

## AN ABSTRACT OF THE THESIS OF

Jason L. Fuller for the degree of Master of Science in Entomology presented on August 22, 2002.

Title: Assessing the Safety of Weed Biological Control: A Case Study of the Cinnabar Moth *Tyria jacobaeae*

Abstract approved: Redacted for Privacy

✓

The cinnabar moth, *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae), was released in 1959 to control the grassland weed tansy ragwort, *Senecio jacobaea* L. (Asteraceae), despite evidence that caterpillars of this species can feed on native plants within the genera *Senecio* and *Packera*. Previous studies confirmed the moth's ability to develop on the native *Senecio triangularis* Hook., although no systematic study has been conducted to determine the extent of non-target impact on all potential host species. To address the lack of systematic studies we conducted a regional survey to determine the consequences of exposure of non-target plants to cinnabar moth caterpillars. We also conducted a local field experiment to determine the influence of habitat on the patterns of association of the moth and non-target plants.

In the regional survey, we mapped the potential distribution of the cinnabar moth in Oregon to determine the extent of exposure of native *Senecio* and *Packera* species, and systematically sampled exposed species to assess the frequency and severity of feeding on these plants. We found that nine of the 20 native non-target species in Oregon were exposed to the cinnabar moth, three of the 10 native *Senecio* and six of the 10 native *Packera*. Ten of the native species escaped exposure because they occur east of the Cascade Mountain Range where the cinnabar moth does not occur. We found feeding damage on three of the nine exposed species: *Packera cymbalarioides*, *P. pseud aurea*, and *S. triangularis* were attacked at one of three (33%), two of six (33%), and seven of 15 (47%) sites that supported populations of each species, respectively. Within sites, attack frequency

of stems was 33% (of six total stems sampled) for *P. cymbalarioides*, and ranged from 53% to 56% (of 20 to 108 total stems sampled) for *P. pseud aurea* and 7% to 64.5% (of 32 to 458 total stems sampled) for *S. triangularis*. Conditional median damage per site (median of attacked stems only) was 10% in *P. cymbalarioides*, 5% to 17.5% in *P. pseud aurea*, and 5% to 37.5% in *S. triangularis*. The attack rate on non-target plants (7.1 to 64.5 percent of stems attacked at a single site) was equal to or greater than on the target weed (8.3 to 50.0 percent of stems attacked at a single site). At three sites, caterpillars attacked non-target plants but the target weed was absent, and at one site, the target was present but caterpillars fed on non-target plants only. We conclude that attack frequency and severity on the three species is not high, but equaled or exceeded the level of attack on the target weed.

We also conducted a mark-release-recapture experiment to relate habitat preference to patterns of non-target host use in the field. We compared adult moth dispersal patterns and larval development between a meadow habitat and a forest habitat. We found that long-term dispersal distance (spanning days) was similar in both habitats but we recaptured a higher percentage of moths from the meadow (47%) compared to the forest (10%). Short-term displacements, based on direct observations of flights immediately after release, differed between habitats: moths in the meadow flew short distances ( $8.5 \text{ m} \pm 1.5$ ,  $n = 13$ ) at or below the herbaceous canopy ( $0.8 \text{ m} \pm 0.2$ ,  $n = 13$ ) while moths in the forest flew longer horizontal ( $22.8 \text{ m} \pm 2.8$ ,  $n = 15$ ) and vertical distances ( $5.9 \text{ m} \pm 0.9$ ,  $n = 15$ ). We recovered seven fifth instar larvae (of 278 eggs) from the meadow habitat but no larvae beyond the second instar (of 119 eggs) were recovered from the forest habitat. We conclude that the cinnabar moth is limited to meadow habitats because adult moths display movement patterns that remove them from forest habitats (possibly due to disorientation) and larvae are unable to survive on plants growing in the forest.

Taken together, the regional survey and the local field-experiment indicate that the cinnabar moth uses only a small proportion of available non-target host plant species. Other species are likely unused because of geographic isolation from

the moth, habitat selection by the moth, or phenological differences between the moth and non-target plants.

©Copyright by Jason L. Fuller  
August 22, 2002  
All Rights Reserved

Assessing the Safety of Weed Biological Control: A Case Study of the Cinnabar  
Moth *Tyria jacobaeae*

by  
Jason L. Fuller

A THESIS

submitted to

Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Master of Science

Presented August 22, 2002  
Commencement June 2003

Master of Science thesis of Jason L. Fuller presented on August 22, 2002.

APPROVED:

Redacted for Privacy

Major professor, representing Entomology

Redacted for Privacy

Chair of the Department of Entomology

Redacted for Privacy

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Redacted for privacy

Jason L. Fuller, Author

## ACKNOWLEDGMENTS

I would like to express my appreciation to Peter McEvoy for his assistance in designing and implementing these studies and for his tireless editorial comments on this thesis. I am grateful to Eric Coombs for his assistance in the field, his availability as a sounding board to air new ideas, and his enthusiasm and comedy. I am grateful to Marjo Schat and Shon Schooler for helping me keep my graduate experience in perspective and offering diversions and laughs in the office. I also thank Nicolle Rager for her support and encouragement throughout this process.

This research was supported in part by two Field Research Grants from NPSO and a Graduate Student Research Grant from the Mazamas.

## CONTRIBUTION OF AUTHORS

Eric M. Coombs provided released data for the cinnabar moth from Oregon Department of Agriculture records and assisted in the entry and interpretation of these data. He also assisted in locating sample sites for the regional survey in Chapter 2.



## TABLE OF CONTENTS

	<u>Page</u>
Chapter 1 .....	1
Chapter 2 - Assessing the Safety of Weed Biological Control: Distribution of the Cinnabar Moth <i>Tyria jacobaeae</i> on Non-target, Native Plant Species in Oregon.	3
Abstract .....	4
Introduction .....	6
Methods .....	12
Results .....	16
Discussion .....	30
Chapter 3 - Assessing the Safety of Weed Biological Control: An Experimental Study on Habitat Selection by the Cinnabar Moth <i>Tyria jacobaeae</i> .	38
Abstract .....	39
Introduction .....	41
Methods .....	42
Results .....	46
Discussion .....	53
Chapter 4 .....	58
Bibliography	60

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
2.1    Locations of <i>Senecio</i> and <i>Packera</i> species, based on OSU Herbarium and Atlas records, grouped as growing west of the Cascade Crest (top), east of the Cascade Crest including the Siskiyou Mountains (middle), and growing across the state (bottom).	17
2.2    Distribution of <i>Senecio jacobaea</i> in Oregon based on ODA biocontrol release records, ODA survey locations, and OSU Herbarium records.	18
2.3    Potential current distribution of the cinnabar moth assessed from release records (grey area), and aggregate distribution of 6 native <i>Packera</i> and 3 native <i>Senecio</i> species assessed from herbarium records (black points).	19
2.4    Twenty-three sites sampled to assess attack frequency and intensity of cinnabar moth feeding on native <i>Senecio</i> and <i>Packera</i> . Numbers correspond to sites in Table 2.2. Insert contains magnification of area near Mount Hood.	22
2.5    Distribution of damage for the target weed and non-target native plants at 10 out of 23 host-bearing sites where attack occurred. Sites listed in bold were determined to be exposed by the potential current distribution of the cinnabar moth. White columns represent stems with no damage and dark columns represent number of stems within each damage level category. Numbers above columns represent number of stems in each category. Median = conditional median percent damage of attacked stems only.	25
2.6    Number of sites sampled for <i>S. jacobaea</i> and 7 native <i>Senecio</i> and <i>Packera</i> species in Oregon, and number of sites attacked (black bars) and not attacked (white bars) by the cinnabar moth. Percentage of sites attacked written above each bar.	26

## LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
2.7 Stem density of <i>S. jacobaea</i> and seven native <i>Senecio</i> and <i>Packera</i> species at sites where no attack by the cinnabar moth was found (open diamonds) and where attack by the cinnabar moth was found (closed squares).	29
2.8 Relationship between longitude and both elevation (top) and precipitation (bottom) for sites sampled to assess impact of the cinnabar moth on native plants. Fifth-order polynomial used to create trend line (Excel XP, Microsoft).	31
2.9 Proportion of plants flowering by week for <i>S. jacobaea</i> (data from Mary's Peak, OR) and 7 native <i>Senecio</i> and <i>Packera</i> species (data from OSU Herbarium records), and moth development (vertical lines, from observations on Mary's Peak). N = number of herbarium specimens used to construct flowering distribution.	32
2.10 Relative size of 7 native <i>Senecio</i> and <i>Packera</i> species exposed to the cinnabar moth, and two introduced plants <i>S. jacobaea</i> and <i>S. vulgaris</i> . Species attacked are labeled in bold.	33
3.1 Mary's Peak, Oregon. Light polygons represent habitat areas into which cinnabar moth adults were released.	43
3.2 Adult cinnabar moth long-term displacements (black lines = displacements, black points = release locations) in forest (A) and meadow (B) habitats. Outlines are habitat areas sampled.	47
3.3 Distribution of long-term cinnabar moth displacements in forest and meadow habitats on Mary's Peak, OR. Mean displacement (= 9.55 m/day) was not different for the two habitats (Two-sample t-test, $T = 0.44$ , $P = 0.66$ ). All displacements were calculated as distance traveled per day.	48

## LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
3.4 Distribution of vertical (top) and horizontal (bottom) distances traveled immediately after release for adult cinnabar moths classified as mobile in two habitats on Mary's Peak, OR.	50
3.5 Temperature profile for meadow and forest habitats at the time of the adult mark-release-recapture experiment. The black line represents the forest habitat and the gray line represents the meadow habitat. Temperature each day was based on the mean of maximum, minimum, and current (at the time of sampling) temperatures. Error bars represent standard error of the mean temperature each day.	52
3.6 Survival of adult cinnabar moths caged within forest and meadow habitats on Mary's Peak, OR. Each column represents one cage, filled columns representing the forest habitat and open columns the meadow habitat.	52

## LIST OF TABLES

<u>Figure</u>	<u>Page</u>
2.1 Native <i>Senecio</i> and <i>Packera</i> taxa in Oregon. Taxa listed in bold are exposed to the cinnabar moth.	20
2.2 Locations of sites sampled to assess non-target impact of the cinnabar moth on native plants. Numbers refer to locations on Fig. 2.4.	23
2.3 Sites sampled, native species found, frequency of attack, conditional median percent damage, stem density, and habitat sampled for all 23 sites visited to assess frequency and severity of attack on native plants. Locations in bold are areas where cinnabar moth feeding occurred. Sites that occurred within the potential current distribution of the cinnabar moth are listed as exposed.	24
2.4 Site by species matrix of attack by the cinnabar moth on native plants. Columns are frequency of stems attacked at a site and conditional median percent damage on attacked stems. Sites listed in bold are located within the potential current distribution of the cinnabar moth.	27
2.5 The influence of stem density, precipitation, and elevation on the conditional median percent damage of attacked plants.	29
3.1 Mean vertical and horizontal distance traveled immediately after release for adult cinnabar moths classified as mobile in two habitats on Mary's Peak, OR.	50
3.2 Number of marked cinnabar moths classified according to recapture, habitat, post-release behavior, wing condition, and gender.	51
3.3 Influence of gender, wing condition, post-release behavior and habitat on the odds of recapture for individual moths.	51

## LIST OF TABLES (Continued)

<u>Figure</u>		<u>Page</u>
3.4	Survival of cinnabar moth caterpillars on Mary's Peak, OR. Columns represent numbers of each stage observed on sample dates in two habitats.	54

# Assessing the Safety of Weed Biological Control: A Case Study of the Cinnabar Moth *Tyria jacobaeae*

## CHAPTER 1

We evaluated the interaction between the cinnabar moth *Tyria jacobaeae* and native, non-target species in the genera *Senecio* and *Packera* in Oregon. The cinnabar moth provides us with an ideal case study of the risk posed to non-target plants by a biological control insect for several reasons. First, the moth is well studied and its distribution in Oregon is well known, enabling us to estimate the probability of encounter and determine the consequences of encounter in the field. Second, the moth has had many opportunities to interact with non-target plants because of its wide geographic distribution, the large numbers of potential non-target hosts, and the amount of time that has transpired since first release in 1959. Third, this system is representative of a class of cases in which the host range estimated in the lab appears to be much broader than the host range reported in the field. By combining observational and experimental studies, we assessed the exposure and consequences of exposure of non-target plants to the cinnabar moth, and we examined how habitat influences this interaction.

In the first part of our study, we determined which non-target species have been exposed to the cinnabar moth by mapping the potential distribution of the moth and native *Senecio* and *Packera* species. Then, we conducted a systematic survey of sites where non-target plants were exposed to assess the frequency and severity of attack on non-target plants and the target weed, *Senecio jacobaea*. We also explored patterns in site variables: stem density, habitat type, elevation, and precipitation.

In the second part of our study, we evaluated the response of the cinnabar moth to two habitats, sunny meadow and shaded forest. We conducted a mark-release-recapture experiment to compare dispersal patterns for adult moths between

the two habitats, and we compared larval development and survival between egg batches laid in both habitats. We examined differences in adult survival and temperature between the two habitats to determine if they could explain the observed patterns in adult dispersal and larval development.

These studies estimated the pattern of exposure of native plants to the cinnabar moth, the frequency and severity of attack on exposed plants, and the influence of habitat selection on these patterns of association. Studies such as these will allow us to assess the impact that biological weed control insects have on non-target plants more accurately than previous, haphazard reports.



## **CHAPTER 2**

# **Assessing the Safety of Weed Biological Control: Distribution of the Cinnabar Moth *Tyria jacobaeae* on Non-target, Native Plant Species in Oregon.**

**Jason L. Fuller, Eric M. Coombs, Peter B. McEvoy**

## ABSTRACT

This research examines possible adverse ecological effects of insects introduced for biological control of weeds. The cinnabar moth, *Tyria jacobaeae*, was released in California in 1959 to control tansy ragwort, *Senecio jacobaea*. Prior to release, larvae were shown to feed and develop on other *Senecio* and *Packera* species in laboratory tests, and after release they were shown to use the native *S. triangularis* in the field. It is possible that non-target host use in the field may go unreported or may be constrained by ecological conditions operating in the field that are not present in the lab. This study examined the interactions between the cinnabar moth and native *Senecio* and *Packera* in Oregon. Detailed release records enabled fine-scale mapping of the cinnabar moth distribution in Oregon that is presently impossible at a continental scale.

Of the 132 species and infraspecific taxa of potential non-target hosts in these genera in the continental United States, 10 native *Senecio* and 10 native *Packera* species occur in Oregon. We found that nine species in Oregon were exposed to the cinnabar moth, 3 *Senecio* and 6 *Packera*, based on overlap in plant and insect distribution. From observations in 2001, we found 3 of the 9 exposed species were attacked, one *Senecio* and two *Packera*. Among sites with populations of focal moth and plant species, *P. cymbalarioides* was attacked at one of three (33%) sites, *P. pseud aurea* was attacked at 2 of 6 (33%) sites, and *S. triangularis* was attacked at 7 of 15 (47%) sites. Within sites with populations of each species, attack frequency of stems was 33% (of six stems sampled) for *P. cymbalarioides*, and ranged from 53% to 56% (of 20 to 108 stems sampled) for *P. pseud aurea* and 7% to 64.5% (of 32 to 458 stems sampled) for *S. triangularis*. Median damage for attacked stems only was 10% in *P. cymbalarioides*, 5% to 17.5% in *P. pseud aurea*, and 5% to 37.5% in *S. triangularis*. The attack rate on non-target plants (7.1 to 64.5 percent of stems across all sites attacked) was equal to or greater than on the target weed (8.3 to 50.0 percent of stems across all sites attacked). At three sites, caterpillars attacked non-target plants but the target weed

was absent, and at one site, the target was present but caterpillars fed on non-target plants only.

Some native *Senecio* and *Packera* in Oregon are segregated geographically. Ten grow in the continental climate east of the Cascade Mountain Range, where the cinnabar moth is absent, four grow in the Mediterranean climate west of the Cascade Mountain Range, where the moth is present, and six grow in both areas. Species that occur on the west side are exposed to the moth, species on the east side are protected, and species that straddle east and west are partially protected.

Of the 20 potential non-target hosts in Oregon, we found larval feeding damage on only three species. The rates of attack on these species were as high or higher than on the target weed, suggesting that as weed populations decreased, the moth moved on to native, non-target plants. Our systematic survey gives us confidence that the remaining species escaped attack because of ecological constraints acting on the moth and not because cases of non-target use go unreported or undetected. Now that we have reliable estimates of exposure and attack rates, future studies should focus on the impact that observed levels of feeding by cinnabar moth caterpillars have on these attacked plant species.

## INTRODUCTION

Non-target feeding by biological control agents has gained attention in the last decade. Some insects imported for biological weed control interact with native plant species that are closely related to the target weed. The frequency of such interactions and their consequences for native biodiversity are not well known, despite increasing attention focused on the ecological impacts and overall safety of biological control (Harris 1988, Harris 1990, Howarth 1991, Simberloff and Stiling 1996, Follett and Duan 2000, Louda and Arnett 2000, Pemberton 2000, Wajnberg et al. 2000, Louda et al. 2002). An increasing number of cases are reported, but the number of cases that go unreported is unknown. Systematic surveys that estimate the frequency and severity of effects with known probability are needed to characterize the possible harm that biological weed control insects impose on native plants. We addressed this question by first predicting encounters between a biological control insect and non-target hosts using a Geographical Information System (GIS) model and then confirming interactions using field surveys to refine estimates of the distribution of the cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae), on non-target, native plant species in Oregon.

