mind-boggling, and may be one of the most compelling mysteries of animal ecology. Other animals use celestial cues (the sun, moon, or stars), the earth's magnetic field, landmarks (mountain ranges or bodies of water), polarized light, infra-red energy perception, or some combination of these cues to migrate, but the degree to which these cues are used by monarchs is not known. Calvert and Wagner (1999) proposed that mountain ranges and river valleys might be used by monarchs to orient during their migration, but celestial cues and the earth's magnetic field have been studied the most.

Many researchers agree that the sun is the celestial cue most likely to be used by southward migrating monarchs. Kanz (1977) and Schmidt-Koenig (1985, 1993) suggested that monarchs use the angle of the sun along the horizon in combination with an internal body clock to maintain a southwesterly flight path, and Mouritsen and Frost (2002) confirmed this hypothesis. Because monarchs often migrate on cloudy days, this sun compass must be combined with the use of some other cue. Scientists have suggested that monarchs may use a magnetic compass to orient, as has been demonstrated in some migratory birds (Wiltschko and Wiltschko 1972, Emlen et al. 1976). However, Mouritsen and Frost (2002) showed that migratory monarchs exhibited randomly oriented flight when presented with only magnetic field cues and did not respond to magnetic field shifts, suggesting that monarchs do not use the earth’s magnetic field to orient during migration. They propose that monarchs may use polarized light patterns, which penetrate cloud cover, to orient on cloudy days.

The first large-scale study of the fall monarch migration began in 1937 when Dr. Fred Urquhart recruited volunteers for his insect migration study, which involved putting small paper tags on the leading edge of the monarch forewing and obtaining both release and capture locations for tagged butterflies (Urquhart and Urquhart 1977). In the fall of 1992, a new tagging program was established (Monarch Watch 2001) to continue the study of fall migratory routes. These tagging programs have revealed much information about the patterns and timing of the fall monarch migration. Several studies have shown that monarchs generally migrate in a south to southwest direction (Gibo 1986; Schmidt-Koenig 1985), with a shift from south to southwest as the origin of flight moves from west to east (Rogg et al. 1999). More recently,Wassenaar and Hobson (1998) used stable isotopes to estimate the origin of monarchs overwintering in central Mexico. They found that about half of the monarchs collected from 13 overwintering sites had migrated from the midwestern US, with smaller numbers originating from the northeastern US and Canada. While tagging reveals patterns of individual fall migrants, stable isotope studies show promise for revealing population-level migratory patterns.

Behavior during migration: Like migratory birds, monarchs make frequent stops during migration, forming roosts at night and during inclement weather that range in size from a few dozen to a few thousand individuals (Fig. A.18). Little is known about this roosting phenomenon, but recently Davis and Garland (2004) used methods from ornithological studies to investigate factors influencing monarch stopover decisions. They found that monarchs commonly stayed at roosting sites for at least 2 days, and proposed that levels of energy reserves may influence monarch migration and stopover decisions, with monarchs staying longer at stopover sites when their lipid reserves are small. Both Borland et al. (2004) and Gibo and McCurdy (1993) found that monarchs collected in the south were heavier than those captured in the north, suggesting that nectaring along the migratory path results in weight gain and increased energy reserve (Fig. A.19). These findings support the suggestion that energy reserves may influence monarch migration decisions. While orientation mechanisms have gained much attention from researchers, few studies have addressed stopover ecology or characteristics of monarchs that increase migratory success.

Fig. A.18: Small monarch night roost in Ohio (photo courtesy of Candy Sarikonda).

Fig. A.19: Late blooming summer flowers provide migrating monarchs with necessary nutrients during their fall migration (photo courtesy of Dallas Hudson).

Overwintering Ecology

Monarchs regularly congregate in two major regions of North America during the winter: central Mexico and coastal California (Brower 1995). They also reside in southern Florida throughout the year, but this population receives an influx of migratory individuals from the eastern migratory population each fall (Knight 1997; Altizer 2001). The degree to which monarchs from Florida move back into the larger population is not understood.

It has been generally assumed that monarchs spending the summer breeding season west of the Rocky Mountains overwinter along the coast of southern California, although the recent observations by Pyle (1999) described above suggest that there are exceptions to this pattern.

