The Tachinidae represent the largest family of dipteran parasitoids, with ~10,000 species. Most of their hosts are Lepidoptera, and it is generally assumed that tachinid flies have wide host ranges (i.e., many suitable host species) (Stireman et al. 2006). However, it is likely that tachinid host ranges have been overestimated; in a long-term study of tachinid flies reared from hosts collected in Costa Rica, many species that appeared to be generalists were shown to be host-specific cryptic species (Smith et al. 2007).

Lespesia archippivora (Riley) (Tachinidae) has been reported to parasitize larvae of 25 Lepidoptera species in 14 families, and one species of Hymenoptera (Arnaud 1978). It is widespread throughout North and Central America, has been found in Brazil (Arnaud 1978), and was introduced into Hawaii for biocontrol in 1898 (Etchegaray and Nishida 1975). Except for its occurrence in multi-host species-rearing projects, L. archippivora has only been studied in detail in monarchs (Danaus plexippus L.) and beet armyworms (Spodoptera exigua Huber). It parasitizes monarch larvae in the continental U.S. and Hawaii (Etchegaray and Nishida 1975, Pryby 2004, Oberhauser et al. 2007), with one long-term, broad-scale monitoring project documenting an overall parasitism rate of ~13% (Oberhauser et al. 2007). In the southern U.S., the beet armyworm is reported to be a preferred L. archippivora host (Stapel et al. 1997).

North American monarchs complete multiple generations on their milkweed host plants (Asclepias spp.) within a summer breeding season, and overwinter in central Mexico (eastern migratory population) or coastal California (western migratory population). They remain in their wintering sites in a state of reproductive diapause from early November through mid-March, before returning to their spring breeding grounds. In the east, returning migrants lay eggs in the southeastern U.S. (Texas to Florida and Oklahoma to North Carolina) and their offspring recolonize the summer breeding range (roughly the northeastern quarter of the U.S. and southern Ontario and Quebec), where they undergo two to three non-migratory generations before the final generation returns to Mexico. There is some

Instant Symposium

Tachinid Flies and Monarch Butterflies:
Citizen Scientists Document Parasitism Patterns over Broad Spatial and Temporal Scales

Karen Oberhauser

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fall breeding by southward migrants in the southern U.S., resulting in another generation that presumably migrates to Mexico. Although some monarchs remain throughout the winter in the southern U.S., where at least some of them continue to breed (Prysby & Oberhauser 2004), tagging records and host plant fingerprint studies suggest that the vast majority of northern monarchs that eclose after mid- to late-August migrate to Mexico. The smaller western population undergoes a shorter migration between breeding ranges west of the Rocky Mountains and coastal California.

Immature monarchs have a large suite of invertebrate predators, with approximately 92% mortality during the egg and early larval stages (Prysby 2004 and references therein). Twelve species of tachinid flies, at least one braconid wasp (Arnaud 1978), and a pteromalid wasp (Pteromalus puparum L., personal observation) have been reported in monarchs. However, many of these may represent incidental or very rare parasitism events.


Methods

Volunteer citizen scientists in the MLMP have documented temporal and spatial variation in monarch egg and larval abundances since 1997. Their monitoring sites include gardens, railroad right-of-ways, roadsides, abandoned fields and pastures, natural habitats, and restored prairies (see Prysby and Oberhauser 2004 for details). In this study, I used two types of MLMP data. First, volunteers estimate weekly monarch density per milkweed ramet1 by checking tens to hundreds of ramets and noting the number of monarch eggs and larvae observed. They enter these data into an online data repository. Second, from 1999-2011, a subset of MLMP volunteers have collected thousands of monarch larvae to measure tachinid parasitism rates. Most volunteers collect and rear 4th or 5th instars, but have contributed records from hundreds of monarchs collected as eggs and younger larvae. They rear them in their homes, recording the date, location, and larval stadium at collection, as well as the outcome of each rearing (adult monarch; died of unknown cause; died accidental death; parasitized by fly; parasitized by wasp). A “notes” data field allows volunteers to record additional information that they consider relevant. Most also record the number of parasitoids that emerge from each host. Volunteers only identify parasitoids to order; but all of the flies that we have identified to species (several dozen from throughout the U.S.) have been L. archippivora (Oberhauser et al. 2007).

