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Causes and Consequences of Local Variability in Aroga Websteri Clarke Abundance Over Space and Time

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CAUSES AND CONSEQUENCES OF LOCAL VARIABILITY IN *AROGA*

WEBSTERI CLARKE ABUNDANCE OVER SPACE AND TIME

by

Virginia L.J. Bolshakova

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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UTAH STATE UNIVERSITY
Logan, Utah

2013

ABSTRACT

Causes and Consequences of Local Variability in *Aroga websteri* Clarke

Abundance over Space and Time

by

Virginia L.J. Bolshakova, Doctor of Philosophy

Utah State University, 2013

Major Professor: Edward W. Evans
Department: Biology

With increasing pressures on sagebrush steppe ecosystems, the sagebrush defoliating *Aroga* moth, *Aroga websteri* Clarke (Lepidoptera: Gelechiidae) has become a critical organism of concern. Despite the cyclic nature of *A. websteri* outbreaks throughout the Great Basin, there is limited information on the moth's population dynamics. The goal of this dissertation was to develop effective means of assessing and describing population trends of the *Aroga* moth across space and time, and potentially promoting biological control of the moth to prevent unnaturally large, prolonged and destructive outbreaks. Field studies were conducted to: 1) monitor and quantify activity of the *Aroga* moth and its damage to sagebrush across a montane landscape, 2) assess the effects of parasitoid and floral diversity on parasitism of the moth, and 3) develop a degree-day (°D) model to describe the phenology of the insect, as well as field

populations studied previously. North-facing stands of sagebrush, characterized by low

values of solar radiation, appear to be especially suitable local habitats for the *Aroga*

moth. High habitat suitability may result from favorable microclimate, both in its direct

effects on the *Aroga* moth and in indirect effects tied to sagebrush plant community

productivity and performance. Parasitoid and floral diversity differed strongly and

predictably across space and time, with greatest overall parasitism occurring when three

major parasitoid species were present. Field experiments revealed individual species of

parasitoids differed substantially and complemented one another in their patterns of

attack among local populations of the *Aroga* moth across the montane landscape.

Differing responses to provision of floral resources and methyl salicylate (an herbivore-

induced plant volatile) support the general hypothesis that over large scales of space and

time, species diversity of natural enemies promotes suppression of insect herbivores.

Lastly, degree-day models were developed and least variation among years in (°D)

phenology resulted with the single-sine method with base temperature of 5°C. Years of

historical *Aroga* moth outbreaks had characteristic seasonal patterns of °D accumulation

that were intermediate and characterized by high precipitation in June and July during

late stage larval development. Thus, it appears that periodic outbreaks of the defoliator

are due to favorable weather conditions.

PUBLIC ABSTRACT

Causes and Consequences of Local Variability in *Aroga websteri* Clarke

Abundance over Space and Time

Virginia L.J. Bolshakova, PhD, Ecology

Sagebrush steppe habitat is rapidly declining in the Intermountain West in both

quality and quantity. Observed reductions in animal and bird populations associated with

sagebrush, invasion of exotic annual grasses such as cheatgrass (*Bromus tectorum*), and

other concerns with climate change have led to a growing awareness of the need to

monitor and better understand the rate of habitat loss. Sagebrush lands are subject to

periodic loss caused by insect feeding damage, and human activities have the potential to

promote unnaturally high levels of such loss. The sagebrush defoliating *Aroga* moth,

Aroga websteri Clarke (Lepidoptera: Gelechiidae), can kill large stands of sagebrush over

a short period of time. Despite the cyclic nature of *A. websteri* outbreaks throughout the

Great Basin, there is limited information on the moth's population dynamics. The goal of

this dissertation was to develop effective means of assessing and describing how the

Aroga moth abundance changes across the landscape over time, and potentially

promoting biological control of the moth (by natural enemies) to prevent unnaturally

large, prolonged and destructive outbreaks. Field studies were conducted to: 1) monitor

and quantify activity of the *Aroga* moth and its damage to sagebrush across a montane

landscape, 2) assess the effects of parasitoid and floral diversity on parasitism of the