The California sites are usually wooded areas dominated by eucalyptus trees, Monterey pines, and Monterey cypresses, and are located in sheltered bays or farther inland. These sites provide moderated microclimate extremes and protection from strong winds. More than 300 different aggregation sites have been reported (Frey and Schaffner 2004; Leong et al., 2004).

North American monarchs that spend the summer breeding season east of the Rocky Mountains overwinter in oyamel fir (Abies religiosa) forests in the Transvolcanic mountains of central Mexico. The location of these overwintering sites was unknown to the scientific community until 1975 when associates of Dr. Fred Urquhart located colonies on Cerro Pelón and Sierra Chincua in the state of Michoacan (Urquhart 1976; Brower 1995). Since then, several more overwintering locations have been located; colonies within the Monarch Butterfly Biosphere Reserve are found in the states of Michoacán and México (Cerro Altamirano, Cerros Chivatí-Huacal, Sierra Chincua, Sierra El Campanario and Cerro Pelón). Outside the Reserve, colonies are found in San Andres, Pizcuaro, Puerto Morillo and Puerto Bermeo (Michoacán) and Palomas, Piedra Herrada and San Francisco Oxtotilpan (México) (Garcia-Serrano et al. 2004). While scientists have learned much about the phenomenon of monarch overwintering in the past few decades, several basic questions remain. Measuring the density of an organism that congregates by the millions presents a formidable challenge. Scientists also seek to understand the characteristics of the overwintering sites that are most important to monarch survival, and the factors that influence patterns of colony formation and dispersal.

Colony formation and dispersal: Throughout the winter, North American monarchs cluster together, covering whole tree trunks and branches (Fig. A.20). Calvert (2004b) describes four phases typical of colony development in Mexico sites: recruitment and consolidation, settling and compaction of clusters, expansion and rapid movement, and mating and dispersal. This pattern is similar in California (Frey and Schaffner 2004). Initially monarchs occupy many local habitats, but abandon many of them by late November and join nearby colonies. Before the monarchs disperse, many of them become reproductive, and the colonies are often filled with mating pairs (Fig. A.21).

Fig. A.20: Overwintering monarchs clustered on oyamel fir trees at the El Rosario preserve, Mexico (photo courtesy of Laura Molenaar).

Fig. A.21: Mating monarchs (photo courtesy of Holly Holt).

The timing of the last phase, mating and dispersal, depends on the timing of completion of reproductive diapause, which varies considerably among individuals. Goehring and Oberhauser (2004) studied post-diapause reproductive development in monarchs overwintering in Mexico. They found a great deal of variation in reproductive status of monarchs collected in late February and early March, with some butterflies fully reproductive while most were still in diapause. Females collected while mating were more likely to have developed oocytes (an indication that they were no longer in diapause) than females collected from clusters. If there is a cause and effect relationship that results in this correlation, it is not clear whether females were more likely to be mating because they were further along in their reproductive development, or if mating actually triggered the end of diapause. Both Van Hook (1993) andOberhauser and Frey (1999) found that males which began mating first at the end of the overwintering period had shorter wingspans, were lighter, and had poorer wing condition than males that were collected in roosts at the same time. They suggest that these males are unlikely to survive the return migration north, and are thus taking advantage of their last, and only, opportunity to mate.

Overwintering densities: Scientists use many methods to estimate population sizes of insects and other animals, but determining overwintering monarch abundance is particularly challenging because of their mobility and huge numbers. Nearly 30 years after the discovery of the Mexican overwintering sites, scientists are still debating how to best estimate monarch density there. Calvert (2004b) used mark, release, recapture techniques to estimate the population densities of 7 to 61 million monarchs per ha, with higher densities occurring later in the season when the colony had contracted. At a different colony, he measured monarch density on sub-samples of tree branches and trunks to estimate 12 million monarchs per hectare. These numbers are within the ranges suggested by Brower (1977) and Brower et al. (1977), but the large variation suggests that densities probably are not constant across the season and between different colonies.

Garcia-Serrano et al. (2004) monitored 22 Mexican overwintering sites from 1993 to 2002. Using an estimate of 10 million monarchs per hectare, they found that the overwintering population ranged from 23 million monarchs in 2000-2001 to 176 million in 1996-1997. They measured the highest mortality (27.7%) during a low population year (1997-1998, 45.5 million monarchs) and suggest that mortality rate may decrease with increasing population size.

