Overview of Monarch Breeding Biology

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Many people are attracted to the biology of monarchs by their spectacular migration and the unequaled phenomenon of millions of butterflies blanketing a few hectares of land in central Mexico. However, every adult that carries out this migration and joins millions of conspecifics in Mexico or thousands in California began its life as an egg on a milkweed plant and faced a myriad of environmental challenges as it developed. In addition, most generations of monarchs do not undergo the long-distance migrations to and from the overwintering sites. Preadult stages and the adult behaviors that produce them provide the subjects of this section: mating, egg laying, and the many challenges faced by eggs and larvae as they develop into adults.

EGGS AND LARVAE

Monarchs lay their eggs on milkweed plants; hence monarch biology is tied closely to milkweed biology. They utilize most of the over 100 North American species (Woodson 1954) in the milkweed family (Asclepiadaceae), the only group of plants that provide food for developing larvae. By laying eggs on the only plants their offspring can eat, females ensure that the larvae will have a ready supply of food on hatching.

Monarchs breed over a broad geographic and temporal range, and their numbers vary a great deal in space and time. Documenting variation in monarch egg and larva abundance is the topic of a citizen science effort reported in chapter 2 by Prysby and Oberhauser. In this project, volunteers throughout the breeding range have measured monarch densities for the past 6 years. Because densities of eggs and larvae are so much easier to quantify than those of the adults, researchers can use comparable methods in many areas to produce data that allow spatial and temporal comparisons.

It is difficult to tell just how many eggs each female butterfly lays during her life, but the average in the wild is probably 300 to 400. Captive monarch butterflies average about 700 eggs/female over 2 to 5 weeks of egg laying, with a record of 1179 eggs (Oberhauser 1997). 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, with individuals in warmer environments developing more rapidly (Zalucki 1982).

Females have a limited amount of resources to allocate to egg production, and the proteins that are an important constituent of eggs must be either 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 1/1000th the mass of an adult, females often lay more than their own mass in eggs throughout their lives. With this large an investment, there is likely to be a trade-off between the egg number and egg size. Oberhauser explores factors that affect monarch egg size in chapter 3. She found that larger females lay larger eggs, and that egg size decreases with female age.

Monarchs complete almost all of their growth during the larval stage. These insect “eating machines” take few breaks even to rest. They typi-
cally begin life by eating their eggshell, then move on to the milkweed leaves on which they were laid. The larval stage lasts from 9 to 14 days under normal summer temperatures. Larvae molt (shed their skin) as they grow, and the stages between larval molts are called instars. All monarchs go through five separate larval instars. From hatching to pupation, they increase their body mass about 2000 times (pers. observ.).

Monarch eggs and larvae have a slim chance of reaching adulthood; several previous studies documented mortality rates of over 90% during the egg and larval stages (Borkin 1982; Zalucki and Kitching 1982; Oberhauser et al. 2001). In chapter 2, Prysby and Oberhauser present additional data collected by citizen scientist volunteers on survival rates of eggs and larvae.

There are both abiotic and biotic sources of monarch mortality during the breeding season. Abiotic (nonliving) factors include environmental conditions such as adverse weather and pesticides. Biotic (living) factors that affect the survival of monarchs include natural enemies, and interactions with their milkweed hosts. Many monarchs in natural populations are killed by invertebrate predators that eat the monarchs themselves, or by parasitoids whose larvae develop in and eventually kill the monarch larvae. Diseases caused by bacteria, viruses, fungi, and other organisms are also significant sources of monarch mortality.

Chapters 4, 5, and 6 by Prysby, Rayor, and Calvert focus on invertebrate predators of monarchs. Prysby describes the overall impacts of natural enemies on monarch survival. In one experiment, she limited the access of predators to monarch eggs and larvae by constructing cages around milkweed plants. She found that excluding both terrestrial and aerial predators increased monarch survival. In another experiment, she found that monarch eggs were less likely to survive on plants on which ants had been observed. Finally, she found that over 14% of the monarchs that survive to late instar larval stages are killed by tachinid fly parasitoids. Rayor and Calvert focused on the effects of a single predator on monarch survival in their studies. Rayor (chapter 5) studied how predation by paper wasps is affected by larval size and the host plant species on which the larvae are feeding. She found that medium-sized larvae are most susceptible to paper wasp predation, and that the wasps generally preferred larvae that consumed milkweed host plants with lower levels of cardenolides. Since paper wasps are abundant throughout the entire monarch breeding range, Rayor concludes that they are likely to be a significant source of mortality. Calvert (chapter 6) used exclosures to study the impact of invasive fire ants on monarchs, and found that monarchs inside exclosures were much more likely to survive than those outside the structures. Despite the large amount of mortality from fire ants, Calvert suggests that pre–fire ant mortality may have been similarly high, since these invasive ants displaced native ants that also preyed on monarchs.

While the mortality described here appears to indicate that monarchs are helpless in the face of an onslaught of predators, monarchs have an effective chemical defense against many predators. They sequester cardenolides (also called cardiac glycosides) present in the milkweed (Brower and Moffit 1974). These compounds are poisonous to most vertebrates; hence monarchs face limited predation from frogs, lizards, mice, birds, and other animals with backbones. The insects described in the previous paragraph, as well as some bacteria and viruses, may be unharmed by the toxins or be able to overcome them. However, Rayor’s 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.