moth, and 3) develop a degree-day (°D) model to describe the insect's development over time as well as field populations studied previously. North-facing stands of sagebrush, characterized by low values of solar radiation, appear to be especially favorable local habitats for the *Aroga* moth. High habitat suitability may result from favorable microclimate, both in its direct effects on the *Aroga* moth and in indirect effects tied to sagebrush plant community productivity and performance. Parasitoid and floral diversity differed strongly and predictably across space and time, with greatest overall parasitism occurring when three major parasitoid species were present. Field experiments revealed individual species of parasitoids differed substantially and complemented one another in their patterns of attack among local populations of the *Aroga* moth across the montane landscape. Differing responses to provision of floral resources and methyl salicylate (an herbivore-induced plant volatile) support the general hypothesis that over large scales of space and time, species diversity of natural enemies promotes suppression of insect herbivores. Lastly, degree-day models were developed and least variation among years in (°D) phenology resulted with the single-sine method with base temperature of 5°C. Years of historical *Aroga* moth outbreaks had characteristic seasonal patterns of °D accumulation that were intermediate and characterized by high precipitation in June and July during late stage larval development. Thus it appears that periodic outbreaks of the defoliator are due to favorable weather conditions.

ACKNOWLEDGMENTS

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CHAPTER 1

INTRODUCTION

Sagebrush *Artemisia* spp., Asteraceae is declining in abundance throughout western North America as its habitat becomes increasingly degraded and fragmented (Braun et al. 1976, Bock et al. 1993, Dobkin and Sauder 2004, Welch 2005). Estimates of the Pre-European range of sagebrush exceed 63 million ha, while the present range is estimated to have been reduced by 32-50 percent (Schroeder et al. 2004, Welch 2005, Miller et al. 2011). The conversion of large acreages of rangelands to annual grasslands (D'Antonio and Vitousek 1992, Keeley 2006) and the expansion of human infrastructures (Knick et al. 2003) have contributed significantly to this decline. Observed reductions in populations of birds and mammals associated with sagebrush (Dobkin and Sauder 2004), invasion of exotic annual grasses such as cheatgrass (*Bromus tectorum*), and other factors such as climate change (Wisdom et al. 2005), have led to growing awareness of the need to monitor and better understand the rate of habitat loss.

Sagebrush habitat is also subject to periodic loss caused by insect feeding damage, and human activities have the potential to promote unnaturally high levels of such loss. The sagebrush defoliator *Aroga websteri* Clarke; Gelichiidae, known also as the *Aroga* moth, can kill large stands of sagebrush over a short period of time. For example, it was estimated that the *Aroga* moth killed sagebrush on as much as 10 to 15 thousand acres in Malheur County, Oregon, in a single year during one eruptive episode (Gates 1964). This native moth is common in sagebrush stands throughout much of the Great Basin. While literature on this species is limited, it is apparent that population numbers reach high levels periodically. The *Aroga* moth feeds primarily on species of

Artemisia (sagebrush), especially *Artemisia tridentata* Nuttall (big sagebrush) (Henry 1961). Recently, significant outbreaks of the defoliator have been observed in southeastern Idaho, northern California, central Oregon, Nevada, and northern Utah. Given the current status of sagebrush rangeland, unnaturally large or extended outbreaks of the *Aroga* moth could pose a serious ecological and economic threat.

The ecological mechanisms that cause or prevent insect outbreaks are not often known, although it is generally accepted that, at the onset of an outbreak, the population has escaped from some controlling set of factors (Royama 1997, Berryman 1999). Factors that determine limits of species distributions, including boundaries of local populations, are also often difficult to identify, and include both abiotic, as well as biotic factors (Gaston 2003). This dissertation was completed in a cooperative effort between the State of Utah Division of Wildlife Resources (UDWR), USDA FS Forest Health Protection, Utah Division of Forestry, Fire and State Lands, and Utah State University to enhance the management of sagebrush lands by developing improved tools for detection and assessment of *Aroga* moth populations. This included developing effective means of assessing and describing population trends of the *Aroga* moth (past and present), and potentially promoting biological control of the moth to prevent unnaturally large, prolonged and destructive outbreaks. To address these needs, three major objectives in this project are addressed in the following chapters:

1) Monitor and quantify the activity of the *Aroga* moth at a range of sites in the
   Intermountain West, with emphasis on northern Utah.

2) Assess the degree of parasitism to investigate how *Aroga* moth population

dynamics are influenced by interactions with natural enemies (hymenopteran

parasitoids).

3) Link *Aroga* moth population dynamics to key abiotic variables (i.e., assess the

influences of variations in weather as it affects the *Aroga* moth).