Microclimate conditions in the overwintering sites: Monarchs migrate to specific overwintering sites because they require particular environmental characteristics to survive throughout the winter. Survival of overwintering monarchs in Mexico from November through March depends on a delicate balance of macro- and microclimatic factors that characterize the oyamel fir forests located within the reserve (Calvert and Brower 1986; Alonso-Mejia et al. 1992, 1997). High humidity and temperatures that fluctuate between 3˚ and 18˚ C characterize these forests, and several studies (Calvert and Brower 1981; Calvert and Cohen 1983; Calvert et al. 1982, 1983, 1984, 1986; Alonso-Mejia et al. 1992; Anderson and Brower 1993; Brower 1999) have shown that an intact forest ecosystem promotes winter survival. Butterflies in thinned forests are more likely to get wet during winter storms, and wet monarchs are unable to survive extremely cold temperatures, such as those that occurred during storms in 2002 (Brower et al. 2004) and 2004. In addition, thinned forests become colder at night because heat escapes from them more easily. Thus, an intact forest serves as both an umbrella, protecting the butterflies from snow and rain during winter storms, and a blanket, keeping the butterflies from freezing (Anderson and Brower 1996).

Recent modeling efforts (Bojórquez-Tapia 2003, Missrie 2004) show that preferred habitats of overwintering monarchs share four features: 1) high elevations (most colony sites are located at altitudes over 2890 m); 2) proximity to streams (most sites occur less than 400 m from permanent or ephemeral streams; 3) moderately steep slopes (between 23° and 26°); and 4) south-southwest orientation. In most cases, these conditions occur in oyamel fir forests, but colony sites also exist below these forests, primarily because the butterflies move to lower altitudes (where mixed forest stands occur) as spring advances.

Frey and Schaffner (2004) examined abundance on three temporal scales (spanning 1, 4 and 20 years) for western overwintering sites, using data from the California Department of Fish and Game Natural Diversity Data Base and The Monarch Program Thanksgiving Count (Marriott 2001). During the period 1997 through 2000, from 101 to 141 known sites were surveyed. Numbers of monarchs per site ranged from 0 to 120,000, with large year to year and site to site variation (Frey and Schaffner 2004). Sites near the coast that contained eucalyptus, pine and cypress tended to have more monarchs. Leong et al. (2004) found that higher monarch abundance in central California was associated with high ambient moisture, substantial morning dew and moderate winter temperatures. GIS analyses showed that most winter groves occurred within 2.4 km of the coastline, on slopes with a south to west orientation. Larger winter sites were associated with the lower slope of valleys, bays and coastal inlets.Frey and Schaffner (2004) placed their findings in a continent-wide context by making comparisons between recent population trends in the western and eastern North American populations. While the eastern population is larger than the western by at least two orders of magnitude (Brower 1985), it appears that both populations fluctuate from year to year by about half an order of magnitude. However, because no correlation between abundance in the two populations was found, their patterns may be caused by different factors.

Both Frey and Schaffner (2004) and Leong et al. (2004) advocate the use of these and similar analyses in evaluating land management practices and structuring conservation goals. Leong et al. argue that preservation of the monarch winter aggregations in California will depend on active and long-term habitat management that focuses on enhancement activities, such as tree planting, trimming and, in some cases, removal.

Winter mortality: Monarchs in the overwintering congregations in Mexico and California face numerous threats. Forest degradation and resultant changes in climatic conditions, predation by birds and mice, starvation, desiccation and freezing represent significant sources of mortality. Although monarchs are protected from vertebrate predators by the cardenolides sequestered from the milkweed they consume as larvae, any concentration of potential prey this large is likely to result in predators that evolve to overcome their defenses. Bird predation is an important cause of winter mortality, with mortality rates ranging from 1% to 18% across several colonies studied by Garcia-Serrano et al. (2004) and from 7% to 44% in colonies studied by Brower and Calvert (1985). The two main bird predators are the black-headed grosbeak (Pheucticus melanocephalus) and the black-backed oriole (Icterus abeillei). The grosbeaks consume the entire fat-rich abdomens of the monarchs, somehow tolerating the cardenolide toxins stored below the exoskeleton. The orioles slit open the abdomen with their sharp beak and scoop the contents of the abdomen and thorax out with their tongue, thus avoiding the toxins. These different prey consumption methods make it easy to distinguish which species is responsible for the deaths of monarchs found on the forest floor. At least five species of mice, the most conspicuous of which is Peromyscus melanotis, feed on butterflies that have fallen to the ground.