For the analyses reported here, I omitted data when monarch death was accidental (e.g., dropping the specimen; crushing between the lid and rearing container). I also omitted data from a volunteer who did not understand the data entry protocol and entered data for more than one monarch in a single entry, and another who reared larvae suffered very high rates (47%) of mortality.

To compare rates of tachinid fly parasitism to monarch densities, I calculated regional metrics of immature monarch density collected by MLMP volunteers, using data from the upper midwestern (MN, WI, IA, and MI) and southern (TX, OK, MS, AL, NC, SC, GA, FL) United States. I used egg density (eggs observed/ramets examined) throughout a given region in a given week to represent monarch density during that week. In the upper Midwest, I used the July or August week with peak density to represent annual population size. In the South, I calculated two maxima for each region: one during the spring migration (April through mid-May) and another during the fall migration (September and October). Monarchs are generally absent from this region for most of June–August. I only used data from weeks during which >100 ramets were examined from at least two sites, and did not use data from years in which this criterion was met for fewer than five and six weeks in the spring and fall in the South, respectively. All years of the study had well over 100 observed plants during all July and August weeks in the upper Midwest. These criteria made it more likely that I used true maxima to represent annual monarch densities.

I calculated the marginal rate of parasitism in each larval stadium as:

\[ m_i = 1 - (1 - q_i)^{t_{i-1}/t_i} \]

where \( q_i \) = the apparent mortality from tachinid parasitism of larvae collected during stadium i, and \( t_i = \) the mortality from all combined causes during stadium i (modified from Bellows et al. 1992). This is appropriate because larvae that died from other causes may have been parasitized (in fact, dissections suggest that parasitism often results in host death before the parasitoids mature [personal observations and Ilse Gebhard, personal communication]). Using the marginal rate corrects for the fact that the measured rate of parasitism is likely to underestimate the actual rate.

I estimated the daily risk of parasitism in each stadium (R), correcting for time in each stadium and the relative abundance of each stadium. These calculations assume that both parasitoids and MLMP volunteers encounter monarchs in proportion to their abundance. I estimated relative abundance using MLMP data that met the following criteria: volunteers monitored at least four times during a given year (to eliminate year/site combinations in which volunteers may have missed stages due to monarch phenology); volunteers monitored 10 or more plants per monitoring event (to decrease sampling error); volunteers did not report more larvae than eggs; and volunteers reported at least some eggs (volunteers not meeting following criteria made it more likely that I used true maxima to represent annual monarch densities).

I used the following formula to estimate the relative daily risk of parasitism in each stadium:

\[ R_i = \left[ (m_i - m_{i-1})/t_{i-1} \right] s_i \]

where \( m_i \) is defined above, \( t_i = \) the number of days spent in stadium i and \( s_i = \) survival to stadium i from i=1. Monarchs spend approximately 2 days as 1st–4th instars and 4 days as 5th instars; \( s_i \) is calculated as \( N_i / N_{i-1} \), where \( N_i \) = total number of larvae in stadium i observed by MLMP volunteers.

Results

Data from 130 volunteers who reared 1–996 eggs and larvae over the 13 years of the study (Fig. 1) provided 7,686 usable records. I used all of these records to study rates of parasitism during different stages. To look at annual variation in parasitism rates, I only used data from larvae collected in the fifth (and final) stadium because parasitism rates increase with the age of monarch at collection (see

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1Because many individual Asclepias plants, especially A. syriaca (the most commonly used species in the northeastern quarter of the U.S.), produce multiple ramets from a single plant, or genet, individual milkweed stems, regardless of species, are referred to as ramets throughout this paper.
below). I also limited this analysis to years in which parasitism data from over 10 fifth-instar monarchs were reported in the region of study; this criterion was met every year from 2000-2010 in the upper Midwest (range 87-377, mean = 204) and in eight of these 11 years in the South (range 10-461, mean = 125).