In Chapter 2, I describe the spatial and temporal variation in *Aroga* moth density

and the moth's defoliation of sagebrush stands throughout the 5700 hectare Henefer-Echo

Wildlife Management Area of northern Utah, a UDWR management area dominated by

sagebrush-steppe. The study addresses topographic features in a mountainous terrain as

they may affect the local population density of the *Aroga* moth. Elevation, aspect, and

slope have been demonstrated to be useful surrogates for the spatial and temporal

distribution of factors such as radiation, precipitation, and temperature that influence

species composition and productivity. The objective was to determine how moth

abundance, survivorship, and damage to the host plant varied among local sites, and to

determine how much of this variability could be accounted for by sagebrush abundance,

elevation, slope, aspect, or incident solar radiation. The ultimate goal of the study was to

assess how well the moth's varying abundance and impact on its host plant over space

and time might be predicted from measurements of local habitat characteristics.

In Chapter 3, I assess the complexities of insect and plant species interactions, as

centered on the *Aroga* moth, along an elevation gradient. Sagebrush-steppe ecosystems

support a diverse flora and fauna, but have been increasingly adversely affected

following European settlement and the introduction of agriculture. The introduction of

grazing, for example, has reduced understory floral diversity. Reduced understory floral diversity may exacerbate the effects of naturally occurring episodic outbreaks of the *Aroga* moth. These outbreaks may be limited in scope and duration by parasitism of the moth, and the parasitoids as adults may depend on floral resources. I examined the patterns of abundance of the sagebrush defoliator, its parasitoids, and flowering understory plants along an altitudinal gradient throughout the Henefer-Echo WMA. Solid understanding of the interplay between defoliator, parasitoids, and floral resources may assist managers in promoting high quality habitat for parasitoids to limit adverse effects of defoliator irruptions.

In Chapter 4, I examine potential links between weather (particularly temperature and precipitation) and *Aroga* moth population dynamics. Dynamics that cause or prevent outbreaks are not often known, but likely include both abiotic and biotic factors interacting in important ways. A simple degree-day (°D) model was developed to describe the phenology of the moth. This tool was used to sample the population at critical periods in its life-cycle, as well as to compare growing °D accumulations associated with annual moth population estimates made during my studies and previously in Curlew Valley, ID/UT during 1971-1975 (Hsiao 1984) and in Alturas, CA during 1962-1964 (Hall 1965). Patterns of fluctuating temperature and precipitation associated with key periods in *Aroga* moth development were compared among years with endemic (low) and outbreak levels of the *Aroga* moth.

These three studies build upon each other and collectively contribute to better general understanding of *Aroga* moth population dynamics. This in turn will support

more effective management of sagebrush rangeland. Recent outbreaks throughout the

Great Basin have made the defoliator increasingly a subject of concern. I hope that the

studies presented here will add to the foundation provided by earlier studies of this

species, and will stimulate further research into *Aroga* moth biology and sagebrush

conservation.

<div align="center">**LITERATURE CITED**</div>

Berryman, A. A. 1999. Principles of populations dynamics and their applications.
Stanley Thorns, Cheltenham, England.

Bock, C. E., V. A. Saab, T. D. Rich, and B. S. Dobkin. 1993. Effects of livestock
grazing on neotropical migratory landbirds in western North America. *In* D. M.
Finch and P. W. Stangel, editors. Status and management of neotropical migratory
birds. USDA Forest Service General Technical Report. **GTR-RM-229**.

Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976.
Conservation committee report on effects of alteration of sagebrush communities
on the associated avifauna. Wilson Bulletin **88**: 165-171.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the
grass/fire cycle, and global change. Annual Review in Ecology and Systematics
23: 63-87.

Dobkin, D. S., and J. D. Sauder. 2004. Shrub steppe landscapes in jeopardy:
distributions, abundances, and the uncertain future of birds and small mammals in
the Intermountain West. High Desert Ecological Research Institute, Bend,
Oregon, USA.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, England.

Gates, D. H. 1964. Sagebrush infested by leaf defoliating moth. Journal of Rangeland Management. **17**: 209-210.

Hall, R. C. 1965. Sagebrush defoliator outbreak in Northern California. USDA Forest Service, Research Note **PSW-75**.

Henry, J. E. 1961. The biology of the sagebrush defoliator, *Aroga* websteri Clarke, in Idaho. Thesis. University of Idaho, Moscow, Idaho, USA.