Extreme weather conditions, such as those caused by winter rains and snowstorms, can also kill overwintering monarchs. For example, the intense cold that followed a prolonged period of cloudy, wet weather early in 1992 may have killed up to 80% of monarchs in several overwintering colonies (Brower et al. 2004). Systematic documentation of mortality that followed another severe storm in January 2002 is reported by Brower et al. (2004). They estimated 75-80% mortality at two overwintering colonies, and suggest that similar rates occurred throughout the Mexico sites. Their estimates of the number of monarchs killed per hectare (26-72 million) far exceeded previous estimates of the number of monarchs occupying these sites, but agree with estimates presented by Calvert (2004b) for the same time of year.Oberhauser and Peterson (2003) used ecological niche modeling to delineate the environmental conditions that favor survival, and found that occupied sites exhibited cool temperatures and low precipitation during the wintering months. Unfortunately, global climate change models predict more precipitation in these areas over the next decades, suggesting that those kinds of winter storms may become more frequent.

While there is no documentation of the effects of extremely dry years on monarch survival, the fact that individuals are often observed imbibing water that collects as dew on plants or from streams or wet ground suggests that a lack of moisture would increase mortality. Likewise, little is known about factors that increase the risks of starving. Monarchs eat little during the overwintering period, so it is likely that starvation would be more likely under conditions that promote increased metabolism, such as warm ambient air temperatures, or when monarchs do not obtain enough food as larvae.

Forest dynamics and conservation of overwintering sites: The Mexican overwintering sites first achieved protected status under a 1986 presidential decree. While this was an important first step, the decree did not protect all important overwintering sites, failed to compensate local landowners for imposed restrictions on land use and offered no effective economic alternatives to previous means of subsistence (such as agriculture and logging). A consortium of geographers, monarch biologists and Mexican government officials conducted a geographic information system (GIS) analysis of deforestation that occurred between 1971 and 1999. This analysis revealed that 44% of the high quality forest present in 1971 had been degraded and fragmented, resulting in lower quality forest for overwintering monarchs (Brower et al. 2002). The rate of deforestation had accelerated over this period.

In 1998, an international group of scientists and policy makers joined to redefine the protected area and address some of the concerns with the original decree. Missrie (2004)described the 4-year process that led to a new presidential decree and improved protection of the overwintering sites. The boundaries of the expanded Reserve were determined using models based on current knowledge of the biological requirements of monarchs during the winter. As a result of the new decree, the total amount of land that was protected increased from 16,110 ha (4491 and 11,619 in the core and buffer zones, respectively) to 56,259 ha (13,552 and 42,707 ha in the core and buffer zones respectively). The new reserve protects a contiguous area of land, instead of the separate "islands" of land that were protected by the old decree (Missrie 2004). However, as is the case with all conservation laws, effectiveness requires enforcement of the law, and logging and forest degradation are still occurring.

Keiman and Franco (2004) studied the response of the Mexican oyamel fir forests to disturbance. Their finding that trees within forest patches tend to be similar in size, and that homogeneity tends to increase with stand age, along with the fact that monarchs typically form colonies in mature forests, suggests that it will be important to ensure replacement as forest patches age.

Spring Migration:

Monarch butterflies begin to leave their Mexican wintering sites in mid-March, and have usually all departed by the end of March. At this point, many of them have already mated, but both sexes leave the sites and migrate north and mating continues throughout the journey north.Malcolm et al. (1993) and Cockrell et al (1993)reported the dates of first sightings of eggs, larvae and the larval host plants of adult monarchs arriving at different latitudes in eastern North America. These papers established the general pattern of spring movement and demonstrated that recolonization of the northern ranges of the breeding habitat occurs over two generations. The monarchs that overwinter in Mexico fly north to repopulate the southern half of the US, and their offspring complete the journey to the northern US and southern Canada. This second generation recolonizes the entire northern breeding range, utilizing more northern milkweed species (Fig. A.22). Monarchs may have subsequent third and fourth generations within the same year.