Currently, the decision to release new organisms into the environment is based on evidence that the candidates for release will not harm plants of economic or ecological value (Blossey 1995, Wapshere 1989). McEvoy (1996) reviewed the evolution of host specificity testing that started with expert opinion, moved to testing crops, then to centrifugal/phylogenetic testing (continually testing more distantly related plants until the host range is circumscribed), and now relies on the relatedness procedure (ordering plants based on relationship to the target weed while testing representatives from all levels of relationship to the target). Although host specificity tests and safety protocols are more likely now than before to limit the impact of introduced weed biological control insects, concerns for native plants have increased with reports of attack on non-target species. Fifteen out of 112 (13.4%) insects introduced for classical biological control of weeds were reported

to feed and reproduce on non-target plants in a survey of the United States and Caribbean (Pemberton 2000). The plant species attacked were in the same or a closely allied genus as the target weed, except in one case (*Teleonemia* on *Lantana*). Direct and indirect harm to non-target organisms must be weighed against the benefits of controlling the target weed. Thirteen of the 15 control organisms that feed on non-target plants provide economic and ecological benefits by suppressing target weed populations (Julien and Griffiths 1998). McFadyen (1998) reviewed seven biological control programs where non-target plants were attacked. Of these, five agents were expected to feed on non-target plants because the insect's host range was known at the time of release to include native species in the same genus as the target weed.

Two biological control insects have been widely cited for their adverse impacts on non-target, native plants. *Rhinocyllus conicus* was introduced to Virginia and Montana in 1969 to control the exotic thistle *Carduus nutans* (Surles et al. 1974, Hodgeson and Rees 1976). Host specificity tests prior to release found that *R. conicus* could feed and develop throughout the lifecycle on thistles in four genera (*Cirsium*, *Syllabum*, *Onopordum*, and *Carduus*), one of which, *Cirsium*, contains species native to North America. The insect was released because researchers believed the preference *R. conicus* exhibited for its host would limit damage to native species (Zwolfer and Harris 1984). Twenty-two of the 100 native thistle species in the US are now attacked by *Rhinocyllus conicus* (Pemberton 2000, USDA 2001). One of these species, *Cirsium canescens* is endemic to the Sandhills prairie in Nebraska, and attack by *Rhinocyllus conicus* is estimated to reduce plant density five fold (Gassman and Louda 2001). Another successful biocontrol insect, *Cactoblastis cactorum*, was released in the Caribbean Islands in 1957 to control *Opuntia* cacti, and by 1989 had spread to Florida where it now feeds and reproduces on native cacti (Bennett and Habeck 1995). Zimmermann et al. (2000) predicted that all 79 species of platyopuntias (prickly pears) native to the United States and Mexico are vulnerable to attack. These cases underscore the mixture of environmental benefits and costs of biological control:

biological control insects can suppress introduced weeds, but some can also have a negative impact on native plant species.

The evidence that only fifteen weed-biocontrol organisms have been found to cause damage to native plants does not imply that non-target effects are rare. Van Klinken and Edwards (2002, p. 592) state that, "No systematic records have been kept of predicted or actual incidences of non-target attack." Only 37% of established biocontrol organisms in Oregon are systematically monitored and evaluated for target effects, let alone non-target effects (McEvoy and Coombs 1999). Simberloff and Stiling (1996) state that the probability of detecting non-target feeding is extremely low, citing a large element of chance in the discovery of *Cactoblastis cactorum* on *Opuntia* in Florida. To better assess the risk that biocontrol insects pose to native plants, we need systematic surveys for non-target effects across phylogenetic, spatial, and temporal scales of observation following release of control organisms. Such surveys will help estimate with confidence what fraction of adverse impacts is likely to be detected and reported, and they will address doubts about the adequacy of host specificity and safety protocols.

The cinnabar moth, *Tyria jacobaeae* L. (Lepidoptera: Arctiidae) provides an ideal case study to estimate the risk posed to native plants in Oregon by a biological control agent. The moth was first released in California in 1959 and in Oregon in 1960 to control the invasive weed *Senecio jacobaea* L. (Asteraceae) (Frick and Holloway 1964, Isaacson 1973a), and since that time has become well established west of the Cascade Mountain Range. Cameron (1935) conducted host specificity tests before the moth was introduced to New Zealand. The caterpillars fed on none of the economic plants tested (*Lactuca sativa*, *Chrysanthemum coronarium*, *Helianthus annuus*, *Solidago* sp., *Aster* sp., and *Dahlia* sp.). Host specificity tests prior to introduction in the United States indicated that cinnabar moth larvae could not develop on the ten economic plants tested (*Cynara scolymus*, *Aster* sp., *Cosmos* sp., *Leucanthemum vulgare*, *Lonicera* sp., *Humulus lupulus*, *Calendula* sp., *Carthamus tinctorius*, *Fragaria chiloensis*, and *Zinnia* sp.) (Parker 1960). Tests conducted prior to introduction into Canada indicated that caterpillars could not

develop on most of the closely related plants tested (*Erechtites arguta*, *Arnica longifolia*, *Cacalia suaveolens*, *Carthamus tinctorius*, *Cirsium arvense*, *Taraxacum officinale*, *Erigeron philadelphicus*, *Achillea millefolium*, *Chrysanthemum leucanthemum*, *Eupatorium rugosum*, and *Ambrosia artemisiifolia*) (Butcher and Harris 1961). However, three introduced plants, *Senecio vulgaris*, *S. cineraria*, and *Erechtites hieraciifolia* (introduced to western North America from eastern North America, Barkley 1993), and one native plant, *Packera paupercula*, supported larval development under laboratory conditions (Butcher and Harris 1961). Cinnabar moth caterpillars may have the ability to feed on other plants in the genera *Senecio*, *Packera*, and *Erechtites* as well.

The ability of the moth to feed on non-target plants in the lab does not translate directly into the ability to use those plants as hosts in the field. The ecological host range expressed in the field is often narrower than the physiological host range demonstrated in the lab because consumers express preference, and temporal and spatial heterogeneity restricts insect-plant interactions in the field environment (Harris and Zwolfer 1968). However, recent lab and field tests confirmed that cinnabar moth caterpillars can feed and complete development on *Senecio triangularis* Hook. (Asteraceae) (Diehl and McEvoy 1989). None of the other 19 native species of *Senecio* and *Packera* in Oregon have been tested for suitability as hosts for the cinnabar moth.

The *Senecio* genus is currently under revision and has been split into two genera: *Senecio* and *Packera* (Bain and Jansen 1995, Bain and Walker 1995). Both genera contain many species in North America: *Packera* contains 62 native species and infraspecific taxa, and *Senecio* contains 70 native species and infraspecific taxa in the continental US (USDA 2001). Oregon is home to 10 native *Senecio* species and 10 native *Packera* species; two of these, *S. ertterae* and *P. hesperia*, are candidates for federal listing as endangered (Chambers and Sundberg 1998, Eastman 1990). The probability and consequences of attack on native species by the cinnabar moth have been investigated in only one case, *S. triangularis* (Diehl and McEvoy 1989). Some fraction of native species may escape harm by virtue of

their resistance, phenology, or spatial location. Consumer choice of hosts and habitats, and timing of lifecycle events will reduce the vulnerability of some potential hosts. Generally, we lack sufficient information to weigh the effectiveness of *Tyria jacobaeae* against the risk it poses to native plants as required under law (see Coulson 1999 for a discussion of legal requirements). For example, the USDA Forest Service recently relocated the cinnabar moth to Montana with little consideration of impact to that state's 15 native *Senecio* and 12 native *Packera* species (McEvoy and Coombs 1999, USDA 2001).

We chose the cinnabar moth as a case study because it is well studied (Dempster 1982) and its distribution in Oregon is well known, enabling us to overlay insect distribution on plant distribution to estimate the probability of encounter and interaction with native plants in the field. The large number of potential non-target species (10 *Senecio* and 10 *Packera*), the wide geographic distribution of the moth (all areas west of the Cascade Mountain Range), and the length of time that has transpired since first release (42 years) provide many opportunities for the moth to interact with native plants.

Non-target feeding by biological control organisms on native plants reflects a progression of opportunities and constraints that determine whether impacts will occur (Harris and McEvoy 1995, McEvoy 1999). McEvoy (1999) listed five constraints that act on biological control insects to limit impact, of which three are examined in this study: phylogenetic host range, behavior, and host-plant suitability. The phylogenetic host range reflects the insect's evolutionary history rather than its current environment and is one indicator of the potential for non-target feeding. Butcher and Harris (1961) found all tested *Senecio* and *Packera* to be suitable for development.

Behavioral constraints on insects may limit colonization of non-target plants because habitats occupied by the plants may differ from those selected by the insect, or plants may lack visual, olfactory, or tactile cues that elicit oviposition and/or feeding by the insect. Cinnabar moths are typically found in open, dry habitats with low vegetation (Dempster 1982). Plants that grow under shade within



forests will likely be protected from adult oviposition and larval feeding while those in open meadow and roadside areas will be attacked (Diehl and McEvoy 1989).

Non-target plants must be suitable for oviposition and larval development. It is not clear whether chemicals in ragwort act as cues to stimulate feeding and oviposition. *Senecio* species produce a variety of pyrrolizidine alkaloids and cinnabar moths selectively store senecionine, seneciphylline, and integerrimine in much higher concentrations than found in *S. jacobaea* (Aplin and Rothschild 1972). *Senecio triangularis* and *S. integerrimus* contain senecionine and integerrimine, respectively, as dominant alkaloids (Roitman et al. 1979, Rueger and Benn 1983, Roitman 1983); this may explain the ability of larvae to feed on *S. triangularis*. However, van der Meijden et al. (1989) showed no response to total alkaloid content from ovipositing females. The allelochemicals produced by other *Senecio* and *Packera* native to Oregon have not been studied but may serve as predictors of cinnabar moth attack.

Additionally, phenology and plant structure may be important indicators of suitability when examining larval development on native *Senecio* and *Packera*. Phenology must be, at a minimum, partially coordinated with the life history of the cinnabar moth to insure that larvae have suitable food to support development. Cinnabar moth caterpillars are unlikely to feed on many *Senecio* and *Packera* because the plants complete development and senesce before larvae have completed feeding. In addition, some *Senecio* and *Packera* are also structurally different from *S. jacobaea*; they are smaller and contain only basal leaves. These species may not provide enough food for cinnabar moth larvae to develop into pupae.

Non-target plants that do not support larval development may nevertheless be damaged (Schooler et al. in press). When an agent reaches high enough density it may move to non-target plants where it may inflict feeding damage without completing its lifecycle.

The objectives of this study were to first, predict general patterns of association and interaction between the cinnabar moth and potential non-target plants. We did this by measuring overlap in insect and plant distributions using a GIS model. Our second objective was to observe actual frequency and intensity of interactions from a field survey conducted over one field season in western Oregon. Our third objective was to screen variables to explain the observed frequency and intensity of interactions and help reconcile prediction and observation.

## METHODS

### Exposure

We estimated exposure of native *Senecio* and *Packera* to the cinnabar moth by overlaying the geographic ranges of the insect and plants. Plants in the genus *Erechtites* were not included in this study because they are not native to Oregon, although they may contribute to overall food abundance. We constructed the potential geographic range of the moth by mapping 2,156 locations where the insect was released according to records kept by the Oregon Department of Agriculture (ODA). We recorded township, range, section, and year for each release. We estimated latitude and longitude from the center of the section in which each release was made.

We mapped release locations of cinnabar moths in ArcView (Version 3.2 for Windows, ESRI) to determine the distribution of releases throughout the state. We then buffered release points by a dispersal distance traveled since time of release calculated as:

$$\text{Dispersal distance} = (\text{years since release} - 2) * 119 \text{ m/yr}$$

Our estimate of dispersal distance was based on four assumptions: all releases were made in suitable habitats containing the target host, all releases became established insect populations, two years elapsed before the populations began to spread, and moth populations spread outward in concentric circles at an annual rate of 119 m/yr. Cinnabar moths were released at sites where the density of the target weed was high and merited inoculation with the moth as a weed-control treatment. The moth did not become established at all of the sites, however. Establishment rates of moth releases were high (>80%) at elevations below 350 meters after the first five years of the release program (Coombs pers. comm.). Establishment rates of moth populations at higher elevations (>1000 m) in Oregon from ODA releases were as low as 30% for initial releases, improving with subsequent releases. Therefore, our estimate of moth distribution may be a worst-case scenario because not all releases were successful. On average, the cinnabar moth required two years to establish at a site before spreading outward from the area of release (Coombs pers. comm.). The estimate of yearly spread rate was based on the mean yearly dispersal distance found by Harrison et al. (1995). The buffers we created combine to estimate the potential current distribution of the cinnabar moth.

We mapped the distribution of native *Senecio* and *Packera* in ArcView from 1,632 vouchered Oregon State University (OSU) Herbarium records and unvouchered records from the OSU Atlas database (Sundberg unpublished data, OSU Herbarium 2002). Our estimate of plant distribution was based on three assumptions: all specimens were accurately identified, all plant locations were accurate, and each plant population was represented by a point. Plant records from the Atlas database are not vouchered so some may be misidentified. In addition, plant locations are not verified and may be incorrect. At some sites, plant records may represent a few rare individuals rather than a large population of the plant. Each population was represented by a point because no data were available on the spatial extent of the plant populations.

We compared the distributions of native plants to the distribution of the cinnabar moth estimated by the buffered areas in ArcView. We classified plants falling within the estimated moth distribution as exposed to the cinnabar moth.

### Regional Survey

We conducted a regional survey of exposed sites to confirm interactions between the cinnabar moth and non-target plants. We sampled sites at the Oregon coast, Coast Mountain Range, and Cascade Mountain Range to determine which native *Senecio* and *Packera* species, populations, and individuals are attacked by the cinnabar moth. Sixty-six exposed sites, as determined by the potential distribution of the moth, were considered for the regional survey. We examined the location descriptions of all exposed sites from the herbarium and atlas records to determine whether the sites could be found. Forty-four of 66 sites (66.7%) were not considered for the regional survey because locality information was not precise enough to permit relocation of the site. We selected twenty-two sites for the regional survey based on herbarium and Atlas records, although plants were subsequently found at only 13 (59%) of these sites in field surveys. Two of the exposed species, *P. macounii* and *S. hydrophilus*, were not included in the survey because site descriptions were vague for *P. macounii* (for example, "Brownsville"), and we could not find plants at the single location where exposure of *S. hydrophilus* to the cinnabar moth was predicted.

We located ten additional sites with the help of OSU Botany and Plant Pathology faculty members and US Forest Service employees, or from prior knowledge of the site. Three of these sites were within the potential cinnabar moth distribution while the remaining seven were not. We sampled twenty-three sites after the addition of these 10 sites. Some of these sites were within close proximity to each other (~ 1 km). We considered these distinct sites because natural barriers to movement (forests and lakes) existed between sites.

At each site, we recorded frequency of attack and percent damage along with independent variables: type of habitat (meadow or forest), stem density, elevation, and mean annual precipitation (from Daly and Taylor 1998). We estimated percent damage as total leaf area missing and/or damaged for a random sample of stems within 1m<sup>2</sup> quadrats when stem density was high (> 5 stems/m<sup>2</sup>). In areas with low stem density (< 5 stems/m<sup>2</sup>), we estimated percent damage as total leaf area missing from a random sample of all stems. We calculated frequency of attack as the percent of stems attacked over all quadrats. We used median percent damage of all attacked stems to estimate the severity of damage for each site/species combination because the distributions of damage were heavily skewed with zero and low values for most attacked sites. We used logistic and linear regression models to assess the influence of the independent variables on attack rate and damage level, respectively. We used the Drop in Deviance test to determine the influence of variables for the logistic regression model (Ramsey and Schafer 1997). We also explored longitudinal patterns of elevation and precipitation. We used S-Plus 6.0 (Insightful Corp.) to conduct all statistical tests.

At sites where the target weed was found, we compared the frequency of attack and median percent damage between the native species and *S. jacobaea* to determine whether frequency and severity of attack on non-target, native plants was higher or lower than on the target weed. We also used this comparison to determine if attack on non-target plants was dependent on high levels of feeding on the target.

We compared the flowering time distribution of each exposed *Senecio* and *Packera*, based on collection times of specimens in the OSU Herbarium, to the phenology of *S. jacobaea* and the cinnabar moth on Mary's Peak. We plotted the distribution of flowering times for each species by tallying collection dates of all herbarium specimens in flower into week periods from April 1 to October 31. We estimated the flowering time distribution of ragwort from field observation on Mary's Peak because the majority of herbarium specimens of this species were collected at low elevations within the Willamette Valley. Most native plants were

sampled at higher elevations or on the coast where ragwort flowers later in the season. We approximated the times of adult flight, egg hatch, and pupation of the cinnabar moth from field observations on Mary's Peak.

## RESULTS

### Exposure

Native *Senecio* and *Packera* were classified into 3 groups to diagnose exposure: four species found west of the Cascade Crest (*P. bolanderi*, *P. flettii*, *P. indecora*, and *P. macounii*), ten species found east of the Cascade Crest and in the Siskiyou Mountains (*P. eurycephala*, *P. hesperia*, *P. streptanthifolia*, *S. aronicoides*, *S. crassulus*, *S. ertterae*, *S. fremontii*, *S. hydrophiloides*, *S. serra*, and *S. sphaerocephalus*), and six species found throughout the state (*P. cana*, *P. cymbalarioides*, *P. pseud aurea*, *S. hydrophilus*, *S. integerrimus*, and *S. triangularis*) (Fig. 2.1). *Senecio jacobaea* can be found both west and east of the Cascade Crest, although the cinnabar moth has not been released east of the Cascade Crest (Fig. 2.2).

Oregon Department of Agriculture recorded 2,156 cinnabar moth releases made over 25 years between 1971 and 1996. The potential current distribution of the cinnabar moth predicted from release data covers a combined 25,938 km<sup>2</sup> and spans all 18 counties west of the Cascade Crest (Fig. 2.3). Nine of twenty native species (3 of the 10 native *Senecio* (30%) and 6 of the 10 native *Packera* (60%)) were judged to have been exposed at 66 locations west of the Cascade Crest (Table 2.1).