Hsiao, T. H. 1984. Biology and demography of the sagebrush defoliator and its impacts on big sagebrush. Pages 191-198 *in* E. D. McArthur and B. L. Welch, editors. Proceedings, Symposium on the Biology of Artemisia and Chrysothamnus, 9-13 June 1984, Provo, UT. USDA Forest Service General Technical Report **GTR-INT-200.**

Keeley, J. E. 2006. Fire management impacts on invasive plants in the western United States. Conservation Biology **20**: 275-38.

Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, M. W. Vander Hagen, and C. Van Riper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. The Condor **105**: 611-634.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom, and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. Pages 145-184 *in* S. T. Knick and J. W. Connelly, editors. Greater sage-grouse: ecology and conservation of a landscape species and

its habitats. Studies in avian biology. University of California Press, Berkeley, California, USA.

Royama, T. 1997. Populations dynamics of forest insects: are they governed by single or multiple factors? Pages 37-48 *in* A. D. Watt, N. E. Stork, and M. D. Hunter, editors. Forests and Insects. Chapman and Hall, New York, New York, USA.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D. Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardern, M. A. Hilliard, G. D. Kobrider, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V. Riderson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America. The Condor **106**: 363-376.

Welch, B. L. 2005. Big sagebrush: a sea fragmented into lakes, ponds, and puddles. General Technical Report **RMRS-GTR-144**.

Wisdom, M., M. Rowland, L. Suring, L. Shueck, C. Meinke, C. and S. Knick. 2005. Evaluating species of conservation concern at regional scale. Pages 289-307 *in* M. Wisdom, M. Rowland, and L. Suring, editors. Habitat threats in the sagebrush ecosystem: Methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, Kansas, USA.

CHAPTER 2

SPATIAL AND TEMPORAL DYNAMICS OF *AROGA* MOTH (LEPIDOPTERA: GELICHIIDAE) POPULATIONS AND THEIR DAMAGE TO SAGEBRUSH IN LOW-TO-HIGH ELEVATION SHRUB STEPPE[1]

ABSTRACT This study examines spatial and temporal variation in the density of the *Aroga* moth, *Aroga websteri* Clarke (Lepidoptera: Gelechiidae), and in its damage to its host plants, sagebrush, in northern Utah. Such variation during and following an outbreak of the moth is examined in relation to physical attributes of the habitat for local moth and sagebrush populations. Topographic features (elevation, aspect, and slope) have been demonstrated to be useful surrogate variables for determining the spatial and temporal distribution of factors, such as radiation, precipitation, and temperature that influence species composition and productivity. The objective of the present study was to determine how moth abundance, survivorship, and damage to the host plant varied among local sites, and to determine how much of this variability could be accounted for by sagebrush abundance, elevation, slope, aspect, or incident solar radiation. The ultimate goal of the study was to assess how well the moth's abundance and the impact on its host plant over space and time might be predicted from measurements of local habitat characteristics. North-facing stands of sagebrush, characterized by lower values of incident solar radiation, appear to be especially suitable local habitats for the *Aroga* moth. This high habitat suitability may result from favorable microclimate, both in its direct effects on the *Aroga* moth and in indirect effects tied to sagebrush plant community

productivity and performance. Further study is called for to determine how environmental variables that are fixed (e.g. aspect), and those that are not (e.g. precipitation), interact to influence the population dynamics of the *Aroga* moth and the sagebrush stands that it attacks.

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[1] Co-author: Edward W. Evans. Written following *Annals of the Entomological Society of America* Journal specifications.

Episodic defoliation of sagebrush (*Artemisia* spp.) has been reported throughout the Great Basin, leading to significant mortality in localized areas. Periodic outbreaks of the native moth *Aroga websteri* Clarke (Lepidoptera: Gelechiidae) cause severe defoliation (Gates 1964, Hsiao 1984). Commonly called the sagebrush defoliator or *Aroga* moth, *A. websteri* feeds primarily on *A. tridentata* (big sagebrush) (Henry 1961), a widely distributed, dominant plant in much of western North America (West 1983, West and Young 2000). At outbreak, larvae defoliate and kill *A. tridentata* shrubs in large numbers within as little as one or two years after defoliation (Hall 1965, Kirkland 1972, Temte 1977). Even at moderate larval densities, damage by the *Aroga* moth significantly reduces *A. tridentata* seedset (Hsiao 1984). Loss of foliage in sagebrush stands, as well as outright death of individual shrubs, decreases forage and cover for wildlife, increases hazardous fuel loads across the landscape, and heightens the susceptibility of the plant community to foreign invaders such as cheatgrass, *Bromus tectorum* (Hall 1965, Widsom et al. 2005, Chambers et al. 2007).