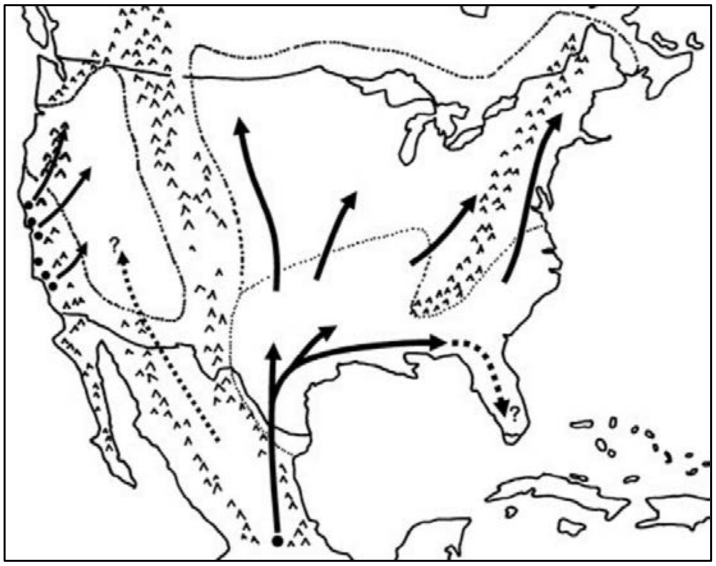


Fig. A.22: Monarch spring migration. The first part of the spring migration is made by the same adults that flew south in the fall, but these migrants do not recolonize the entire summer breeding range. It is their offspring, laid as eggs in late March and April, that complete the spring journey north (drawing courtesy of Sonia Altizer and Michelle Solensky).

Spring migratory routes are considerably more difficult to identify and study than fall routes because in the spring monarchs are dispersed and consequently less noticeable than the fall migrants which form spectacular roosts. We are still learning a great deal about this portion of the monarchs' annual cycle from individuals that report their monarch observations as part of Citizen Science programs, such as Journey North (Howard and Davis 2004). This program involves school children and other interested individuals from every US state and seven Canadian provinces, who report their first sightings of monarch butterflies every spring. Through these reports, we can learn about when and where monarchs travel as they migrate north in the spring.

Howard and Davis (2004) described the patterns of spring migration and monarch abundance based on data collected by Journey North participants over a 6-year period from 1997 to 2002. They found a striking regularity of the migratory pattern from year to year, although the average arrival date at different latitudes and the duration of migration varied between years. They suggest that this annual variation may stem from differences in environmental conditions or timing of milkweed emergence, and are continuing to investigate these factors using additional data collected by Journey North participants.

Threats to Monarchs

Breeding habitat loss (Monarch Joint Venture, 2015a)**:** Immature monarch butterflies (caterpillars) only eat milkweed (*Asclepias* spp.). Thus, in order to successfully reproduce, female monarchs must locate and lay eggs on milkweed plants. The Midwestern US (also called the Corn Belt) used to be an important source of milkweed habitat for monarchs. Milkweed used to grow abundantly in agriculture fields and surrounding areas, but the growing farming industry and development of Round-Up ready crops have devastated milkweed abundance in much of this landscape. Round-Up ready crops are genetically modified to be resistant to the herbicide glyphosate. Planting Round-Up ready crops enables farmers to control weeds by spraying glyphosate, which kills weeds but not the crops. Prior to the incorporation of Round-Up ready corn and soybeans, and thus, post-emergence applications of glyphosate, plowing was the main means for ridding fields of weeds. This allowed some persistence of milkweed habitat within agricultural fields and surrounding areas, whereas the shift to increased glyphosate use totally eradicates milkweed from the field and spray drift can have harmful effects on areas surrounding agriculture fields.

Additionally, corn that is genetically modified to contain a toxin from the bacterium *Bacillus thuringiensis* may have a harmful effect on monarchs if exposed to it. This “Bt-corn” is toxic to the European corn borer, but also to other Lepidoptera. Pollen and anthers from Bt-corn can be harmful to monarch larvae if ingested, but it is thought that since milkweed is essentially gone from agricultural areas, exposure to this pollen is low and thus, the effect on monarchs is negligible.

In the past few decades, there has been an increase in the amount of agricultural land conversion in the Corn Belt, due to an increasing demand for corn and advancing agricultural technology, allowing farmers to efficiently manage more acres. Research by scientists from the Universities of Iowa and Minnesota in 2012 showed a direct correlation between declining monarch numbers and increasing adoption of herbicide tolerant soybeans and corn. With the loss of agricultural habitat, it is key that we ensure that milkweed and monarch nectar plants are available in other areas (Fig A.23).