The benefits gained by monarchs from the sequestered cardenolides are not without cost. While cardenolides help monarchs in their defense against predators, these compounds are actually produced by milkweed plants as a chemical defense against herbivores. In addition, the plants produce a sticky substance called latex; this is the source of the name “milkweed.” This substance also provides a mechanical defense against herbivores, whose mandibles may be glued together by the material or whose bodies may become mired in a drop of latex formed when the plant is injured. Several researchers have shown that monarch larvae are negatively affected by these defenses (Zalucki and Brower 1992; Malcolm and Zalucki 1996; Zalucki and Malcolm 1999; Zalucki et al. 2001). In chapter 7, Hoevenaar and Malcolm present a study of how defenses in Asclepias curassavica and A. incarnata milkweed plants affect the behavior of monarch larvae. Surprisingly, there were no differences in the monarch
response to these two species, which vary in cardenolide content and latex volume, and Hoevenaar and Malcolm conclude that monarchs are well-adapted specialists that can handle the defenses in these two species without negative impacts on their performance.

Monarchs require specific abiotic conditions to survive. Eggs do not hatch in very dry conditions. Very hot weather also causes mortality; several studies have shown that temperatures above approximately 35°C (95°F) can be lethal to all stages (Zalucki 1982; Malcolm et al. 1987). 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., this volume). Threats due to very hot or very cold temperatures are magnified during the breeding season, since monarchs are indirectly affected by conditions that affect the health and survival of milkweed. Freezing temperatures and extremely dry conditions can be especially damaging to milkweed, and thus to monarchs.

**PUPAE**

During the pupal stage, the transformation to the adult stage is completed in a process that takes about 9 to 15 days under normal summer temperatures. From the outside, few of these changes are apparent until the final day, when the black, orange, and white wing patterns of the adults are visible through the pupal covering. This results from the development of the scale pigmentation at the very end of the pupal stage. However, most of the physiological and morphological changes that produce an adult monarch actually begin to 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 it pupates, the monarch has already begun the major changes to the adult form. As it forms the pupa, the antennae, proboscis, wings, and legs move to the surface just inside the exoskeleton, and the most notable changes that occur after this involve a major reorganization of the flight muscles in the thorax. Sperm also mature during the pupal stage, although eggs do not mature until after adult eclosion.

The ecology of monarch (or any other lepidopteran) pupae is not well studied, and unfortunately, this book does not add to our knowledge of pupal ecology. This is probably 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 issues remain to be studied: 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.

**ADULTS**

The primary goal during the adult stage is to reproduce—to mate and lay the eggs that will become the next generation. Adults in summer generations live from 2 to 5 weeks, while those that migrate may live up to 9 months. This difference 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 hibernation sites slow their metabolism, allowing them to live longer.

Summer-generation monarchs first mate when they are 3 to 8 days old (Oberhauser and Hampton 1995), and females begin laying eggs immediately after their first mating. Monarchs that overwinter do not lay eggs until spring (although they may mate before this). 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). Since male reproductive success in most animals depends on the number of females with which they are able to copulate (Bateman 1948), determining the factors that affect male mating success is a major focus of many behavioral ecologists. Solensky and Oberhauser (chapter 8) discuss factors that affect the mating success of male monarchs. They found that mating success is a heritable trait; males that mate more often than other males tend to have sons that mate more often. Since males attempt to mate with many more females than they actually successfully copulate with, Solensky and Oberhauser tested whether males that mated more...
often simply tried to mate with more females, or whether they were more likely to be successful during any given mating attempt. They found that the latter was true; something about some males makes their mating attempts more likely to end in success. The characteristics that result in more frequent success remain unidentified.

Since there is a delay between adult emergence and egg laying and because monarch adults 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 understudied area of monarch biology, despite its importance to monarch population dynamics. Important research topics that remain to be addressed include 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.

**HUMAN-INDUCED MORTALITY DURING THE BREEDING SEASON**

Humans often change the environment in ways that may kill monarchs. The most important source of human-caused mortality is loss of habitat, especially the destruction of milkweed and nectar sources. Some people consider milkweed a noxious weed and often destroy it. In addition, herbicides used to kill plants in agricultural fields, near roadsides, and in gardens may harm milkweed and nectar sources and may also kill monarchs directly. Monarchs can also be exposed to insecticides used to control pests in agricultural fields, forests, and gardens. Many people worry that the use of insecticides to combat mosquito-borne diseases like the West Nile virus will kill monarchs and other beneficial insects.

A potential source of monarch mortality that has received a great deal of attention recently is corn genetically modified to contain *Bacillus thuringiensis* (Bt) toxin (Losey et al. 1999; Jesse and Obrycki 2000; Oberhauser et al. 2001; Sears et al. 2001; Brower 2001). This corn produces a protein that is toxic to lepidopteran larvae and effective against the European corn borer, an important agricultural pest. However, the wind-dispersed pollen produced by Bt corn also carries the toxin. The toxicity of the pollen produced by different genetically modified corn varieties varies significantly, and the varieties now on the market have lower levels of toxin than some of the earlier varieties (Hellmich et al. 2001; Sears et al. 2001). If pollen with high levels of Bt is blown onto plants growing in or near cornfields, it could pose a threat to nontarget Lepidoptera that consume these plants. Most researchers who have assessed the risks of this technology isolated corn pollen from other material shed by the plant (particularly the pollen-bearing anthers) (Hellmich et al. 2001; Sears et al. 2001). Jesse and Obrycki (chapter 9) describe what happened when larvae were exposed to Bt corn pollen and anthers naturally deposited on milkweed plants within a cornfield. They found a consistent trend of lower survival in Bt fields than non-Bt fields. While this finding was not statistically significant (there is a 10% chance that their findings could have been due to random variation, versus the 5% generally taken to mean statistical significance), it clearly indicates that there is a good chance that the blanket conclusion that Bt corn poses no risks to monarchs (Sears et al. 2001) should be revisited.

**References**