Despite the cyclic nature of *A. websteri* outbreaks throughout the Great Basin, there is only limited information on the spatial and temporal dynamics of these outbreaks (Hsiao 1984). Defoliator outbreaks can occur over areas of several hundred to several thousand hectares. It is not well known how density among local moth populations varies within an outbreak area at any point in the cycle. Density is likely to vary with local habitat suitability, but it is unknown what general factors may determine habitat suitability. It is also unknown whether the densities of local populations of the moth rise and fall synchronously with each other during outbreaks that may extend over very large geographic areas.

In this study, spatial and temporal variation in moth density and damage inflicted on sagebrush during and surrounding the years of an outbreak in northern Utah was examined in relation to physical attributes of the habitat for local moth and sagebrush populations. Insect species typically vary widely in local population density across multiple spatial scales (Root 1988, Brewer and Gaston 2003, Gripenberg and Roslin 2007). The causes and consequences of such variation in local insect population density can be investigated by considering spatial variation in physical attributes of the habitat (Andresen et al. 2001, Irwin and Lee 2003). These attributes may influence underlying demographic rates of an insect species (Thomas and Kunin 1999). This study addresses topographic features (elevation, aspect, and slope) in a mountainous terrain as they may affect the local population density of the *Aroga* moth. Aspect and slope are considered both individually and as linked together in an index that estimates incident solar radiation.

Topographic heterogeneity often plays a key role in the population dynamics of broadly distributed terrestrial invertebrates (Janzen 1967, Hodkinson 2005, Garrick 2011). Across an elevation gradient, populations at the lower and upper extremes experience highly divergent local environmental conditions (McCoy 1990, Hodkinson 2005, Straw et al. 2009). Similarly, across gradients of slope, aspect, and incident solar radiation in mountainous terrain, local populations may differ greatly in the local environmental conditions that they experience, thereby influencing species distributions and habitat selection. Keating et al. (2007), for example, found niche separation along a gradient of solar radiation among three ungulate species on northern Yellowstone winter range dominated by big sagebrush. Abundances of insect species can be expected to vary similarly along such an environmental gradient.

The abundance of the *Aroga* moth was measured in this study at multiple local sites within sagebrush-steppe during 2008-2012. In addition, moth survivorship and feeding damage inflicted on sagebrush were compared among these sites. The objective was to determine how moth abundance, survivorship, and damage to the host plant varied among local sites, and to determine how much of this variability could be accounted for by sagebrush abundance, elevation, slope, aspect, and/or incident solar radiation. The ultimate goal of the study was to assess how well the moth's abundance and impact on its host plant over space and time might be predicted from measurements of local habitat characteristics.

Materials and Methods

Study System. The study was conducted at the Henefer-Echo Wildlife

Management Area (WMA) (41.024°N, 111.444°W), an area in north central Utah that is

owned and managed by the state's Division of Wildlife Resources. Henefer-Echo WMA

lies at the eastern edge of the Great Basin in the western foothills of the Wasatch

Mountain Range. It is a sagebrush-steppe ecosystem dominated by big sagebrush,

encompassing 5700 hectares of shrubland and grassland that vary in elevation from 1500

to 2700 m. Sagebrush grows abundantly on the steep slopes that characterize much of the

area. The management area is maintained primarily to provide critical winter range for

elk, moose, and mule deer, though it provides habitat also to many small mammals and

birds, including sage grouse.

The *Aroga* moth inhabits sagebrush stands at Henefer-Echo WMA. Females

oviposit in the cracks of sagebrush bark during late summer (late July through

September) (Henry 1961, Hsiao 1984). Both eggs and early instars (young larvae) may

overwinter (Henry 1961, Kirkland 1972, Hsiao 1984). After hatching either in the fall or

early spring, larvae move by mid-April to sagebrush leaves where feeding occurs.

Significant damage and defoliation of the sagebrush plant is generally not apparent until

mid-June, at which time larvae are generally entering the fourth (of five) stadium (Hsiao

and Temte 1975). These older caterpillars construct large webbed tubes (the webbing is a

signature of the *Aroga* moth) that are readily visible from moderate distances (5-10 m).