The percentage of sites exposed for each native species was low when compared to the total number of sites: *Packera bolanderi* = 22.0% of 141 sites, *P. cana* = 2.2% of 183, *P. cymbalarioides* = 4.8% of 62, *P. flettii* = 33.3% of 9, *P.*

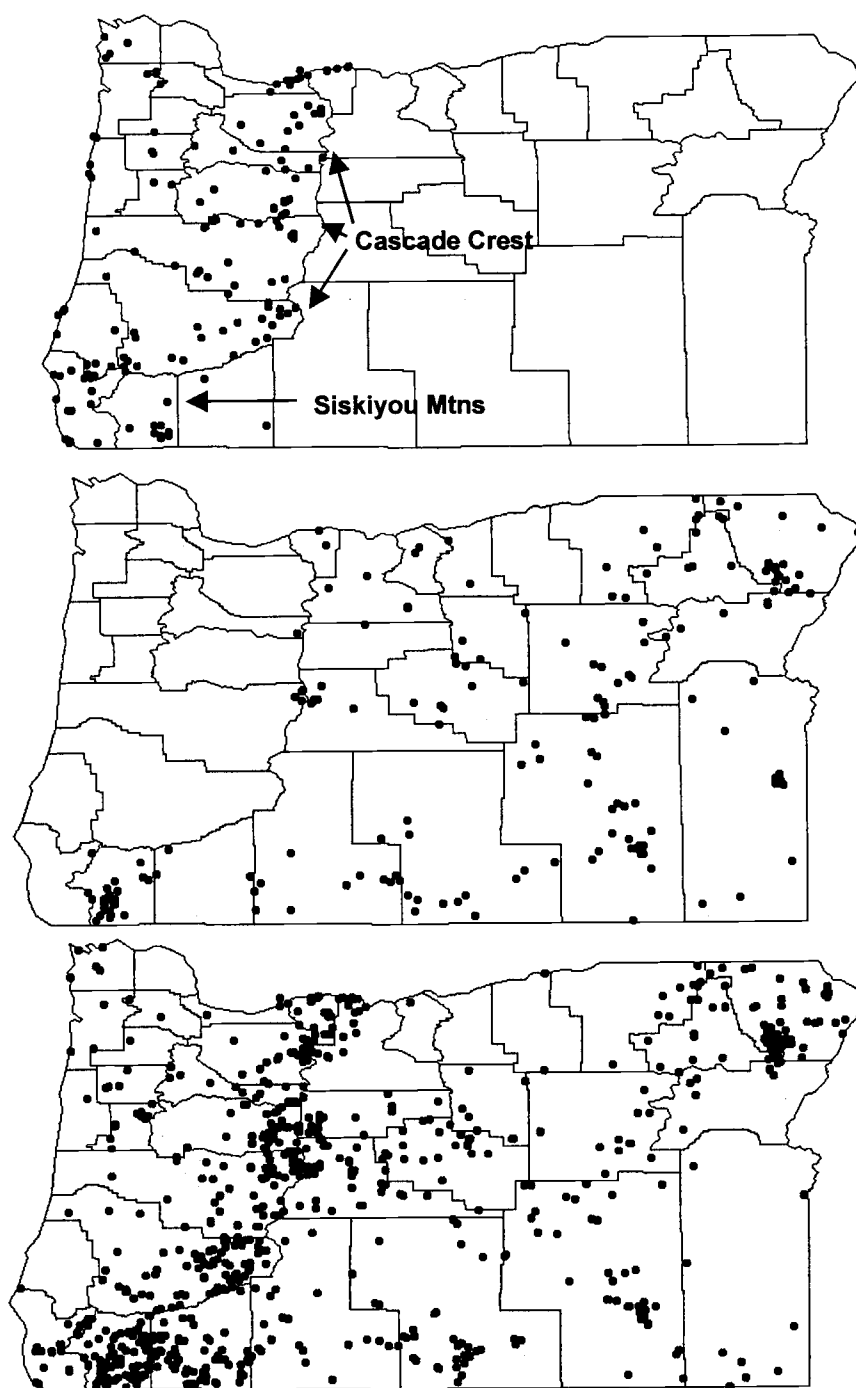


Figure 2.1. Locations of *Senecio* and *Packera* species, based on OSU Herbarium and Atlas records, grouped as growing west of the Cascade Crest (top), east of the Cascade Crest including the Siskiyou Mountains (middle), and growing across the state (bottom).

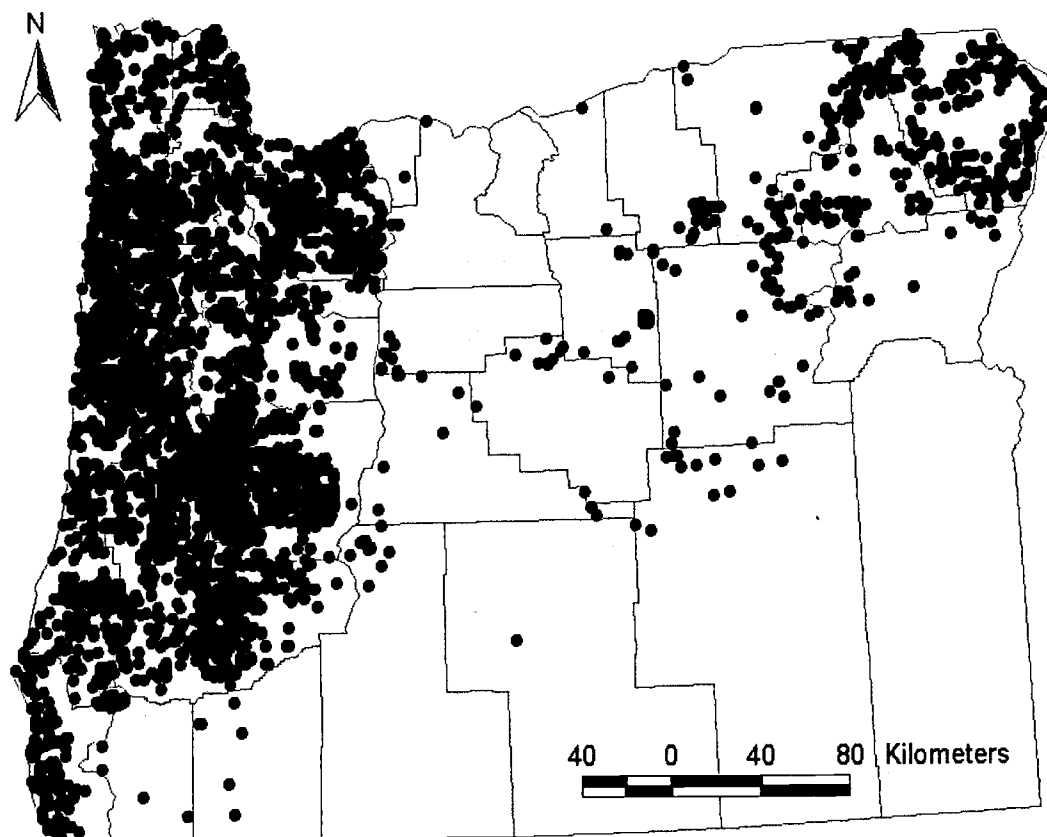


Figure 2.2. Distribution of *Senecio jacobaea* in Oregon based on ODA biocontrol release records, ODA survey locations, and OSU Herbarium records.



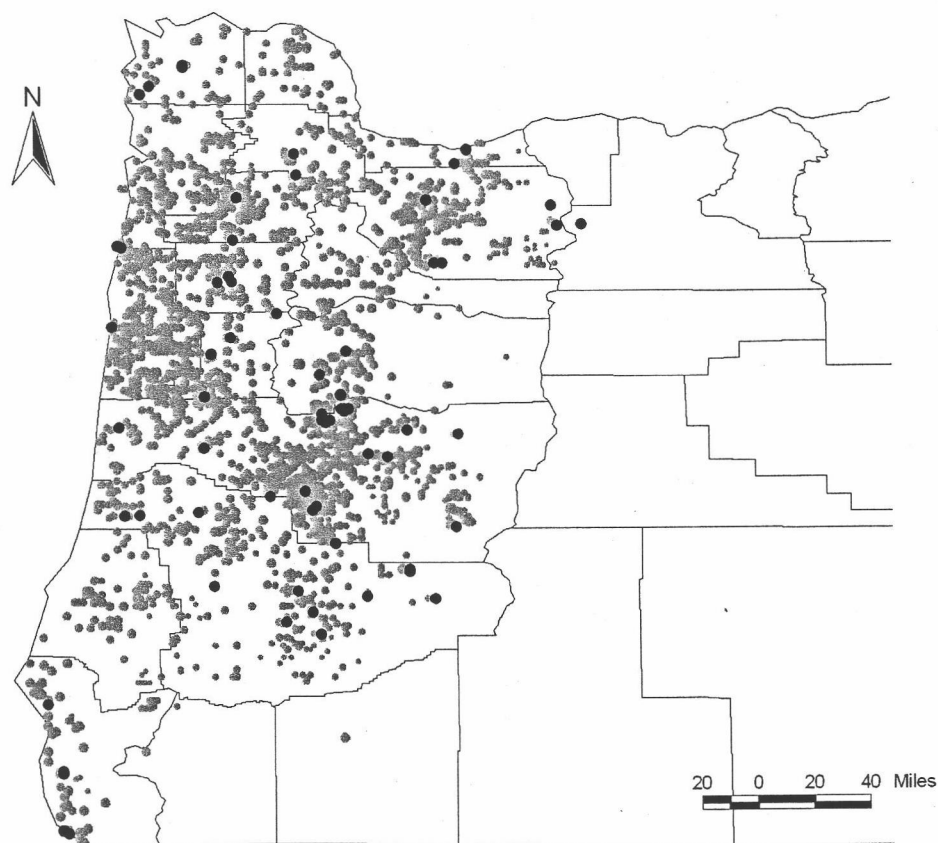


Figure 2.3. Potential current distribution of the cinnabar moth assessed from release records (grey area), and aggregate distribution of 6 native *Packera* and 3 native *Senecio* species assessed from herbarium records (black points).

Table 2.1. Native *Senecio* and *Packera* taxa in Oregon. Taxa listed in bold are exposed to the cinnabar moth.

Species	Authority	Life History
<b>Packera bolanderi</b>	(Gray) W.A. Weber & A. Love	perennial
<b>Packera cana</b>	(Hook.) W.A. Weber & A. Love	perennial
<b>Packera cymbalarioides</b>	(Buek) W.A. Weber & A. Love	perennial
Packera eurycephala	(Torr. & Gray ex Gray) W.A. Weber & A. Love	perennial
<b>Packera flettii</b>	(Weig.) W.A. Weber & A. Love	perennial
Packera hesperia	(Greene) W.A. Weber & A. Love	perennial
Packera indecora	(Greene) A. & D. Love	perennial
<b>Packera macounii</b>	(Greene) W.A. Weber & A. Love	perennial
<b>Packera pseud aurea</b>	(Rydb.) W.A. Weber & A. Love	perennial
Packera streptanthifolia	(Greene) W.A. Weber & A. Love	perennial
Senecio aronicoides	DC.	biennial/perennial
Senecio crassulus	Gray	perennial
Senecio ertterae	T.M. Barkl.	annual
Senecio fremontii	Torr. & Gray	perennial
Senecio hydrophiloides	Rydb.	biennial/perennial
<b>Senecio hydrophilus</b>	Nutt.	biennial/perennial
<b>Senecio integerrimus</b>	Nutt.	biennial/perennial
Senecio serra	Hook.	perennial
Senecio sphaerocephalus	Greene	perennial
<b>Senecio triangularis</b>	Hook.	perennial

*macounii* = 26.3% of 19, *P. pseudaura* = 2.9% of 69, *S. hydrophilus* = 2.6% of 38, *S. integerrimus* = 4.6% of 369, and *S. triangularis* = 8.2% of 314.

### Regional survey

We sampled five of six exposed *Packera* species and two of three exposed *Senecio* species at 23 sites in Oregon (Fig. 2.4, Table 2.2, Table 2.3). Two of the five exposed *Packera* species (40%) sampled and one of the two exposed *Senecio* species (50%) sampled were attacked by the cinnabar moth: *Packera cymbalarioides*, *P. pseudaura*, and *Senecio triangularis* (Fig. 2.5). We used median percent damage to estimate attack severity because the distribution of damage for these species was skewed to the right: most damage values were low or zero. We calculated the median of all stems sampled, and the conditional median of only attacked stems. Median percent damage was zero in 10 of the 16 attacked site/species combinations. The majority of attacked stems sustained low levels of damage (Fig. 2.5).

The proportion of sites where attack occurred varied slightly among attacked species. *Packera cymbalarioides* and *P. pseudaura* were attacked at 33% of the sites sampled for those species ( $n = 3$  and  $n = 6$  respectively), while *S. triangularis* was attacked at 47% of the sites ( $n = 15$ ) (Fig. 2.6). Measuring attack frequency by the mean proportion of stems attacked within each site we found that attack frequency varied little for *P. pseudaura* (53.3 to 55.6% of stems attacked), but varied more for *S. triangularis* (7.1 to 64.5% of stems attacked) (Table 2.4). The highest proportion of attacked *P. pseudaura* stems (55.6%) was recorded at Little Crater Meadows in Mount Hood National Forest and the highest proportion of attacked *S. triangularis* stems (64.5%) was recorded at Timothy Lake, also in Mount Hood National Forest. The conditional median percent damage for attacked stems at these sites varied more widely, between 5.0 and 17.5% damage for *P. pseudaura* and between 5.0 and 37.5% damage for *S. triangularis*. The greatest amount of damage occurred on *P. pseudaura* stems at Timothy Lake and on *S.*

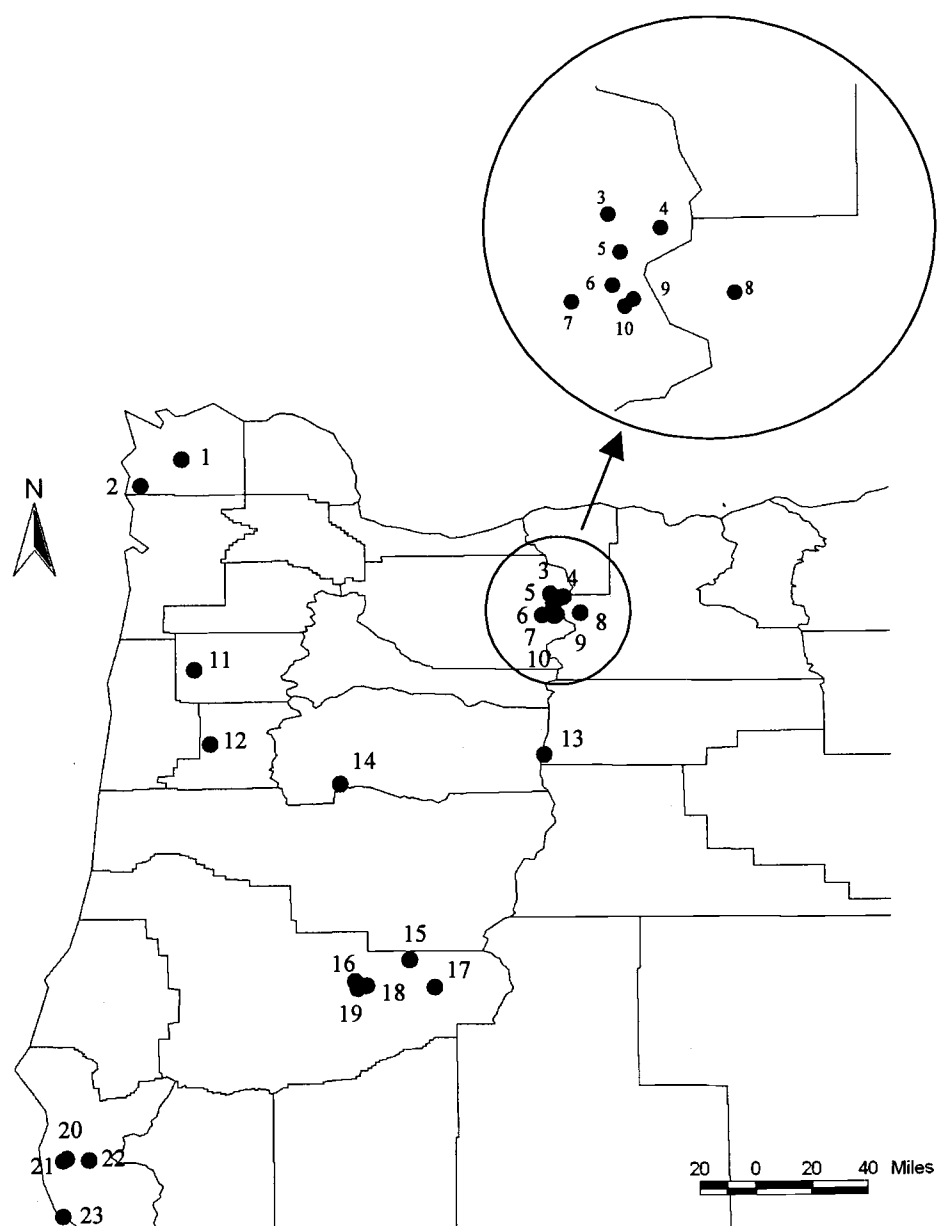


Figure 2.4. Twenty-three sites sampled to assess attack frequency and intensity of cinnabar moth feeding on native *Senecio* and *Packera*. Numbers correspond to sites in Table 2.2. Insert contains magnification of area near Mount Hood.

Table 2.2. Locations of sites sampled to assess non-target impact of the cinnabar moth on native plants. Numbers refer to locations on Fig. 2.4.