Fig. A.23: With the advent of glyphosate, milkweed has been eliminated from most agricultural fields, increasing the importance of milkweed and nectar plants in other habitats (photo courtesy of Karen Oberhauser.

The loss of milkweed in agricultural fields is a major cause of decline in monarchs, though there are other factors contributing to the decline in milkweed availability. Herbicide application and increased mowing in roadside ditches and agricultural margins is eradicating milkweed habitat even more from rural areas. If managed appropriately, roadsides could provide millions of acres of habitat suitable for monarchs and other pollinators. These areas are often mowed or sprayed regularly throughout the growing season to control weedy species, but if transformed into a native plant community, they could require significantly less maintenance once established while providing important habitat. If mowing is used to manage weedy species or invasives, it is best to do it during times when monarchs will be least affected by the disturbance. In addition, leaving sections of the habitat untouched will allow pollinators and other wildlife to find refuge in those areas while the disturbed portion of the site recovers.

Urban sprawl and continuing industrial development are also major factors influencing the decline in quality monarch habitat. Other anthropogenic factors, such as ozone pollution or increased carbon dioxide levels, can affect the health and distribution of milkweed plants.

Overwintering habitat loss (Monarch Joint Venture, 2015d): Eastern North American monarchs travel to the same locations in Mexico each year to spend the winter. These overwintering sites are being threatened by forest degradation due to legal and illegal logging, land conversion for farming, and climate change that may negatively affect oyamel fir stands. The degradation of these sites can have very harmful effects on overwintering monarch populations. The oyamel fir stands serve as both a blanket and umbrella during the winter, protecting monarchs from extreme cold temperatures and precipitation. The encroachment of logging near overwintering sites and forest degradation from other causes can alter the microclimate there which may increase monarch mortality.

While many government policies promote sustainable forest management and ban most logging in the areas in which monarchs overwinter in Mexico, these regulations and incentives have not been 100% effective. While illegal logging accounts for much of the forest loss in the Monarch Butterfly Biosphere Reserve, a smaller number of trees are still removed by authorized extraction or by individuals cutting down trees for firewood or building houses.

Subsistence-farming activities may also impact oyamel fir forests and the monarchs that overwinter there. With the diversion of water for human use, monarchs may be forced to travel further in search of water, which may deplete their lipid reserves more quickly. Oyamel fir stands may also be threatened by the impending effects of climate change. Recent climate change models suggest that these forests may be exposed higher stress from heat and drought which may cause them to be more vulnerable to insects and disease. Some level of forest and overwintering habitat degradation may also be caused by unregulated tourism in the monarch overwintering areas.

Monarchs of western North America migrate to many locations along the Pacific coast of California, though some monarchs tagged in western states have been recovered in Mexico, suggesting there is some interchange between eastern and western populations. Overwintering populations in California have been estimated annually for over 15 years by citizen scientist volunteers through the Western Monarch Thanksgiving Count. These data, along with other historic overwintering site evaluations, were pooled by the Xerces Society for Invertebrate Conservation into a comprehensive database of current and historic western monarch overwintering locations. While not all of these sites are monitored each year, and year-to-year population fluctuation may be the result of drought or other climate conditions, the long-term trend of the western monarch overwintering population is downward.

The cause of this downward trend in the western population is not fully understood, but habitat loss in overwintering locations is a major issue of concern. Municipal and commercial development in these areas is conceivably the most damaging to western overwintering habitat. Numerous known overwintering locations have been lost as a result of new housing developments or expansions. While increasing awareness of monarchs and their decline can help to boost conservation efforts, increasing tourism inspired by monarchs can drive an increase in development and pollution near overwintering sites, which can have harmful effects on overwintering clusters.

Western overwintering sites have a similar microclimate to that of sites in Mexico, though they generally contain some combination of exotic eucalyptus, Monterey cypress, Monterey pine, and western sycamore trees, rather than oyamel firs. Monarchs do cluster in the non-native eucalyptus trees, but this is perhaps because they are the primary species available in the area. Research suggests that it may not actually be a preferred species used by overwintering monarchs in California. Land management to restore these sites is difficult because native trees are generally much more slow-growing than the non-native eucalyptus. Long-term management plans need to be in place to restore these sites back to their native state to ensure the future and abundance of quality western overwintering habitat.