Volunteers collected and reared monarchs in all immature stages (N: egg = 654, L1 = 619, L2 = 417, L3 = 493, L4 = 1458, L5 = 3999, pupa = 46). From one to 12 flies emerged from individual monarchs. Later stages tended to produce more flies per monarch, although this relationship is only statistically significant when comparing 1st–3rd to 4th–5th instars (Fig. 2). Monarchs collected during later stadia were more likely to be parasitized and the daily risk of parasitism was higher during the middle three stadia (Fig. 3).

There is a correlation between tachinid parasitism rates and monarch population densities in the upper Midwest the previous year (Fig. 4; Pearson coefficient = 0.663, N = 11, p = 0.0262). There is no relationship between tachinid parasitism rates and current-year monarch densities in the upper Midwest, nor between parasitism and tachinid flies parasitize monarchs as first or fifth instars, their daily risk of parasitism is lower than in the middle three stadia. Further study could help determine whether these larvae are less likely to be encountered by the flies, or simply less attractive once they're encountered.

In the upper Midwest, high monarch densities one year are followed by high *L. archippivora* parasitism rates in the next year. One explanation for this coupling is that monarchs drive *L. archippivora* numbers. This hypothesis seems contrary to the assumption that *L. archippivora* is a generalist, but could result if *L. archippivora* identified from different hosts are actually host races or cryptic species, or if monarchs are the primary *L. archippivora* host and other host species represent spill-over parasitism. Alternatively, the coupling may not be causal, and could result if multiple *L. archippivora* hosts follow similar cycles, perhaps tracking abiotic conditions. The hypothesis that monarchs are the primary *L. archippivora* host is supported by Janzen and Hallwachs’ (2009) extensive caterpillar-rearing study in Costa Rica, in which all of 27 rearings of *L. archippivora* were from monarchs (out of 292 monarch rearings and 51,425 total rearings).

Monarch migratory patterns in the eastern U.S. result in temporally separated spring and fall generations in the South, and continuous summer generations in the North (Prysby and Oberhauser 2004). Unless the parasitoids undergo summer diapause, they must use alternate hosts during the summer in the southern U.S. Thus, phenological overlap between monarchs and *L. archippivora* may differ throughout the breeding range in ways that could affect *L. ar-
The Lost Ladybug Project:
Citizen Spotting Surpasses Scientist’s Surveys

John Losey, Leslie Allee, and Rebecca Smyth

Coccinellids, known as ladybugs, ladybeetles, or ladybird beetles, are among the most common and easily recognizable invertebrate components of almost every terrestrial ecosystem in the U.S. and Canada (Gordon 1985). Species in this family are so ubiquitous and yet so sensitive to environmental conditions that they have been proposed as indicator species (Iperti 1999). In addition to their ubiquity, the bright coloration and gentle nature of this group make them a favorite wild creature of adults and youth alike. Like honeybees, ladybugs are revered for their industriousness and their important ecological role as well as their beauty.

This respect is well deserved, as ladybugs contribute to the control of many pest insect species (reviewed in Hodek and Honěk 1996). Given their potential to control pest species, many programs have tried to supplement extant populations or introduce new species. Ladybugs have been the subject of many scientific studies, and from these studies we know that ladybug species vary greatly in their ability to suppress pest populations (reviewed in Hodek and Honěk 1996) and their response to changing environmental conditions (Iperti 1999; Bazzocchi et al. 2004). Thus, long-term regional shifts in species composition may have important implications for the functioning of this complex and its response to environmental changes.

Over the past twenty years, several native ladybug species that were once very common have become extremely rare (Harmon et al. 2006). During this same time, several species of ladybugs from

Chippivora specificty. The fact that the correlation between monarch densities and parasitism rates the following year was only found in the upper Midwest supports the hypothesis that the L. archippivora /monarch interaction is more specific in this region, as does the fact that Stireman and Singer (2003) reared L. archippivora from five other hosts in the southwestern U.S.

This research demonstrates the value of detailed and long-term records on host distribution and abundance as well as parasitism rates that have been collected by MLMP volunteers. A study of this magnitude would have been impossible without their contributions.

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