Number	Location	County	Latitude	Longitude	Elevation	Precipitation
					m	cm / yr
1	Saddle Mountain	Clatsop	45.95	-123.68	980	368
2	Onion Peak	Clatsop	45.82	-123.90	738	394
3	Veda Lake	Clackamas	45.26	-121.79	1282	206
4	Salmon River Meadow	Clackamas	45.24	-121.72	1005	145
5	Jackpot Meadow	Clackamas	45.21	-121.77	510	287
6	Cooper Creek Bog	Clackamas	45.17	-121.78	1088	155
7	Dinger Lake	Clackamas	45.15	-121.83	1213	170
8	Hickeyville Junction Bog	Wasco	45.16	-121.63	1027	99
9	Little Crater Meadow	Clackamas	45.15	-121.75	986	140
10	Timothy Lake	Clackamas	45.14	-121.76	985	145
11	Fanno Meadow	Polk	44.88	-123.63	873	368
12	Mary's Peak	Benton	44.50	-123.54	1194	287
13	Square Lake	Jefferson	44.44	-121.82	1474	196
14	Horse Rock Ridge	Linn	44.29	-122.87	830	165
15	Grassy Ranch	Douglas	43.39	-122.52	1603	150
16	Reynold Ridge	Douglas	43.39	-122.52	1561	150
17	Watson Creek Falls	Douglas	43.25	-122.39	834	130
18	Lookout Mountain	Douglas	43.26	-122.74	1504	150
19	Emily Shelter	Douglas	43.24	-122.79	1203	160
20	Pine Point	Curry	42.37	-124.29	595	297
21	Hunter Springs Bog	Curry	42.36	-124.31	510	287
22	Fairview Meadow	Curry	42.36	-124.17	1197	343
23	Harris Bog	Curry	42.07	-124.31	60	201

Table 2.3. Sites sampled, native species found, frequency of attack, conditional median percent damage, stem density, and habitat sampled for all 23 sites visited to assess frequency and severity of attack on native plants. Locations in bold are areas where cinnabar moth feeding occurred. Sites that occurred within the potential current distribution of the cinnabar moth are listed as exposed.

Location	Species	Freq.	Damage	Density	Habitat	Attack	Exposed
		%	%	stems / m <sup>2</sup>			
Cooper Creek Bog	<i>P. pseud aurea</i>	0.0	0.0	2.00	meadow	0	0
Cooper Creek Bog	<i>S. jacobaea</i>	0.0	0.0	0.15	meadow	0	0
Cooper Creek Bog	<i>S. triangularis</i>	0.0	0	0.25	meadow	0	0
Dinger Lake	<i>P. pseud aurea</i>	0.0	0.0	1.00	forest	0	0
Dinger Lake	<i>S. triangularis</i>	0.0	0.0	0.25	meadow	0	0
Emily Shelter	<i>S. jacobaea</i>	50.0	10.0	0.07	meadow	1	0
Emily Shelter	<i>S. triangularis</i>	7.1	40.0	11.00	meadow	1	0
Fairview Meadow	<i>S. integerrimus</i>	0.0	0.0	0.20	meadow	0	0
Fairview Meadow	<i>S. jacobaea</i>	25.8	51.3	0.16	meadow	1	0
Fanno Meadow	<i>S. triangularis</i>	48.0	27.8	9.28	meadow	1	0
Grassy Ranch	<i>S. integerrimus</i>	0.0	0.0	0.04	meadow	0	1
Grassy Ranch	<i>S. jacobaea</i>	0.0	0.0	0.11	meadow	0	1
Grassy Ranch	<i>S. triangularis</i>	0.0	0.0	8.00	meadow	0	1
Harris Bog	<i>S. jacobaea</i>	0.0	0.0	0.00	meadow	0	1
Harris Bog	<i>S. triangularis</i>	0.0	0.0	0.35	meadow	0	1
Hickeyville Junction Bog	<i>P. pseud aurea</i>	0.0	0.0	5.00	meadow	0	1
Hickeyville Junction Bog	<i>S. triangularis</i>	0.0	0.0	0.22	meadow	0	1
Horse Rock Ridge	<i>S. integerrimus</i>	0.0	0.0	0.03	meadow	0	1
Horse Rock Ridge	<i>S. jacobaea</i>	33.3	9.0	0.18	meadow	1	1
Hunter Springs Bog	<i>P. bolanderi</i>	0.0	0.0	6.00	forest	0	1
Hunter Springs Bog	<i>P. cana</i>	0.0	0.0	0.07	meadow	0	1
Hunter Springs Bog	<i>S. jacobaea</i>	0.0	0.0	0.50	meadow	0	1
Jackpot Meadow	<i>P. cymbalarioides</i>	33.3	10.0	0.37	meadow	1	0
Jackpot Meadow	<i>S. triangularis</i>	40.0	4.4	1.14	meadow	1	0
Little Crater Meadow	<i>P. pseud aurea</i>	55.6	9.4	23.86	meadow	1	1
Little Crater Meadow	<i>S. triangularis</i>	53.6	13.0	1.29	meadow	1	1
Lookout Mountain	<i>P. bolanderi</i>	0.0	0.0	0.12	forest	0	1
Lookout Mountain	<i>S. integerrimus</i>	0.0	0.0	0.16	meadow	0	1
Mary's Peak	<i>S. integerrimus</i>	0.0	0.0	0.04	meadow	0	1
Mary's Peak	<i>S. jacobaea</i>	9.4	18.3	0.18	meadow	1	1
Mary's Peak	<i>S. triangularis</i>	30.9	17.2	2.33	meadow	1	1
Onion Peak	<i>P. flettii</i>	0.0	0.0	8.00	meadow	0	1
Onion Peak	<i>S. jacobaea</i>	20.0	5.0	0.87	meadow	1	1
Pine Point	<i>P. cana</i>	0.0	0.0	0.20	meadow	0	0
Pine Point	<i>S. jacobaea</i>	0.0	0.0	0.40	meadow	0	0
Reynolds Ridge	<i>S. jacobaea</i>	0.0	0.0	0.13	meadow	0	1
Reynolds Ridge	<i>S. triangularis</i>	0.0	0.0	4.00	meadow	0	1
Saddle Mountain	<i>P. cana</i>	0.0	0.0	0.07	meadow	0	1
Saddle Mountain	<i>P. flettii</i>	0.0	0.0	0.05	forest	0	1
Salmon River Meadow	<i>P. cymbalarioides</i>	0.0	0.0	0.00	meadow	0	0
Salmon River Meadow	<i>P. pseud aurea</i>	0.0	0.0	0.90	meadow	0	0
Salmon River Meadow	<i>S. triangularis</i>	0.0	0.0	0.24	meadow	0	0
Square Lake	<i>P. cymbalarioides</i>	0.0	0.0	0.47	meadow	0	0
Square Lake	<i>S. triangularis</i>	31.6	41.4	1.18	meadow	1	0
Timothy Lake	<i>P. pseud aurea</i>	53.3	37.6	5.00	meadow	1	0
Timothy Lake	<i>S. jacobaea</i>	8.3	6.0	1.75	meadow	1	0
Timothy Lake	<i>S. triangularis</i>	64.5	23.7	1.30	meadow	1	0
Veda Lake	<i>P. bolanderi</i>	0.0	0.0	4.00	forest	0	1
Veda Lake	<i>S. triangularis</i>	0.0	0.0	0.24	forest	0	1
Watson Creek Falls	<i>P. bolanderi</i>	0.0	0.0	1.00	forest	0	1

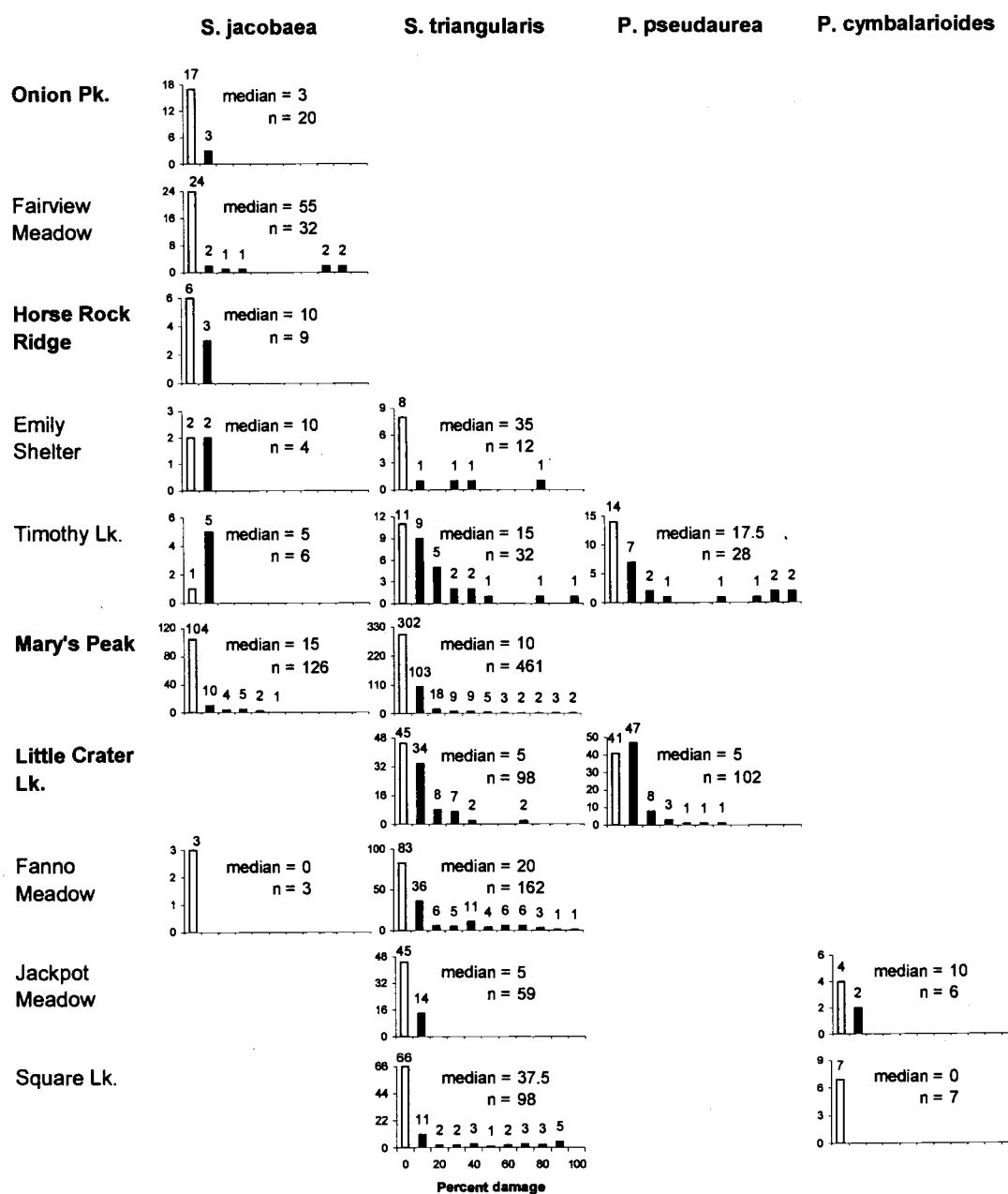


Figure 2.5. Distribution of damage for the target weed and non-target native plants at 10 out of 23 host-bearing sites where attack occurred. Sites listed in bold were determined to be exposed by the potential current distribution of the cinnabar moth. White columns represent stems with no damage and dark columns represent number of stems within each damage level category. Numbers above columns represent number of stems in each category. Median = conditional median percent damage of attacked stems only.

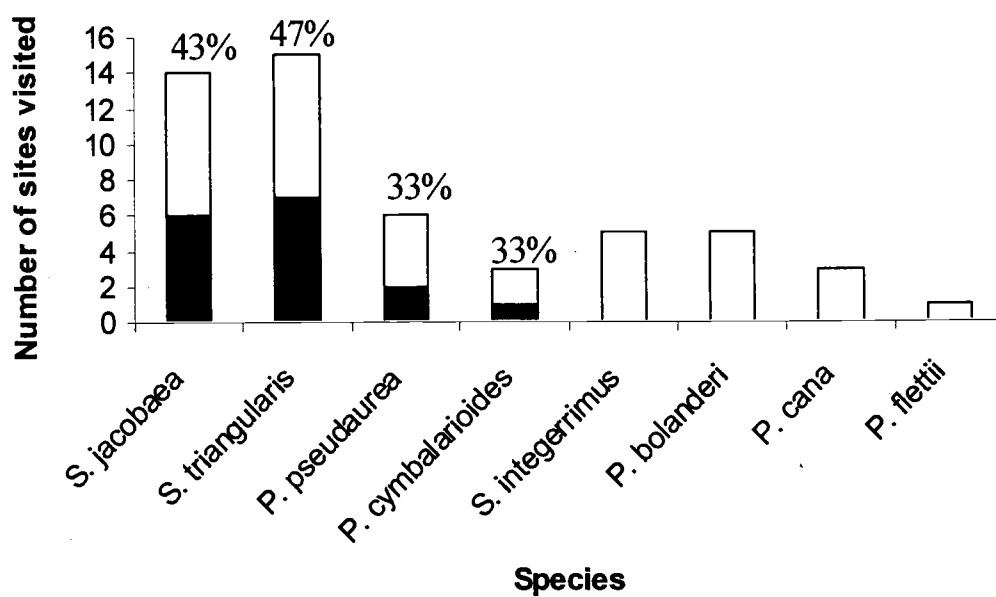


Figure 2.6. Number of sites sampled for *S. jacobaea* and 7 native *Senecio* and *Packera* species in Oregon, and number of sites attacked (black bars) and not attacked (white bars) by the cinnabar moth. Percentage of sites attacked written above each bar.



Table 2.4. Site by species matrix of attack by the cinnabar moth on native plants. Columns are frequency of stems attacked at a site and conditional median percent damage on attacked stems. Sites listed in bold are located within the potential current distribution of the cinnabar moth.

Site	cinnabar moth presence	S. jacobaea			S. triangularis			P. pseudaura			P. cymbalarioides			S. integerrimus			P. bolanderi			P. cana			P. flettl			Species attacked / total
		freq	dam	n	freq	dam	n	freq	dam	n	freq	dam	n	freq	dam	n	freq	dam	n	freq	dam	n	freq	dam	n	
Onion Peak	1	20.0	5.0	20																		0	0	15	1 / 2	
Fairview Meadow	1	25.8	55.0	32										0	0	20									1 / 2	
Horse Rock Ridge	1	33.3	10.0	9										0	0	10									1 / 2	
Emily Shelter	1	50.0	10.0	4	7.1	35.0	52																		2 / 2	
Timothy Lake	1	8.3	5.0	6	64.5	15.0	32	53.3	17.5	26															3 / 3	
Mary's Peak	1	9.4	15.0	126	30.9	10.0	458							0	0	10									2 / 3	
Little Crater Meadows	1				53.6	5.0	98	55.6	5.0	108															2 / 2	
Fanno Meadow	1	0	0	3	48.0	20.0	162																		1 / 2	
Jackpot Meadow	1				40.0	5.0	59				33.3	10.0	6												2 / 2	
Square Lake	1				31.6	37.5	98				0	0	7												1 / 2	
Cooper Creek Bog	0	0	0	15	0	0	25	0	0	20															0 / 3	
Grassy Ranch	0	0	0	3	0	0	50							0	0	8									0 / 3	
Harris Bog	0	0	0	2	0	0	7																		0 / 2	
Reynolds Ridge	0	0	0	8	0	0	58																		0 / 2	
Hunter Springs Bogs	0	0	0	22													0	0	20	0	0	10			0 / 3	
Pine Point	0	0	0	2																0	0	4			0 / 2	
Saddle Mountain	0																0	0	3	0	0	4			0 / 2	
Dinger Lake	0				0	0	40	0	0	3															0 / 2	
Hickeyville Junction Bog	0				0	0	9	0	0	20															0 / 2	
Salmon River Meadows	0				0	0	24	0	0	16	0	0	1												0 / 3	
Veda Lake	0				0	0	10										0	0	5						0 / 2	
Lookout Mountain	0	0	0	4										0	0	4	0	0	12						0 / 3	
Watson Creek Falls	0																0	0	15						0 / 1	
Sites (attacked / total)	9 / 23	6 / 14			7 / 15			2 / 6			1 / 3			0 / 5			0 / 5			0 / 3			0 / 1			

*triangularis* stems at Square Lake in the Mount Jefferson Wilderness. *Packera cymbalarioides* stems were attacked at one location, Jackpot Meadow in the Mount Hood National Forest. Damage was found on two stems within the meadow and median percent damage was 10% for those stems.

*Senecio jacobaea* occurred at 14 of the 23 sites sampled and was attacked by the cinnabar moth at 6 (43%) of these sites (Fig. 2.6). The level of attack on non-target plants at sites where both target and non-target plants occurred was similar to or greater than the level of attack on target plants. Frequency of attack on *S. jacobaea* ranged from 8.3% to 50.0% of stems attacked and conditional median percent damage of attacked stems ranged from 5.0% to 55.0%. *Senecio jacobaea* was found with *S. triangularis* at four sites (Emily Shelter, Timothy Lake, Mary's Peak, and Fanno Meadow) where attack occurred. At Fanno Meadow, we found larvae feeding on 48.0% of *S. triangularis* stems but no damage was found on *S. jacobaea* that occurred there (Table 2.4). Damage was more frequent on *S. triangularis* than on *S. jacobaea* at Timothy Lake (64.5% on the non-target compared to 8.3% on the target) and at Mary's Peak (30.9% on the non-target compared to 9.4% on the target). We found *S. jacobaea* growing with *P. pseudoaurea* at one site, Timothy Lake. As with *S. triangularis* at this site, attack was more frequent on the non-target species *P. pseudoaurea* than on the target host (53.3% compared to 8.3%). In addition, attack occurred on non-target plants in the absence of the target host at three sites: Little Crater Meadow, Jackpot Meadow, and Square Lake.