Climate change (Monarch Joint Venture, 2015b): Predicting species' responses to climate change is especially challenging for migratory species, like monarchs, because they could respond to climate change in two fundamentally different ways. First, because they depend on diverse resources across a vast landscape, and because the timing of migration is driven by environmental cues, migratory species could be especially vulnerable to environmental changes. On the other hand, their propensity to move could buffer them against shifting resources, with the outcome being little net change to their population sizes and distributions. Monarchs' response to climate change will also be driven by how milkweed responds; even if temperatures allow monarch survival, if conditions cause their milkweed host plants to go dormant, become too dry, or die altogether, monarchs will need to move to other areas.

Climate change models suggest that monarchs will need to move northward from their current range in June and July, and then return southward in August to track the conditions they currently use for reproduction. Currently, only the spring generation appears to move northward before laying eggs, so this would represent a change from their current migratory pattern. Climate models also predict that the overwintering grounds in Mexico may soon no longer be suitable for monarchs, indicating that the eastern North American monarch population may require different overwintering habitat. Whether monarchs can successfully overwinter in other areas depends in part upon their being able to survive the colder temperatures and different habitats present in areas such as the southern U.S.

To minimize the impacts of climate change, it is important to maintain corridors of suitable monarch and milkweed habitat, and ensure that other pressures on their populations are minimized.

Pesticides (Monarch Joint Venture, 2015e): Most insecticides (and all other pesticides, including herbicides, fungicides and nematocides) are used in agricultural applications. The widespread loss of milkweed in agricultural fields reduces the risk of immature monarchs (eggs, larvae, pupae) being killed by agricultural insecticide applications, simply because without milkweed, these stages no longer occur in high numbers within these fields. Adult monarchs traveling across agricultural fields in search of milkweed or nectar during times of insecticide application are at higher risk, however. Insecticide use in agriculture is a concern for other pollinators that forage for pollen and nectar in agricultural landscapes. Additionally, insecticide drift into ditches and field borders can affect monarchs. Insecticide use by commercial and government entities (to control herbivores and pests like mosquitoes and black flies), as well as in yards and gardens, often kills monarchs.

One group of insecticides that is raising concern is neonicotinoids, which are used on farms and around homes, schools, and city landscapes. While harm to humans and other mammals is minimal, these insecticides are extremely toxic to arthropods. They are systemic, meaning that when they are applied, plants absorb and distribute the compounds to all parts of the plant, making the leaves, nectar, pollen, and woody tissue toxic to insects and other arthropods that feed on them. A variety of application methods make neonicotinoids popular for use in pest control. Crop seeds can be treated before being planted, allowing uptake by the plant during growth, and thus protection from plant pests for a period of time while the chemical remains in the plant tissues. Neonicotinoids can also be applied topically on plant foliage or as drenches to the ground.

Pollinators and other insects exposed to neonicotinoids* while foraging face lethal or sublethal effects. As treated crop seeds are planted, particles of neonicotinoid compounds are often carried with dust and settle onto nearby vegetation; this can cause direct mortality in bees. Additionally, pollinators can be directly exposed to these chemicals if they are foraging at the time when crops, garden plants, or natural areas are being sprayed with insecticide. Further concern with neonicotinoids arises because they persist in the soil and plants much longer than other compounds, making them dangerous to pollinators for a longer period of time after the initial application. Because they are systemic, nectar and pollen gathered from treated plants are contaminated. While this may not be a lethal dose for bees, sublethal effects such as decreased ability to locate food sources or their hive may impact the productivity of the colony. Compounds that are not absorbed by the plants remain in the soil for extended periods of time, and often leach into the groundwater or run-off into natural water bodies.

Neonicotinoid and other insecticides, like organophosphates, carbamates, and inseciticidal soaps that are often used in plant nurseries can have a negative impact on pollinators. High plant density and a controlled temperature environment can foster insect pests that damage the plants being grown in a greenhouse or nursery. For this reason, nurseries (even those growing plants specifically for native plant gardens with the purpose of attracting and benefiting pollinators!) often resort to the use of insecticides to control unwanted insect pests. Because some insecticides persist in the plant tissues for months after the initial application in the greenhouse, nursery plants that have been treated with systemic insecticides pose an ongoing risk to pollinators. It is important to determine if plants have been treated before purchasing and planting them.