The aggregate density of all non-target plant species influenced the odds of being attacked at a site (Drop-in-deviance,  $\chi^2 = 7.19$ ,  $P < 0.01$ ). Attacked sites tended to support higher plant densities than sites that were not attacked (Fig. 2.7). The odds of attack at each site did not vary with habitat, elevation, or precipitation (Drop-in-deviance,  $\chi^2 = 1.64$ ,  $P > 0.25$ ). Although habitat did not influence which sites were attacked, no forest sites were attacked. The conditional median percent damage did not vary with stem density, elevation, or precipitation (Table 2.5). We found aggregate stem densities ranging from 0.02 to 20.64 stems/m<sup>2</sup>, and elevation

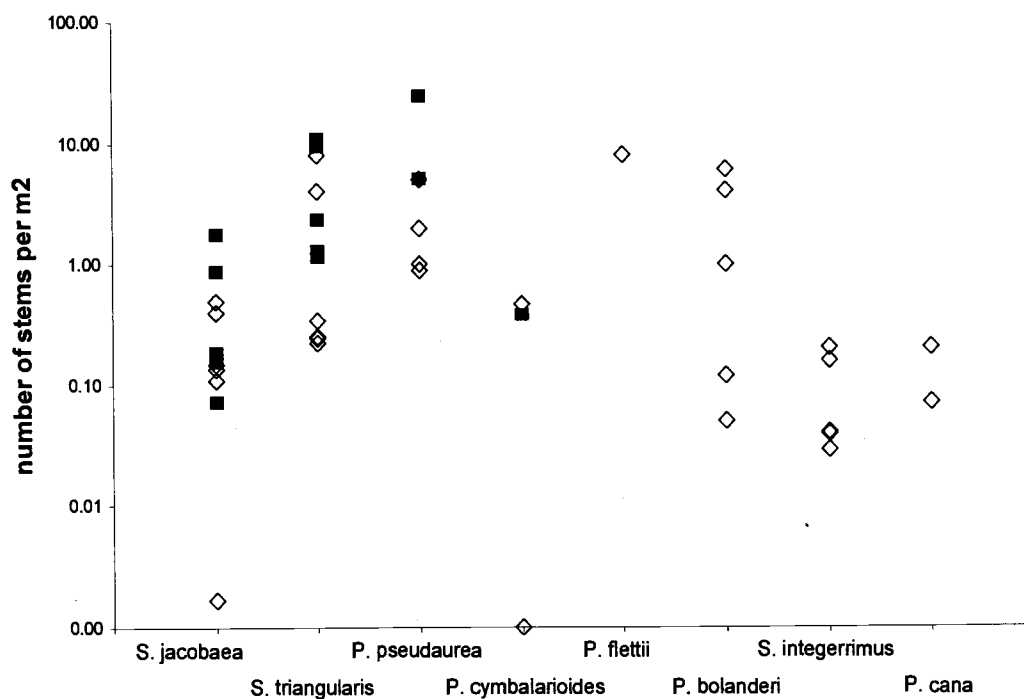


Figure 2.7. Stem density of *S. jacobaea* and seven native *Senecio* and *Packera* species at sites where no attack by the cinnabar moth was found (open diamonds) and where attack by the cinnabar moth was found (closed squares).

Table 2.5. The influence of stem density, precipitation, and elevation on the conditional median percent damage of attacked plants.

Source	sum-of-squares	df	F-ratio	P
Ln (Stem Density)	64.01	1	0.267	0.64
Precipitation	41.43	1	0.173	0.71
Elevation	259.68	1	1.084	0.37
Error	718.82	3		

and precipitation ranged from 60 to 1561 meters and 39 to 155 cm/yr, respectively. Longitude influenced both precipitation and elevation: as one moves from the coast to the Cascade Mountain Range precipitation and elevation increase in the Coast Mountain Range, decrease in the Willamette Valley (although we did not sample within this region because most non-target plants occur in the mountains), and increase in the Cascade Mountain Range (Fig. 2.8).

The four species that escaped attack flowered later than the attacked species (Fig. 2.9). These four species completed flowering by the time caterpillars were feeding. Caterpillars attacked species that spanned the full range of plant sizes. The tallest species, *S. jacobaea* and *S. triangularis* (average height = 100 cm), and the shortest species, *P. cymbalarioides* (average height = 25 cm), were attacked (Fig. 2.10). In addition, the confirmed non-target host *S. vulgaris* averages only 45 cm tall.

## DISCUSSION

We estimated that all 6 species of *Packera* and all 3 species of *Senecio* growing in western Oregon have been exposed to the cinnabar moth, with the exception of *P. indecora* for which there was only one record in Oregon. The remaining 10 species of *Packera* and *Senecio* are, to date, protected by geographic isolation in eastern Oregon, outside the current range of the cinnabar moth. Six species occur both east and west of the Cascade Crest and have been partially protected from the moth by geographic isolation. Risk to non-target plants may increase, however, if the moth is moved to or naturally expands its range into eastern Oregon.

The procedures and assumptions we used to estimate exposure likely caused us to over represent insect distribution and under represent plant distribution. However, we expect our estimate of exposure to adequately represent which

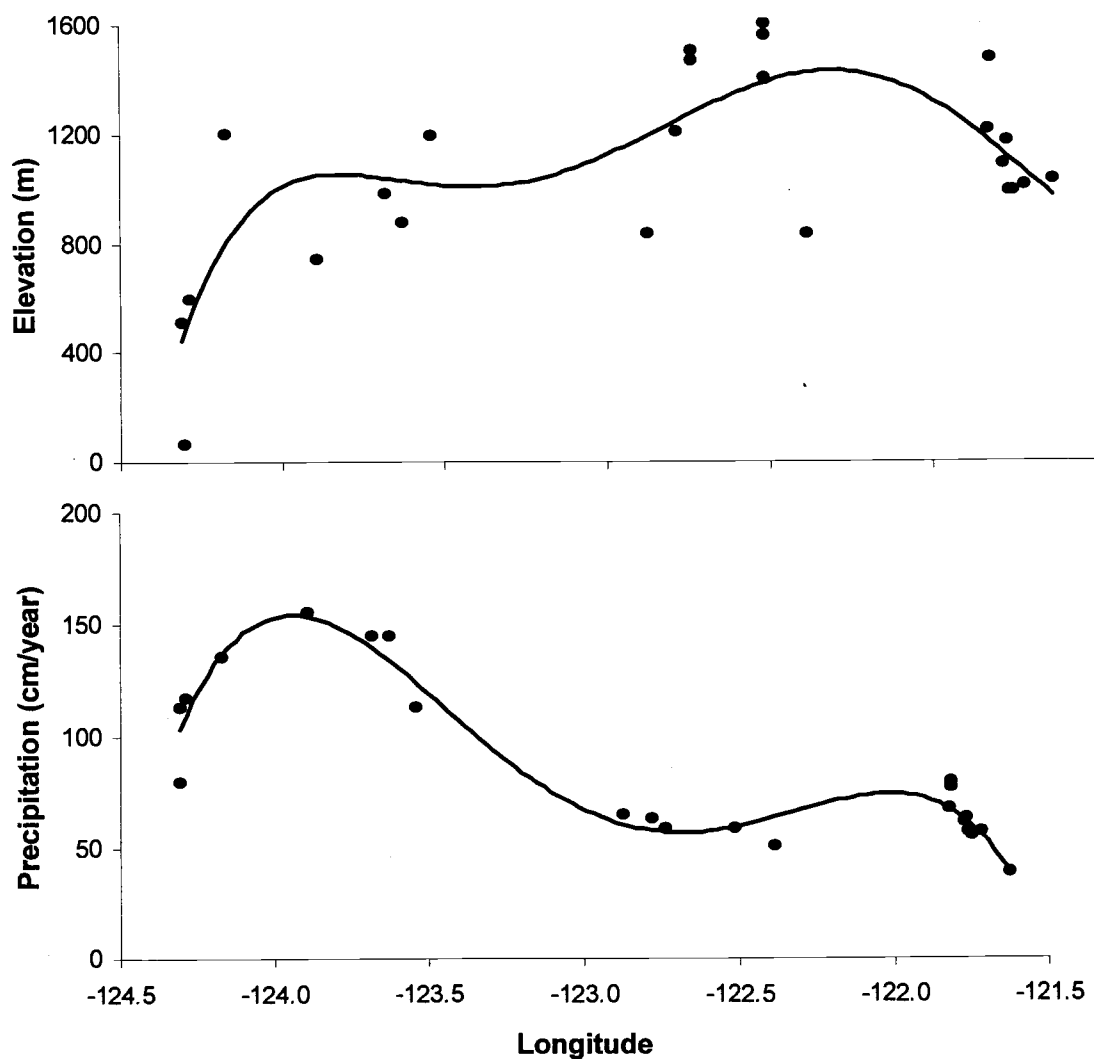


Figure 2.8. Relationship between longitude and both elevation (top) and precipitation (bottom) for sites sampled to assess impact of the cinnabar moth on native plants. Fifth-order polynomial used to create trend line (Excel XP, Microsoft).

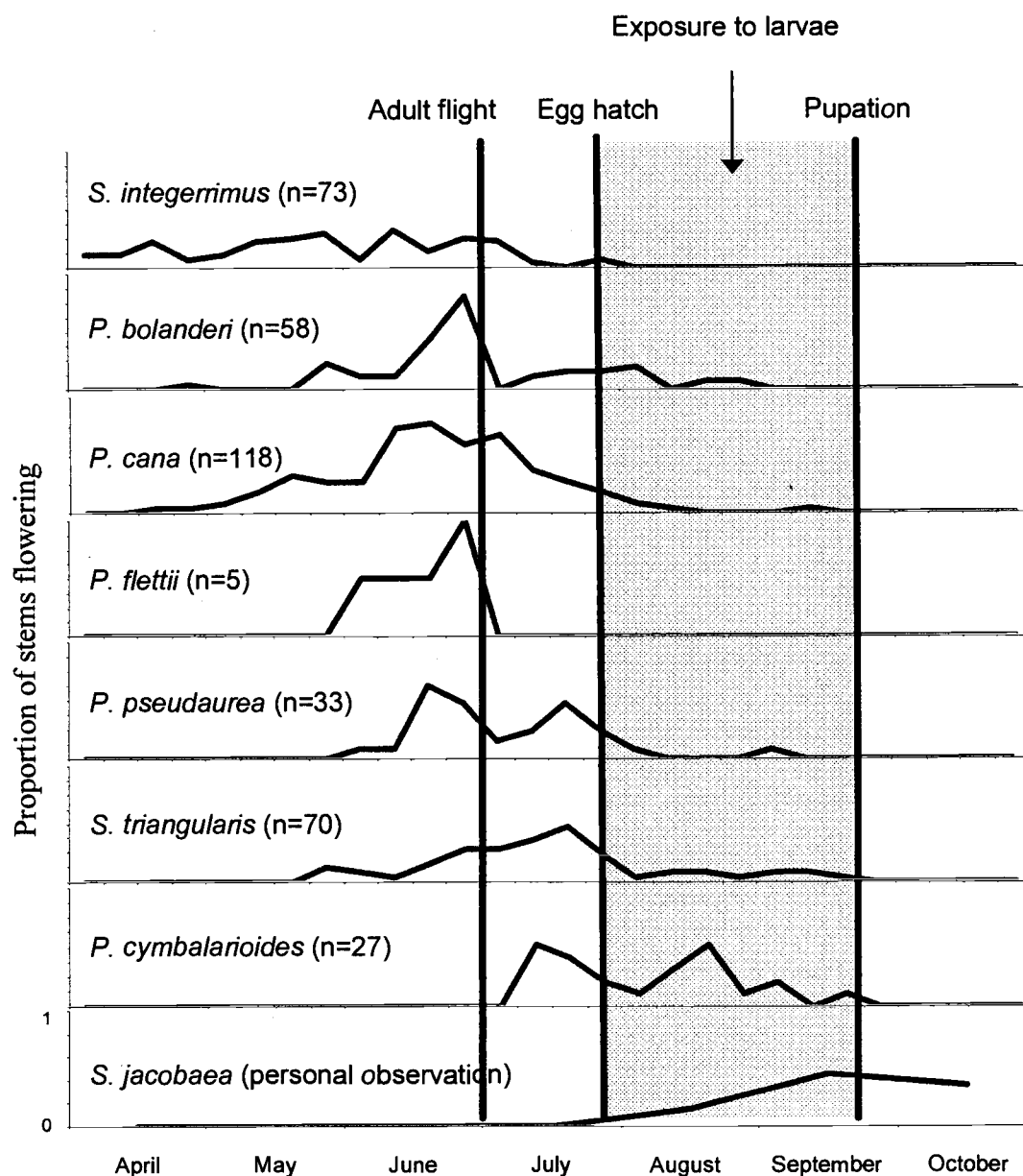


Figure 2.9. Proportion of plants flowering by week for *S. jacobaea* (data from Mary's Peak, OR) and 7 native *Senecio* and *Packera* species (data from OSU Herbarium records), and moth development (vertical lines, from observations on Mary's Peak). N = number of herbarium specimens used to construct flowering distribution.

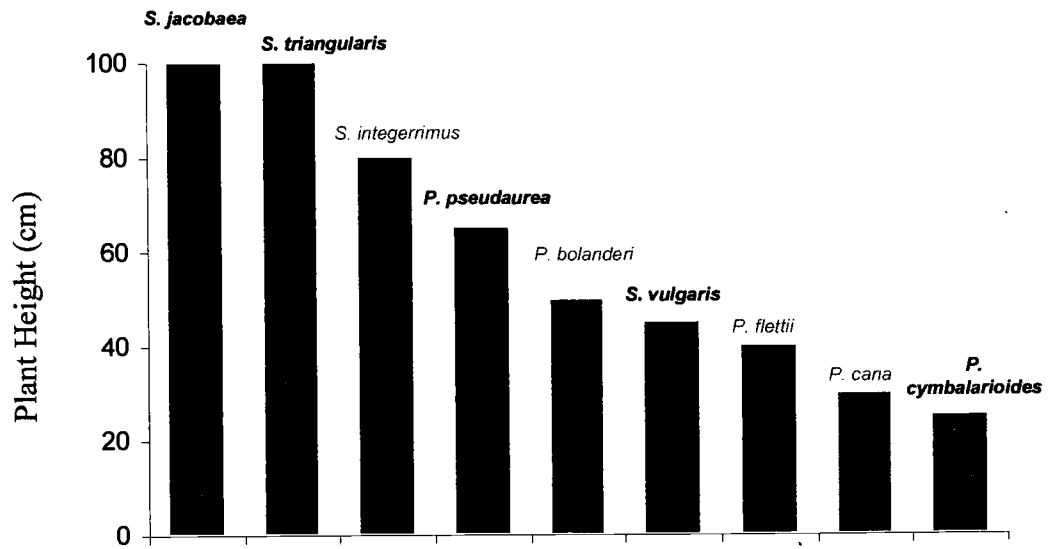


Figure 2.10. Relative size of 7 native *Senecio* and *Packera* species exposed to the cinnabar moth, and two introduced plants *S. jacobaea* and *S. vulgaris*. Species attacked are labeled in bold.

species have been exposed and the frequency of sites at which they have been exposed. We used the 10 additional sites to supplement our regional survey by including more sites where interactions were likely to occur. This study improves upon haphazard reporting of non-target host use by biological control agents.

We found 3 of the 9 exposed species to be attacked in 2001: *Packera cymbalarioides*, *P. pseud aurea*, and *S. triangularis*. Attack frequency for the three susceptible species varied among and within sites. We found low to moderate attack levels on *P. cymbalarioides* (33% of sites attacked, 10% of stems attacked) and *P. pseud aurea* (33% of sites attacked, 50 to 60% of stems attacked). In contrast, *S. triangularis* was attacked at 47% of sites sampled and up to 60% of stems were attacked at one site. Damage levels on stems were low for *P. cymbalarioides* and *P. pseud aurea* (10% and 5 to 17.5% respectively) but moderate for *S. triangularis* (5 to 37.5%).

We were able to find only a few sites with *P. cymbalarioides*, *P. cana*, and *P. flettii*. However, our sample sizes were high compared to the number of sites of each species that fell within the cinnabar moth distribution. We sampled *P. cymbalarioides* at 3 of 6 sites (3 of which fell within the cinnabar moth distribution), *P. cana* at 3 of 4 exposed sites, and *P. flettii* at 1 of 3 exposed sites.

We found non-target and target species to be equally suitable and available hosts. We found similar attack rates and damage severity between host and non-target at sites with both the host weed and native plants. At two sites (Timothy Lake and Mary's Peak), attack was more frequent on non-target plants (64.5% and 30.9%, respectively) than on the target weed (8.3% and 9.4%, respectively). In addition, attack was found at three sites (Little Crater Lake, Jackpot Meadow, and Square Lake) where the host did not occur and at one site (Fanno Meadow) where the host occurred but damage was found only on the native plants. Van Klinken and Edwards (2002) claim that non-target feeding on native plants usually requires a nearby source population of the target weed. Our findings suggest that feeding by the cinnabar moth on native plants is not a "spill-over" effect from feeding on *S. jacobaea*, but that the native species alone are supporting the moth population.



Attack rates on non-target plants may be increasing over time. Comparing our results with those reported by Diehl (1988) suggests that attack by cinnabar moths on *S. triangularis* has increased in frequency on Mary's Peak. He observed low attack rates in 1986 and 1987 (0% and 6% of stems attacked) within a meadow site while we found higher rates of attack in 2001 (49%) within the same meadow. At a nearby roadside site, he found 77% and 23% of stems attacked in 1986 and 1987 respectively, while we found 9.5% of stems attacked in 2001 at the same site. The density of *S. jacobaea* on Mary's Peak is low now compared to when the previous study was conducted. Higher attack rates in the meadow and lower attack rates on the roads may be caused by movement of the moth into higher density stands of an alternate host in absence of the original host. *Senecio triangularis* stems along the road may not offer enough food material to sustain moth populations.

Attack on non-target plants may depend on high aggregate densities of suitable non-target plants. The current study was observational, so we do not know whether stem density has a causative effect on which sites are attacked or if an unknown factor that we did not measure is driving the pattern of attack. Higher stem densities may be needed to support a population of cinnabar moths, and sites with lower densities may not have a large enough food source to sustain the moth year after year.

Attack on non-target plants may also depend on suitable habitats. The cinnabar moth avoided shaded habitats, as no forest sites were attacked in this study. However, only 3 out of 23 total site/species combinations were within forest habitat, so this result may not accurately represent the pattern of attack. Diehl and McEvoy (1989) found high attack rates on *S. triangularis* in open habitats while nearby forest habitats were unused by the moth. The cinnabar moth may avoid shaded habitats, preferring open sunny locations. One native species may escape cinnabar moth feeding by virtue of the habitat in which it grows. No feeding was found on *P. bolanderi*, which grows in shaded, forest habitats along the coast, in the Coast Mountain Range, and in the Cascade Mountain Range.

Plant phenology may limit the suitability of native plants for cinnabar moth development. The three native species that were attacked flower later than the other *Senecio* and *Packera* studied (Fig. 2.9). Cinnabar moth adults prefer to oviposit on large flowering plants of *S. jacobaea*, and the larvae develop faster and larger if flowers are available for consumption when they reach later instars (van der Meijden 1976, Rose 1978). The faster development may be associated with higher nitrogen concentrated in flowers (3.20 - 3.30) compared to leaves (1.94 - 2.60 percent dry weight) (Dempster 1982). When flowers are not available, the larvae must complete their development on leaf material alone, which slows development and lowers pupal size. Low pupal size in turn lowers fecundity (Dempster 1971). The four species that were not attacked undergo peak flowering before cinnabar moths have emerged, and have begun to senesce before the larvae have completed development. Peak flowering time for the three attacked species comes after adult emergence and they do not begin to senesce until later in the season, allowing larvae to complete development (Fig. 2.9).

We did not investigate the consequences of the observed levels of damage on these plant populations. The three species attacked are long-lived perennials (Table 2.1) (Hitchcock and Cronquist 1973). They may be able to compensate for damage in one year by flowering in the next year. Most of the stems of these species developed seed by the time cinnabar moth larvae were ready to move up the stem and feed on flowers. The greatest potential impact, that of destroying flower heads, is thus avoided by the plants. Diehl and McEvoy (1989) provided the best available estimate of impact to a non-target plant by the cinnabar moth. They showed that later defoliation of the stem reduces seed viability on *S. triangularis*, but the impact of reduced seed viability on *S. triangularis* distribution and abundance has not been assessed.

Future studies should focus on the impact that the observed levels of feeding by cinnabar moth caterpillars have on the three native species attacked. Such studies will allow us to more accurately assess the risk posed to native plants by the cinnabar moth.

Our study provides a framework by which biological control workers and managers can assess the potential current or future risks weed biological control agents pose to non-target plants. Our systematic survey improves upon the haphazard reporting of non-target feeding that has, to date, characterized monitoring efforts. It will be possible to accurately assess the harm that biological weed control insects impose on native plants only when we conduct systematic surveys that estimate the frequency and severity of effects with know probability.

## CHAPTER 3

### **Assessing the Safety of Weed Biological Control: An Experimental Study on Habitat Selection by the Cinnabar Moth *Tyria jacobaeae*.**

**Jason L. Fuller, Peter B. McEvoy**

## ABSTRACT

The cinnabar moth *Tyria jacobaeae* was released in North America from Europe to control the weed *Senecio jacobaea*. Caterpillars now feed on native plants that are closely related to the target weed. Growing in shaded habitats may protect native species from attack if the moth is restricted to sunny habitats. Although the cinnabar moth is not normally found within shaded habitats, few studies examine the response of adult moths or caterpillars to plants growing in the shade. This study compares dispersal of the adult cinnabar moth and larval survival in forest and meadow habitats. We use a mark-release-recapture experiment to compare dispersal patterns for adult moths between forest and meadow habitats and we compare larval survival and development from the egg stage in each habitat.

Long-term displacements (spanning days) of adult moths were similar in both habitats with a combined mean dispersal distance per day of  $9.55 \text{ m} \pm 1.02$  (mean  $\pm$  se) for the 51 recaptured moths. However, recapture rates in the meadow (47%, 42 moths recaptured of 89 released) were more than four times higher than in the forest (10%, 9 moths recaptured of 85 released), despite similar survival times of caged moths in the meadow ( $3.5 \text{ days} \pm 0.8$ ,  $n = 6$ ) and forest ( $4.7 \text{ days} \pm 0.8$ ,  $n = 6$ ) over a 6 day period. Short-term displacements (immediately after release) differed between habitats: moths in the meadow habitat flew short distances ( $8.5 \text{ m} \pm 1.5$ ,  $n = 13$ ) at or below the herbaceous canopy ( $0.8 \text{ m} \pm 0.2$ ,  $n = 13$ ) while moths in the forest habitat flew longer horizontal ( $22.8 \text{ m} \pm 2.8$ ,  $n = 15$ ) and vertical distances ( $5.9 \text{ m} \pm 0.9$ ,  $n = 15$ ). We recovered seven fifth instar larvae (from an initial density of 278 eggs) from the meadow habitat but no larvae (from an initial density of 119 eggs) were recovered from the forest habitat after the second instar.

We conclude that concentration of the cinnabar moth in open, meadow habitats rather than closed-canopy forest arises due to a combination of higher

emigration rates in the adult stage and lower survival in juvenile stages in forest compared to meadow habitats.

## INTRODUCTION

Host specificity of biological control organisms is one of the primary criteria that scientists and regulators use to evaluate and rank the risks that these organisms pose for non-target organisms (Zwolfer and Harris 1971, Wapshere 1974, Harris and McEvoy 1995, McEvoy 1996, McEvoy 1999). Host range generally refers to the set of species on which a control organism can feed and develop. Investigators commonly find that the physiological host range revealed in the lab is greater than the ecological host range revealed in the field (Baloch et al. 1969, Dunn and Rizza 1977, Dunn 1978, Wapshere 1989). One reason for this discrepancy is that suitable hosts can occur in unsuitable habitats and thereby enjoy a measure of protection, a refuge, from herbivore attack. To test this possibility, we examined how habitat influences colonization of the native plant *Senecio triangularis* Hook. (Asteraceae) by the cinnabar moth *Tyria jacobaeae* (L.) (Lepidoptera, Arctiidae), introduced to North America from Europe for control of ragwort *Senecio jacobaea* L. We contrast both adult movement and juvenile survival in forest and meadow habitats, and we show that plants growing in the forest are protected by a combination of high emigration rates of adult moths and low survival of caterpillars.

The cinnabar moth was first released in the western United States in California in 1959 to control the pasture weed, tansy ragwort *Senecio jacobaea* (Frick and Holloway 1964). It was released in Oregon in 1960 (Isaacson 1973a), and now feeds on native species in the genera *Senecio* and *Packera* in Oregon (Diehl and McEvoy 1989, Fuller et al. 2002). In a survey of 23 sites in western Oregon, Fuller et al. (2002) found no attack by the cinnabar moth on native plants within forest habitats. This included sites where *S. triangularis* was attacked in meadow habitats but was not attacked in nearby forest habitats. In addition, van der Meijden (1979) found that attack rates on *S. jacobaea* populations decreased as

shading increased. In general, the cinnabar moth is believed to be a primarily open meadow species that does not invade forested habitats.

Movement of adult cinnabar moths has been studied in Europe (Crawley and Gillman 1989, Harrison et al. 1995) and in the United States (Rudd and McEvoy 1996). These three studies yielded three separate estimates of maximum displacement (20 m, 156 m, and > 300 m). Rudd and McEvoy (1996) concluded that maximum displacement depends on scale of observation, because larger areas of observation yield greater maximum displacement estimates.

To date no study has examined adult cinnabar moth movement patterns or larval survival and development in heavily shaded habitats. Our objectives were to contrast adult movement and larval survival and development in forest and meadow habitats. We predicted that the cinnabar moth does not use suitable hosts growing in closed-canopy forest due to a combination of adult preference (relatively high emigration rates) and larval performance (relatively low survival rates).

## METHODS

### Adult transfer

We conducted a mark-release-recapture study over a 14-day period from 3 July to 16 July 2001 near the summit of Mary's Peak, located 16 km west of Philomath, Oregon, within Siuslaw National Forest (N 44.5048 W123.5514) (Fig. 3.1). Two sites were chosen for this study: a 2400 m<sup>2</sup> (~80 m x 30 m) area within a meadow dominated by *Senecio triangularis* (Snow 1984), and a 3200 m<sup>2</sup> (~80 m x 40 m) area within a hemlock-noble fir-Douglas fir community (Merkle 1951) whose understory is dominated by *S. triangularis* and other herbaceous vegetation. These sites were separated by 150 m (Fig. 3.1). Mean *S. triangularis* density was 6.2 stems/m<sup>2</sup> ± 1.3 (mean ± se) at the forest site and 23.9 stems/m<sup>2</sup> ± 3.0 at the meadow site.



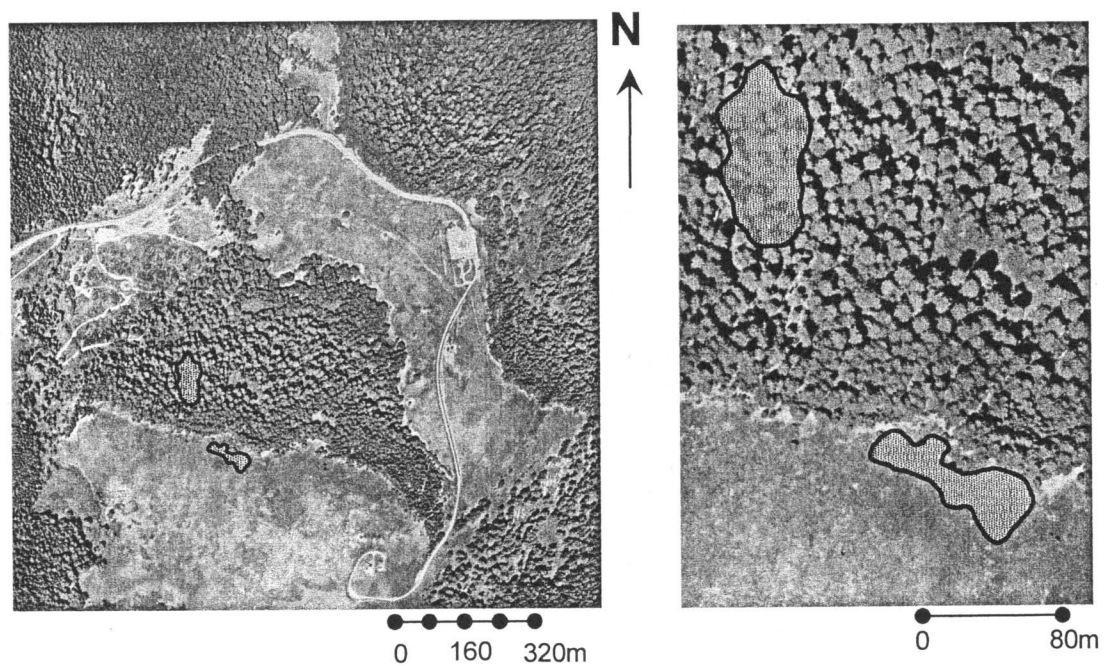


Figure 3.1. Mary's Peak, Oregon. Light polygons represent habitat areas into which cinnabar moth adults were released.

We sampled each site for approximately 90-120 minutes on 11 of the 14 days. Within each sample area, we placed flags at 10 m intervals, creating a grid of 10 x 10 m cells for estimating moth locations. We collected adult cinnabar moths from the meadow habitat by a systematic sweep of the vegetation with sweep nets on each sample day, and then redistributed captured moths between both sites. We lightly brushed all plants within the grid with sweep nets to flush adult moths out of the vegetation, captured all adult moths encountered, and marked them with a Sanford Sharpie felt marker. We marked the moths on the underside of the fore- and hindwings in nine places, three on each hindwing and 3 on the forewings, which allowed us to mark a maximum of 511 individuals. We randomly assigned captured moths to groups of two to four moths, then released them on *Senecio triangularis* at random locations in the meadow and forest sites. Moths were initially captured in the meadow and relocated to the meadow and forest because they are not found naturally in the forest. This procedure allowed us to give equal treatment to both experimental populations. Captured moths that were previously marked were re-released at the point of recapture to avoid disorienting them further. Only previously released moths were encountered in the forest so these were re-released at the point of capture. We assumed the probability of flushing or detecting moths to be equal at both sites. Moths may have been less prone to flush within the forest, but the probability of detecting those that stayed on the stems was higher than in the meadow because *S. triangularis* stems at this site were less dense and more evenly distributed.

Upon initial release and recapture, we recorded: (1) coordinates for the point of release or recapture estimated to the nearest meter; (2) gender; (3) level of wing wear as low (fully scaled) or high (scales worn, color faded, or wings torn); and (4) post-release behavior as mobile (individual moved >1 m) or immobile (individual moved <1 m). For sample days after 12 July, we recorded the vertical and horizontal distance traveled for mobile individuals along with daily maximum, minimum, and current temperatures.

We compared the distribution of long-term displacements (displacements that spanned one day or more) for recaptured moths and used a two-sample t-test to examine differences in long-term dispersal distance between the meadow and forest sites. We used logistic regression to test the relationships between the odds of recapture and independent variables: gender, wing wear, behavior, and habitat. Specifically, we used the Drop in Deviance  $\chi^2$  to test for interactions among all terms, then we used Wald's test to determine the influence of each independent variable on the odds of recapture because this test allowed us to examine each variable while taking into account all other variables (Ramsey and Schafer 1997). We compared the distribution of short-term displacements, vertical and horizontal distance traveled immediately after release of mobile individuals, between sites and used a two-sample t-test to examine differences in mean vertical and horizontal distance. Temperature was compared between the two sites to determine its influence on dispersal and odds of recapture.

We assessed survival of adult moths by placing two cages around *S. triangularis* stems within each site; all cages contained three adults. We confined adults within each cage for 6 days. This experimental design gave us four replicates, two in each habitat. The number of moths alive in each cage was determined on subsequent sample days. We used a two-sample t-test to compare survival times of moths in each habitat. We used S-Plus 6.0 (Insightful Corp.) to conduct all statistical tests.

### **Larval transfer**

We used egg masses laid by caged females from the adult transfer experiment to assess developmental differences between the two sites. We removed the cages on July 16 and recorded the total number of eggs per cage. We recorded stage specific density on 31 July; 10, 17, 23, and 28 August; and 8 September. Larvae begin to wander during the third instar (Dempster 1982), making it difficult to estimate the number of survivors per cohort. For this reason,

we pooled densities for each habitat. Fourth and fifth instar larvae may have wandered far from the original caged area and so were not recovered. We compared survival and developmental time between sites.

We placed two Thermochron iButtons (Dallas Semiconductor) at each site on 31 July to record hourly temperature. The iButtons were taped to the side of 1m long wooden stakes and placed in *S. triangularis* patches within each site. We drove the stakes into the ground until the iButtons were located at the top of the herbaceous canopy, and faced the iButtons north to avoid direct sunlight.

We constructed a degree-day model to explain differences in developmental rates between sites. We set the lower developmental threshold at 5°C, assuming that a more accurate threshold would not be necessary for relative estimates of the heat available for development at the two sites. Only 2% of the hourly temperature readings fell below 5°C. We modeled day degrees on a sine wave curve using the minimum and maximum daily temperatures, then compared the accumulated heat units between sites to help explain any differences in developmental rates.

## RESULTS

### Adult transfer

We released 167 cinnabar moth adults over the 14-day span of this study, 84 in the forest site and 83 in the meadow site. We recovered 8 (10%) moths from the forest, 5 (12%) females and 3 (7%) males, and 36 (43%) from the meadow, 24 (57%) females and 12 (29%) males (Fig. 3.2). Time between release and recapture varied from one to seven days. Few long-term displacements were recorded over multiple days so all displacements were analyzed as distance traveled per day. Long-term dispersal distances were similar for the two habitats (Two-sample t-test,  $T = 0.44$ ,  $P = 0.66$ ) (Fig. 3.3), with a mean displacement per day of  $9.55 \text{ m} \pm 1.02$

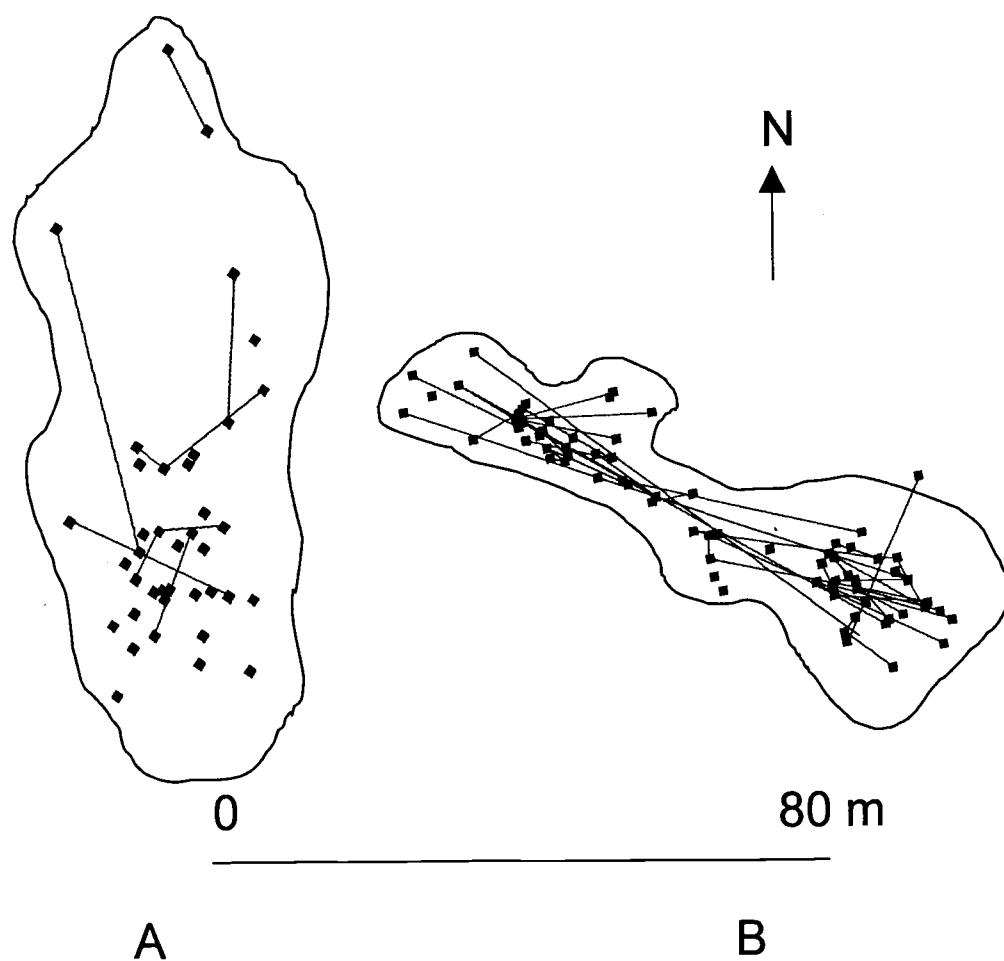


Figure 3.2. Adult cinnabar moth long-term displacements (black lines = displacements, black points = release locations) in forest (A) and meadow (B) habitats. Outlines are habitat areas sampled.