In urban and suburban areas, adult and larval mosquito populations are controlled vigorously and repetitively. Some species of milkweed grow in areas likely to be treated for mosquitoes, thus increasing the risk of monarch exposure to these chemicals. The University of Minnesota conducted research on how monarch larvae and adults were affected by exposure to insecticides commonly used in mosquito control (resmethrin and permethrin). These pyrethroids can be sprayed as ultra-low volume treatments or as barrier treatments. Ultra-low volume treatments are intended to affect insects as they are flying, whereas the barrier treatments remain on leaves, providing a barrier to mosquitoes that may not be out foraging during the day. Both the ultra-low resmethrin study and the barrier permethrin study showed negative impacts on monarch larvae and adults. Leaves from the barrier treatments resulted in higher mortality to monarch larvae than control leaves up to 3 weeks after the initial application. These insecticides do have harmful effects on monarchs if exposed, but population-level impacts will depend on the proportion of host plants treated in a given landscape or how much of the monarch population is directly exposed.

Natural Enemies (Monarch Joint Venture, 2015c): Monarchs become toxic to predators by sequestering toxins from the milkweed they ingest as larvae, and are brightly colored in both the larval and adult stages to warn predators of this toxicity. Despite the fact that milkweeds are assumed to convey some degree of protection from generalist predators and parasitoids, monarchs of all life stages are vulnerable to predation and disease.

Monarch eggs and small larvae face considerable dangers of predation, and only about 5% of monarchs reach the last larval instar. Ants, spiders, true bugs, beetles, and lacewing larvae are some known predators of monarch eggs and larvae. In a laboratory experiment, one lacewing larva was observed consuming 40 monarch eggs. Chinese mantids and paper wasps have also been observed preying on immature monarchs. Adults face less danger of being eaten by predators during the breeding season, but there is a much greater risk of being eaten by bird predators in overwintering locations. In Mexico, the black-headed grosbeak, black-backed oriole, and Scott's oriole are responsible for much of the predation of overwintering monarchs, with some additional predation by mice. In California, Rufous-sided towhees consume adult monarchs in overwintering clusters.

Parasitoids develop by feeding in or on a host organism, causing its eventual death. Monarch parasitoids are reported to include 12 species of tachinid flies and at least one braconid wasp. The best-studied monarch parasitoid is the tachnid fly *Lespesia archippivora*, which attacks larvae, resulting in the death of late-instar larvae or pupae. Some sites where tachinid fly parasitism has been studied have found parasitism rates of up to 90%, but the average rate is between 10 and 20% in the wild. Recent studies have documented a pupal parasitoid of monarchs,*Pteromalus cassotis.* These tiny wasps lay eggs inside a monarch chrysalis, which emerge as adult wasps from the monarch pupa casing a few weeks later. More research is needed to understand *P. cassotis* and the effects this species has on monarch populations. Parasitoids, such as those mentioned here, are often introduced as biological control agents to rid an area of unwanted pests. Bio-control agents often have harmful non-target effects on beneficial species, like monarchs or other pollinators.

Monarch larvae are generally found singly on milkweed plants, unlike the large aggregations of adults in overwintering clusters. Lower larval density in milkweed patches reduces the chance of diseases, such as nuclear polyhedrosis virus and *Pseudomonas* bacteria, spreading between larvae. These diseases are often fatal to monarchs.

Perhaps the most-studied parasite of monarchs is a protozoan parasite called *Ophryocystis elektroschirra* (Oe). This parasite cannot be transferred between larvae or adults simply by contact. To become infected, a larva must ingest dormant Oe spores that fall from the abdomen of an infected adult to the surface of milkweed leaves (Fig. A.23). While it is often not fatal, OE can have negative effects on survival, mass, and life span of monarchs. There is a higher occurrence of this parasite in populations that do not migrate, such as the one in southern Florida. The eastern migratory population has the lowest occurrence of Oe, likely due to the fact that infected monarchs are less likely to make it to their overwintering destinations in Mexico and therefore will not reproduce and spread the parasite. Recent studies about Oe and exotic milkweed describe how the year-round presence of tropical milkweed in some parts of the US may be facilitating the spread of this parasite. To learn more about Oe, visit monarchparasites.org (Project Monarch Health, 2015).

Fig. A.23: Oe spores (small brown football-shaped ovals) next to monarch scales (much larger irregularly-shaped ovals).

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