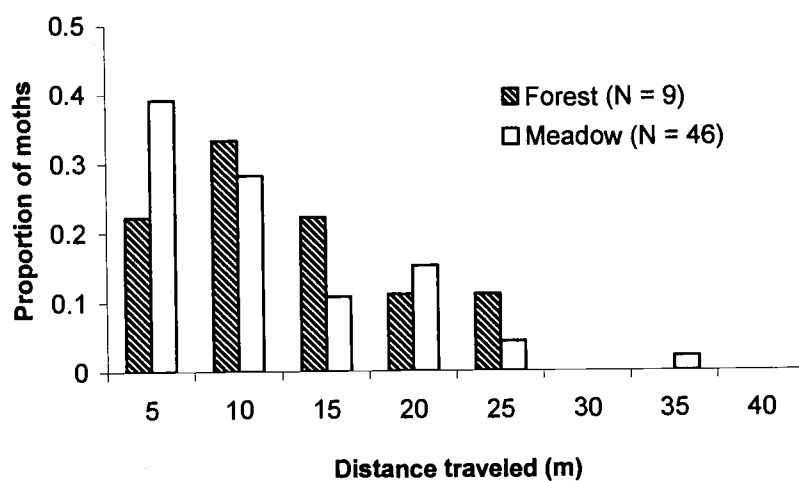


Figure 3.3. Distribution of long-term cinnabar moth displacements in forest and meadow habitats on Mary's Peak, OR. Mean displacement ( $= 9.55$  m/day) was not different for the two habitats (Two-sample t-test,  $T = 0.44$ ,  $P = 0.66$ ). All displacements were calculated as distance traveled per day.

(mean  $\pm$  se). However, short-term displacements differed between the two habitats. Mean vertical distance traveled for mobile moths was significantly higher in the forest,  $5.9 \text{ m} \pm 0.9$  (mean  $\pm$  se), than in the meadow,  $0.8 \text{ m} \pm 0.2$  (Two-sample t-test,  $T = 5.32$ ,  $P < 0.0001$ ) (Fig. 3.4, Table 3.1). Mean horizontal distance traveled for mobile moths was also significantly higher in the forest,  $22.8 \text{ m} \pm 2.8$ , than in the meadow,  $8.5 \text{ m} \pm 1.5$  (Two-sample t-test,  $T = 4.36$ ,  $P = 0.0005$ ).

The odds of recapture for adult moths was associated with gender, post-release behavior, and habitat into which the moth was released (Table 3.2, 3.3). The odds of recapture for female moths was 2.3 times the odds of recapture for male moths (Wald's test,  $Z = -3.333$ ,  $P < 0.001$ ) (95% CI from 1.4 to 3.7 times). The odds of recapture for mobile moths was 2.2 times the odds of recapture for immobile moths (Wald's test,  $Z = 3.206$ ,  $P < 0.001$ ) (95% CI from 1.4 to 3.7 times). The odds of recapture in the meadow was 2.9 times the odds of recapture in the forest (Wald's test,  $Z = 4.628$ ,  $P < 0.001$ ) (95% CI from 1.8 to 4.5 times). The odds of recapture did not vary with wing wear (Wald's test,  $Z = -0.547$ ,  $P = 0.58$ ). Interactions between variables were not significant in our model (Drop in Deviance,  $\chi^2 = 16.05$ ,  $P > 0.1$ ).

Mean daily temperatures and temperatures recorded at the time each moth was collected did not differ between habitats, but the amplitude of temperature variation was higher in the meadow compared to the forest (Fig. 3.5). Mean temperatures declined during the observation period from  $19 \pm 6.0^\circ\text{C}$  to  $7.4 \pm 2.9^\circ\text{C}$  (mean  $\pm$  se).

Caged moths survived an average of 4.2 days. Six out of 12 individuals survived six days until the cages were removed and the moths set free (Fig. 3.6). All three moths in one of the forest cages survived for six days while one moth survived in each of the other cages. We found survival time of caged moths to be similar in the meadow ( $3.5 \text{ days} \pm 0.8$ ,  $n = 6$ ) and forest ( $4.7 \text{ days} \pm 0.8$ ,  $n = 6$ ) habitats (Two-sample t-test,  $T = -0.98$ ,  $P = 0.35$ ).

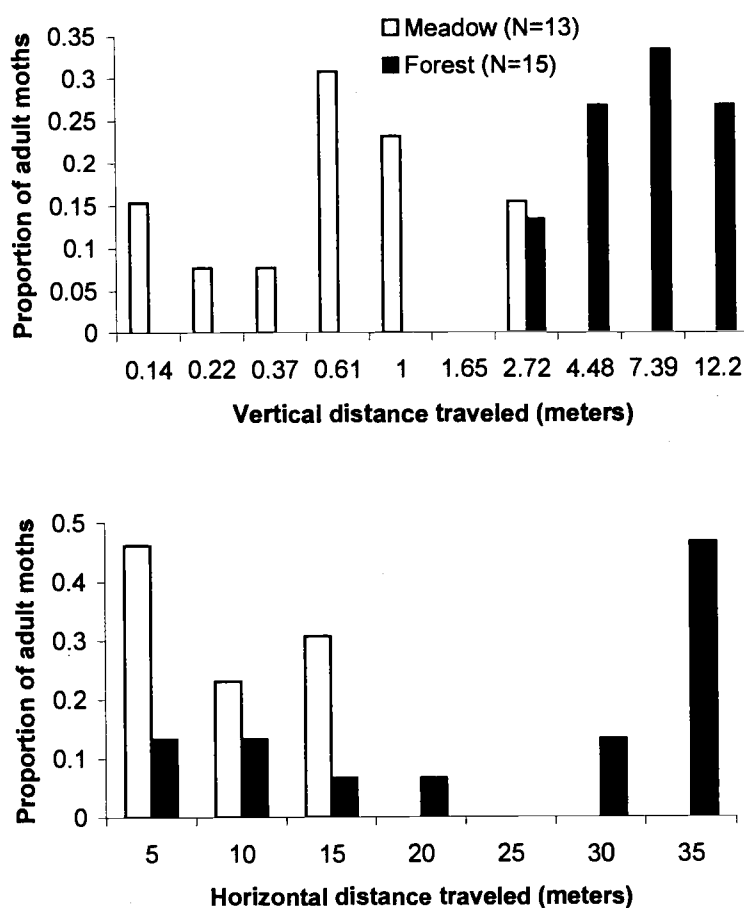


Figure 3.4. Distribution of vertical (top) and horizontal (bottom) distances traveled immediately after release for adult cinnabar moths classified as mobile in two habitats on Mary's Peak, OR.

Table 3.1. Mean vertical and horizontal distance traveled immediately after release for adult cinnabar moths classified as mobile in two habitats on Mary's Peak, OR.

Habitat	Vertical distance traveled (m)		Horizontal distance traveled (m)		Number of moths
	mean	se	mean	se	
Forest	5.9	0.9	22.8	2.8	15
Meadow	0.8	0.2	8.5	1.5	13
		$P < 0.0001$			$P = 0.0005$



Table 3.2. Number of marked cinnabar moths classified according to recapture, habitat, post-release behavior, wing condition, and gender.

Habitat	Behavior	Condition	Number of moths			
			Recaptured		Not Recaptured	
			Female	Male	Female	Male
Forest	immobile	low	3	1	27	6
		high	2	0	8	12
	mobile	low	0	0	2	10
		high	0	2	1	10
			5	3	38	38
Meadow	immobile	low	9	3	12	7
		high	6	1	6	14
	mobile	low	5	1	0	3
		high	4	7	0	5
			24	12	18	29

Table 3.3. Influence of gender, wing condition, post-release behavior and habitat on the odds of recapture for individual moths.

Source	Deviance	df	Z-statistic	P
Gender	5.464	1	-3.333	<0.001
Condition	1.710	1	-0.547	0.58
Behavior	11.312	1	3.206	<0.001
Habitat	26.313	1	4.628	<0.001
Error	147.806	162		

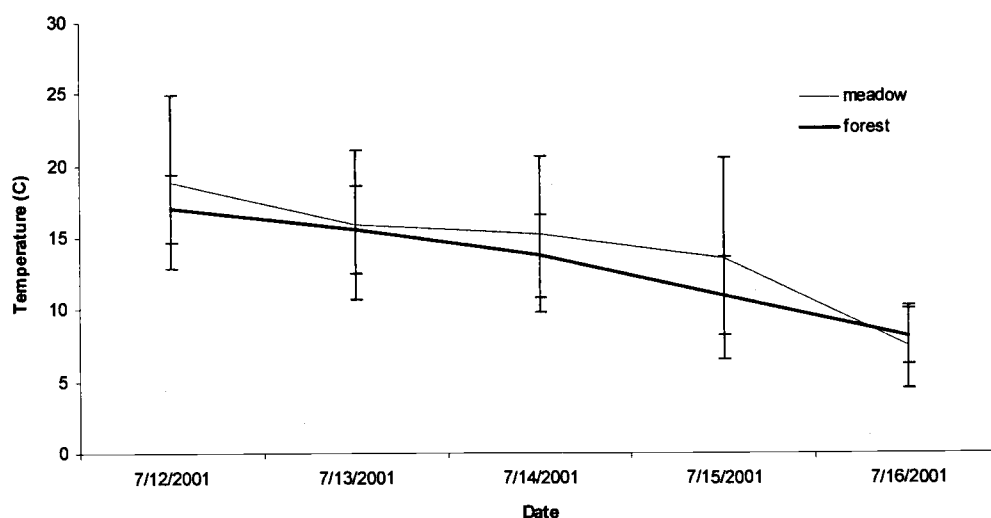


Figure 3.5. Temperature profile for meadow and forest habitats at the time of the adult mark-release-recapture experiment. The black line represents the forest habitat and the gray line represents the meadow habitat. Temperature each day was based on the mean of maximum, minimum, and current (at the time of sampling) temperatures. Error bars represent standard error of the mean temperature each day.

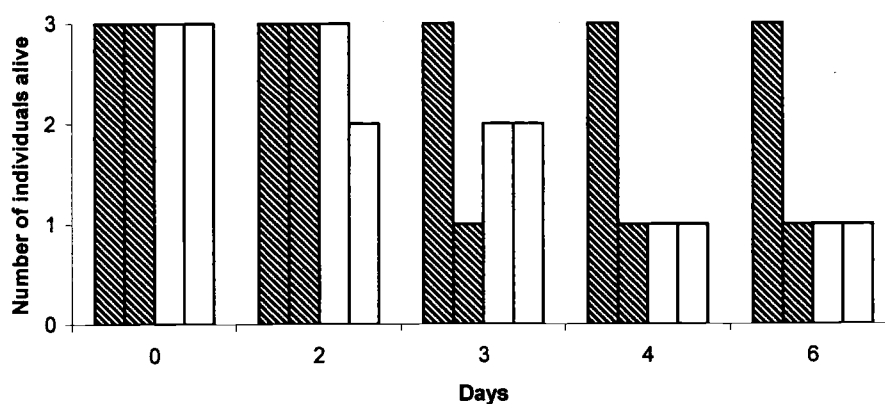


Figure 3.6. Survival of adult cinnabar moths caged within forest and meadow habitats on Mary's Peak, OR. Each column represents one cage, filled columns representing the forest habitat and open columns the meadow habitat.

## **Larval transfer**

Survival and developmental time differed for larvae at the two sites. We recovered only second instar larvae from the forest site, and by the fifth week we found neither larvae nor feeding damage (Table 3.4). Larvae in the meadow had developed past the second instar by the third week, and we recovered seven fifth instar larvae from the meadow site by the end of the sixth week.

The behavior of larvae in the forest differed from those in the meadow. The larvae appeared to feed normally during the first instar but then stopped feeding after the first molt. All second instar larvae observed were not active and were found on areas of the plant that showed no damage.

The meadow accumulated an average of 677.5 heat units between July 31 and September 8 while the forest accumulated an average of 570.8. Most third instar larvae in the meadow were found on August 17. By this date, the meadow had accumulated an average of 194 heat units. The forest accumulated the same number of heat units by August 20, at which time larvae in the forest remained in the second instar.

## **DISCUSSION**

We found habitat selection by the cinnabar moth to be related to adult movement and juvenile survival. When transplanted from the meadow to an unfamiliar site in the forest, adults flew farther and larvae were unable to survive. Short-term displacements differed between habitats: both horizontal and vertical dispersal distances were higher in the forest (Fig. 3.4, Table 3.1). We found no larvae beyond the second instar in the forest, while larvae in the meadow were able to complete development through to the fifth instar. Larvae in the forest also developed slower than those in the meadow.

Table 3.4. Survival of cinnabar moth caterpillars on Mary's Peak, OR. Columns represent numbers of each stage observed on sample dates in two habitats.

Habitat	Date	Eggs	1st	2nd	3rd	4th	5th
Meadow	7/31	278					
	8/10	73		64	1		
	8/17			16	21	6	
	8/23				4	2	
	8/28					6	6
	9/8						1
Forest	7/31	119					
	8/10	63	50				
	8/17	2		82			
	8/23			38			
	8/28			6			
	9/8						

These findings have important consequences for the safety of biological weed control. Suitable hosts growing in forest habitats are protected from the cinnabar moth. Exclusion of the moth from these habitats creates a time-independent spatial refuge for some non-target plants.

Two patterns emerge from this study: the odds of recovering individual moths were higher for females and those that were mobile following release. These results agree with similar findings by Rudd and McEvoy (1996). We observed that male moths were stronger fliers than females, which may explain the higher chance of recovering female moths. Male moths likely emigrated from the study site, whereas females remained within the areas sampled. We expected moths that were immobile immediately after release to be recaptured more often than mobile moths because we assumed mobile moths to be more active and to emigrate from the study site. Our results suggest that we were unable to recapture some immobile moths despite their presence in the area sampled.

Two unsettled points remain in this study: the fate of uncaptured adults and causes of juvenile mortality. Long-term displacements did not differ between habitats. However, recapture rates in the meadow were more than four times higher than in the forest. Forty-seven percent of moths released in the meadow habitat were recovered (62% of females and 31% of males) while only 10% of those released in the forest were recovered (14% of females and 7% of males). Recapture rates of all moths in the meadow were similar to those (41%) reported by Dempster (1971) and the rates for females in the meadow were similar to those (40-70%) reported by Crawley and Gillman (1989) for female moths. Our recapture rates of all moths in the meadow were higher than those reported by Rudd and McEvoy (1996) (13% of males and 16% of females), and the recapture rate of males in the meadow were higher than those reported for males (12-13%) by Crawley and Gillman (1989). Recapture rates for all moths and for each gender were lower in the forest than in these previous studies.

Displacements in the forest may be underestimated relative to displacements in the meadow because moths that eluded recapture likely left the

area sampled. Higher adult emigration is a more likely explanation of the differences in recapture rates than higher mortality because we found no differences in adult survival between the two habitats over the six days moths were caged (although our sample size,  $n = 12$ , may have not been high enough to detect real differences). Short-term displacements provided us with a more accurate estimate of moth dispersal by allowing us to directly observe flights immediately after release.

We were unable to determine the cause of juvenile mortality. Dempster (1971) found that generalist predators killed 23 to 61% of first and second instar larvae. Feeding by generalist predators may help explain the patterns we found because larvae in the forest developed more slowly and were therefore exposed to predation for a longer period of time. Likely, other unknown factors limit survival in the forest. The forest habitat accumulated more heat units than were necessary for larvae to reach the third instar in the meadow, even though it accumulated less total heat units than the meadow habitat. Philogene (1975) and Isaacson (1973b) found that larvae develop faster at higher temperatures, although the lowest temperature tested, 18.3 °C, was above the mean temperatures for both habitats in this study. To characterize the risk that the cinnabar moth poses to non-target plants at high elevation, it would be desirable to obtain better estimates of the effect of low temperatures on development and survival of this insect.

Slower developmental rates do not explain the 100% mortality we found in the forest. Cinnabar moth larvae may depend on behavior to increase the amount of heat they receive. They are often found feeding in full sun and may actively orient themselves in the sunlight to increase their temperature. Larvae in the forest are unable to modify the amount of heat they receive by orienting toward the sun, and thus may not accumulate the required number of heat units to develop past the second instar. In a study of the butterfly *Euphydryas editha bayensis*, Weiss et al. (1988) found that the ability of caterpillars to bask in full sun may be necessary for them to complete development before host plant senescence. In addition, Sipura and Tahvanainen (2000) found that leaf beetles feeding on willows preferred open,

sunny plants to shaded plants even though food quality was higher in the shade. The authors suggest that the preference is due to higher and more variable temperatures in the open habitat.

Host plant quality may differ between meadow and forest habitats. *Senecio triangularis* in the forest may not produce the same feeding cues as in the meadow or may be of lower nutritional quality for some unknown reason. Either difference can limit feeding and development of the larvae. Jansen and Stamp (1996) found host plant differences between tomato (*Lycopersicon esculentum*) grown in shade and sun to influence the growth of *Manduca sexta* caterpillars. Plants grown in the shade produced more protein and less allelochemicals, and caterpillars fed a diet of leaves from the shade grew faster than those fed leaves growing in the sun. In our study, plants growing in the shade may similarly produce less allelochemicals that may act as feeding stimulants, reducing the caterpillar's feeding response. A reduction in allelochemicals would not change the nutritional quality of the plant because cinnabar moth caterpillars appear to be insensitive to alkaloid variation in their diet over the range investigated (Soldaat and Vrieling 1992).

Forest habitats are unfavorable for cinnabar moth adults because they lack appropriate cues that allow adult moths to orient to patches of a suitable host. These habitats are also unfavorable for cinnabar moth caterpillars, which are unable to complete their development on suitable host plants within forest habitats. We did not determine which factors limit survival, although low temperatures, high predation rates, and low host plant quality may contribute to low rates of survival.

## CHAPTER 4

In this thesis, we investigated the patterns of association and interaction between the cinnabar moth, *Tyria jacobaeae*, and non-target *Senecio* and *Packera* species in Oregon, and the influence habitat imposes on these patterns. Our objectives were to determine which plant species were exposed, quantify the frequency and intensity of attack on exposed species, determine which variables help predict the pattern of interaction, and determine how habitat influences the ability of the cinnabar moth to attack native plants.

In our first study, we measured overlap in insect and plant distribution to determine exposure, observed actual frequency and intensity of interactions, and screened variables to help reconcile predicted with observed patterns of interaction. We found that nine of 20 native species (3 *Senecio* and 6 *Packera*) have been exposed to the cinnabar moth in Oregon. Ten of the 11 unexposed species (91%) occurred in areas of the state where the cinnabar moth does not occur. Of the nine exposed species, only three were attacked: *Packera cymbalarioides*, *P. pseud aurea*, and *S. triangularis*. We conclude that patches of non-target plants occur where attack frequency and severity are moderate but many plants escape feeding. Attacked plants may be able to minimize losses to the cinnabar moth by virtue of their life histories.

In our second study, we determined how habitat modifies behavior of adult moths and survival and development of larvae. We found forest habitats to be unfavorable to the cinnabar moth. Adults within the forest flew farther and higher immediately following release compared to those in the meadow. In addition, larvae were unable to complete development in the forest despite seemingly adequate temperature levels. We conclude that forest habitats act as a refuge for suitable non-target hosts.

Taken together, these studies show that only a fraction of potential non-target hosts are used by the cinnabar moth in Oregon because of geographic



separation of insects and plants, habitat selection by the moth, and phenological differences between the moth and native plants. Our systematic survey improved upon haphazard reporting of non-target feeding and our experiment investigated the influence of habitat as a potential refuge for non-target plants. Future studies should focus on the impact of the observed levels of feeding on populations of the attacked species.

## BIBLIOGRAPHY

- Aplin, R.T. and M. Rothschild. 1972. Poisonous alkaloids in the tissues of the garden tiger moth (*Arctia caja* L.) and the cinnabar moth (*Tyria* (= *Callimorpha*) *jacobaeae* L.) (Lepidoptera). Pp. 579-595 in *Toxins of Animal and Plant Origin*. A. de Vries and K. Kochva (eds.). Gordon and Breach, London.
- Bain, J.F. and R.K. Jansen. 1995. A phylogenetic analysis of the aureoid *Senecio* (*Asteraceae*) complex based on ITS sequence data. *Plant Systematics and Evolution* 195:209-219.
- Bain, J.F. and J. Walker. 1995. A comparison of the pollen wall ultrastructure of aureoid and non-aureoid *Senecio* species (*Asteraceae*) in North America. *Plant Systematics and Evolution* 195:199-207.
- Baloch, G. M., A. I. Mohyuddin, M.A. Ghani. 1969. Biological control of *Cuscuta* spp. III. Phenology, biology and host specificity of *Herpystis cuscutae* Bradley (Lepidoptera: Tortricidae). *Entomophaga* 14:119-128.
- Barkley, T. 1993. *Erechtites*. p. 250 In *The Jepson manual: Vascular plants of California*. Hickman, J. (ed.). University of California Press, Berkeley.
- Bennett, F.D. and D.H. Habeck. 1995. *Cactoblastis cactorum*: A successful weed control agent in the Caribbean, now a pest in Florida. Proc. VIII Int. Symp. Biol. Contr. Weeds, 2-7 Feb 1992, Canterbury, New Zealand. Delfosse, E.S. and R.R. Scott (eds.). pp. 21-26.
- Blossey, B. 1995. Host specificity screening of insect biological weed control agents as part of an environmental risk assessment. Pp. 84-89 In *Biological control: Benefits and risks*. Hokkanen, H.T.M. and J.M. Lynch (eds.). Cambridge University Press, Cambridge, UK.
- Bucher, G.E and P. Harris. 1961. Food-plant spectrum and elimination of disease of Cinnabar Moth larvae, *Hypocrita jacobaeae* (L.) (Lepidoptera: Arctiidae). *Canadian Entomologist* 93:931-936.
- Cameron, E. 1935. A study of the natural control of ragwort (*Senecio jacobaea* L.). *Journal of Ecology* 23:265-322.
- Chambers, K.L. and S. Sundberg. 1998. Oregon vascular plant checklist: *Asteraceae*. Oregon Flora Project, Oregon State University, Corvallis, Oregon. 54 pp.

- Coulson, J.R. 1999. Developing safe weed biocontrol in the United States. pp. 2-3 in Weed biocontrol: extended abstracts from the 1997 interagency noxious-weed symposium. Isaacson, D.I. and M. Brookes (eds.). US Department of Agriculture, Forest Service, Morgantown, West Virginia, USA.
- Crawley, M. J. and M. P. Gillman 1989. Population dynamics of cinnabar moth and ragwort in grassland. *Journal of Animal Ecology* 58: 1035-1050.
- Daly, C. and G. Taylor. 1998. Western U.S. Average Monthly or Annual Precipitation, 1961-90. Water and Climate Center of the Natural Resources Conservation Service. Portland, Oregon, USA.
- Dempster, J.P. 1971. The population ecology of the cinnabar moth, *Tyria jacobaea* (Lepidoptera, Arctiidae). *Oecologia* 7:26-67.
- Dempster, J.P. 1982. The ecology of the cinnabar moth, *Tyria jacobaea* L. (Lepidoptera: Arctiidae). *Advances in Ecological Research* 12:1-36.
- Diehl, J.W. 1988. Feeding, colonization and impact of the cinnabar moth, *Tyria jacobaea*, on *Senecio triangularis*, a novel, native host plant. M.S. Thesis. Oregon State University. 85 pp.
- Diehl, J.W. and P.B. McEvoy. 1989. Impact of the Cinnabar Moth (*Tyria jacobaea*) on *Senecio triangularis*, a non-target native plant in Oregon. Proc. VII. Int. Symp. Biol. Contr. Weeds, 1988, Rome, Italy. Delfosse, E.S. (ed.). pp. 119-126.
- Dunn, P. H. 1978. Shortcomings in the classic tests of candidate insects for biocontrol of weeds. Proc. V. Int. Symp. Biol. Contr. Weeds, 1976, Gainesville, Florida, USA. Freeman, T.E. (ed.). pp.51-56.
- Dunn, P. H. and A. Rizza 1977. Host specificity of *Psylliodes chalconera*, a candidate for biological control of musk thistle. *Environmental Entomology* 6: 449-454.
- Eastman, D.C. 1990. Rare and endangered plants of Oregon. Beautiful America. Wilsonville, OR. 194 pp.
- Follett, P.A. and J.J. Duan, editors. 2000. Nontarget effects of biological control. Kluwer Academic, Boston, MA, USA. 316 pp.
- Frick, K.E. and J.K. Holloway. 1964. Establishment of the cinnabar moth, *Tyria jacobaea*, on tansy ragwort in the western United States. *Journal of Economic Entomology* 57: 152-154.

- Fuller, J.F., E.M. Coombs, and P.B. McEvoy. 2002. Assessing the safety of biological weed control: Distribution of the cinnabar moth *Tyria jacobaeae* on non-target, native plant species in Oregon. Unpublished Manuscript.
- Gassmann, A. and S.M. Louda. 2001. *Rhinocyllus conicus*: Initial evaluation and subsequent ecological impacts in North America. pp. 147-183 in Evaluating indirect ecological effects of biological control. Wajnberg, E., J.K. Scott, and P.C. Quimby (eds.). CABI Publishing, New York, NY, USA.
- Harris, P. 1988. Environmental impact of weed-control insects. *BioScience* 38:542-548.
- Harris, P. 1990. Environmental impact of introduced biological control agents. Pp. 289-300 in Critical issues in biological control. M. Mackauer, L.E. Ehler, and J. Roland (eds.). Intercept, Andover, England.
- Harris, P. and P. McEvoy. 1995. The predictability of insect host plant utilization from feeding tests and suggested improvements for screening weed biological control agents. *Proc. VIII Int. Symp. Biol. Contr. Weeds*, 1992, Canterbury, New Zealand. Delfosse, E.S. and R.R. Scott (eds.). pp. 125-131.
- Harris, P. and H. Zwolfer. 1968. Screening of phytophagous insects for biological control of weeds. *Canadian Entomologist* 100:295-303.
- Harrison, S., C.D. Thomas, and T.M. Lewinsohn. 1995. Testing a metapopulation model of coexistence in the insect community on ragwort (*Senecio jacobaea*). *American Naturalist* 145:546-562.
- Hitchcock, C.L. and A. Cronquist. 1973. *Flora of the Pacific Northwest: An illustrated manual*. University of Washington Press, Seattle, USA.
- Hodgson, J.M. and N.E. Rees. 1976. Dispersal of *Rhinocyllus conicus* for biocontrol of musk thistle. *Weed Science* 24:59-62.
- Howarth, F. G. 1991. Environmental impacts of classical biological control. *Annual Review of Entomology* 36: 485-509.
- Isaacson, D.L. 1973a. A life table for the cinnabar moth, *Tyria jacobaeae*, in Oregon. *Entomophaga* 18:291-303.
- Isaacson, D.L. 1973b. Population dynamics of the cinnabar moth, *Tyria jacobaeae* (Lepidoptera: Arctiidae). M.S. Thesis, Oregon State University. 65 pp.

- Jansen, M.P.T. and N.E. Stamp. 1997. Effects of light availability on host plant chemistry and the consequences for behavior and growth of an insect herbivore. *Entomologia Experimentalis et Applicata* 82: 319-333.
- Julien, M.H. and M.W. Griffiths. 1998. Biological control of weeds: A world catalogue of agents and their target weeds. CABI Publishing, New York, NY, USA. 223 pp.
- van Klinken, R.D. and O.R. Edwards. 2002. Is host-specificity of weed biological control agents likely to evolve rapidly following establishment? *Ecology Letters* 5:590-596.
- Louda, S.M. and A.E. Arnett. 2000. Predicting non-target ecological effects of biological control agents: Evidence from *Rhinocyllus conicus*. Proc. X Int. Symp. Biol. Contr. Weeds, 4-14 July 1999, Montana State University, Bozeman, Montana, USA. Spencer, N.R. (ed.). pp. 551-567.
- Louda, S.M., R.W. Pemberton, M.T. Johnson, and P.A. Follett. 2002. Non-target effects – The achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. *Annual Review of Entomology*. In press.
- McEvoy, P.B. 1996. Host specificity and biological pest control: How well is research on host specificity addressing the potential risks of biological control? *Bioscience* 46: 401-405.
- McEvoy, P.B. 1999. Host-specificity as a measure of safety in weed biocontrol. Pp. 17-19 in *Weed biocontrol: Extended abstracts from the 1997 interagency noxious weed symposium*. Isaacson, D. and M.H. Brookes (tech. coords.) Dec. 2-4, 1997. Corvallis, OR. Forest Health Technology Enterprise Team FHTET-98-12. Morgantown, WV: USDA, FS, Forest Health Technology Enterprise Team, and Salem, OR: ODA.
- McEvoy, P.B. and E.M. Coombs. 1999. Why things bite back: unintended consequences of biological weed control. pp. 167-194 in *Nontarget effects of biological control*. P.A. Follett and J.J. Duan (eds.). Kluwer Academic Publishers, Boston, Massachusetts, USA.
- McFadyen, R. E. C. 1998. Biological control of weeds. *Annual Review of Entomology* 43: 369-393.
- van der Meijden, E. 1976. Changes in the distribution pattern of *Tyria jacobaeae* L. in relation to soil properties. *Acta Botanica Neerlandica* 23:681-690.

- van der Meijden, E. 1979. Herbivore exploitation of a fugitive plant species: local survival and extinction of the cinnabar moth and ragwort in a heterogeneous environment. *Oecologia* 42: 307-323.
- van der Meijden, E. A.M. van Zoelen, and L.L. Soldaat. 1989. Oviposition by the cinnabar moth, *Tyria jacobaeae*, in relation to nitrogen, sugars and alkaloids of ragwort, *Senecio jacobaea*. *Oikos* 54: 337-344.
- Merkle, J. 1951. An analysis of the plant communities of Mary's Peak, western Oregon. *Ecology* 32: 618-640.
- OSU Herbarium. 2002. <http://www.orst.edu/dept/botany/herbarium/db>.
- Parker, H.L. 1960. Starvation tests with larvae of the cinnabar moth. *Journal of Economic Entomology* 53: 472-473.
- Pemberton, R.W. 2000. Predictable risk to native plants in weed biological control. *Oecologia* 125:489-494.
- Philogene, B.J.R. 1975. Responses of the cinnabar moth *Hypocrita jacobaeae* to various temperature/photoperiod regimes. *Journal of Insect Physiology* 21: 1415-1417.
- Ramsey, F.L. and D.W. Schafer. 1997. *The statistical sleuth: A course in methods of data analysis*. Duxbury Press, Belmont, CA. 742 pp.
- Roitman, J.N. 1983. The pyrrolizidine alkaloids of *Senecio triangularis*. *Australian Journal of Chemistry* 36:1203-1213.
- Roitman, J.N., R.J. Molyneux, and A.E. Johnson. 1979. Pyrrolizidine alkaloid content of *Senecio* species. Pp.23-33 in *Symposium on pyrrolizidine (Senecio) alkaloids: toxicity, metabolism, and poisonous plant control measures*. P.R. Cheeke (ed.). The Nutrition Research Institute, Oregon State University, Corvallis, Oregon.
- Rose, S.D. 1978. Effect of diet on larval development, adult emergence and fecundity of the cinnabar moth, *Tyria jacobaeae* (L.) (Lepidoptera: Arctiidae). M.S. Thesis, Oregon State University. 88 pp.
- Rudd, N. T. and P. B. McEvoy 1996. Local dispersal by the cinnabar moth *Tyria jacobaeae*. *Ecological Applications* 6(1): 285-297.

- Rueger, H. and M.H. Benn. 1983. The alkaloids of *Senecio triangularis* Hook. Canadian Journal of Chemistry 61:2526-2529.
- Schooler, S.S., E.M. Coombs, and P.B. McEvoy. 2001. Field tests of nontarget impact to crape myrtle by *Galerucella pusilla* and *G. californiensis* (Chrysomelidae), biological control agents of purple loosestrife. *In press* Weed Science.
- Simberloff, D. and P. Stiling 1996. How risky is biological control? Ecology 77: 1965-1974.
- Sipura, M. and J. Tahvanainen. 2000. Shading enhances the quality of willow leaves to leaf beetles – but does it matter? Oikos 91:550-558.
- Snow, B. D. 1984. Plant communities of the grassy balds of Marys Peak, Oregon. M.S. Thesis, Oregon State University. 109 pp.
- Soldaat, L.L. and K. Vrieling. 1992. The influence of nutritional and genetic factors on larval performance of the cinnabar moth, *Tyria jacobaeae*. Entomologia Experimentalis et Applicata 62: 29-36.
- Sundberg, S. Oregon State University, Department of Botany and Plant Pathology.
- Surles, W.W., L.T. Kok, and R.L. Pienkowski. 1974. *Rhinocyllus conicus* establishment for biocontrol of thistles in Virginia. Weed Science 22:1-3.
- USDA, NRCS. 2001. The PLANTS Database, Version 3.1 (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
- Wajnberg, E., J.K. Scott, and P.C. Quimby, editors. 2000. Evaluating indirect ecological effects of biological control. CABI Bioscience, New York, NY, USA. 261 pp.
- Wapshere, A. J. 1974. A strategy for evaluating the safety of organisms for biological weed control. Annals of Applied Biology 77:201-211.
- Wapshere, A.J. 1989. A testing sequence for reducing rejection of potential biological control agents for weeds. Annals of Applied Biology 114:515-526.

- Weiss, S.B., D.D. Murphy, and R.R. White. 1988. Sun, slope, and butterflies: Topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69:1486-1496.
- Zimmermann, H.G., V.C. Moran, and J.H. Hoffmann. 2000. The renowned cactus moth, *Cactoblastis cactorum*: its natural history and threat to native *Opuntia* floras in Mexico and the United States of America. Diversity and Distributions 6:259-269.
- Zwolfer, H. and P. Harris 1971. Host specificity determination of insects for biological control of weeds. Annual Review of Entomology 16: 159-178.
- Zwolfer, H. and P. Harris. 1984. Biology and host specificity of *Rhinocyllus conicus* (Froel.) (Col, Curculionidae), a successful agent for biocontrol of the thistle, *Carduus nutans* L. Zeitschrift fuer Angewandte Entomologie 97:36-62.