Development of the insect and defoliation of the plant proceed rapidly from June through

August (Hsiao and Temte 1975, Temte 1977). In mid-summer the larvae pupate, and two

to three weeks thereafter adults emerge and mate. Adult activity has been known to last

for two to three months, although a single adult is unlikely to be active for that length of

time (Kirkland 1972).

Measurements of Larval Abundance. Measurements of moth abundance were

initiated in 2008 in response to the severe damage from the *Aroga* moth to localized

patches of sagebrush throughout Henefer-Echo WMA noted by Division of Wildlife

Resources personnel in 2005-2006. Damage from the moth in 2005-2006 was estimated

at the time to have killed 3-5% of sagebrush plants throughout the area, with the damage

spread across the landscape in a patchy mosaic. Populations of the *Aroga* moth were

sampled weekly during the growing season in permanent 100x50m plots that were

created in open habitats at varying elevation (1615 m-2286 m). An initial set of 28 plots

was created and sampled in 2008. With the addition of 10 more plots the next year, 38

plots were sampled in 2009-2011. Intensive sampling at the time of peak moth

abundance in 2012 was conducted at 13 of these plots (nine of the initial sites created in

2008, plus an additional four sites added in 2009); this set of 13 sites hence was sampled

at peak larval abundance for four to five years during 2008-2012.

Nearest sites were situated approximately 200 to 1600 meters apart throughout the

most northerly and southerly sections of Henefer-Echo WMA (Fig. 2.1). The sites were

restricted to these two distinct areas within Henefer-Echo WMA because of their

accessibility; the interior of Henefer-Echo WMA is accessible only to authorized 4x4

vehicles driven by land management personnel. Collectively, populations of the *Aroga*

moth at the study sites were taken as representative of the localized populations of the

moth that occurred across the entire land area encompassed by Henefer-Echo WMA during the time of the study *(personal observations).*

Throughout 2008-2011, individual sites were visited weekly from April through August. In 2012, sites were sampled only once, at the time that peak larval abundance was estimated to have occurred in the second stadium based on degree-day accumulation (Chapter 4). During each visit, sites were sampled for larval abundance of the *Aroga* moth by randomly selecting and collecting vegetative stems (terminal segments approximately 15 cm long) from sagebrush plants. During a ten-minute sampling period (census) at each site, a single stem per plant was collected from individual shrubs growing throughout the plot. An effort was made to collect a representative sample of stems by selecting and clipping a single, blindly chosen stem from systematically alternating top, middle, and bottom positions on individual shrubs. Nearest shrubs were selected as encountered (without regard to plant height or volume) at ten meter intervals along a haphazardly, zig-zagging transect through each half of the plot. On average, approximately 70 terminal stems were collected from each site (0.4 HA-plot).

The sagebrush stems collected each week were placed in Ziploc bags, stored in a cooler, and transported back to the lab for further processing. In the laboratory, stems were counted and measured for length. *Aroga* moth larvae were extracted by placing the stems in Berlese funnels for 96 hours (a preliminary study demonstrated that over the course of 96 hours in a Berlese funnel, 99% of larvae were extracted from a sample of stems). In the latter part of the season (late June-July) when larvae had become 4th and 5th instars, stems were first visually inspected to remove caterpillars before placing the

stems in Berlese funnels for 96 hours. Larvae collected by Berlese funnel extraction and by initial visual inspection of stems were counted and scored for stage of development (instar, as determined by measuring the width of the head capsule; Henry 1961). Abundance of larvae in each plot at each census was quantified as the number of larvae per unit stem (i.e., per 15 cm of terminal stems).

Vegetation Sampling. Each of the 38 permanent plots was sampled for sagebrush cover during 9-23 June 2009. Percent cover of sagebrush was measured at each site using a ground-based line-intercept technique (Canfield 1941). Canopy cover was estimated along each of three 50 m transects per site. These transects were spaced 25 m apart, and were marked by a meter tape pulled taught from edge to edge across the 50 m wide plots. Two teams of two persons worked to measure and score total sagebrush cover along the transects. Detailed measurements were taken on each sagebrush plant with canopy intercepted along the transect line. Each plant was scored for percentages of the entire plant that accounted for material that was (1) live and undamaged by the moth, (2) defoliated by the moth (as evidenced by clipped yellowed leaves and silken larval tubes from the current season), or (3) dead stems and branches (from previous defoliation by the moth or other causes).

Thirteen of the permanent plots (those that subsequently were sampled for peak moth abundance in 2012) were selected for additional vegetation sampling in 2009. Percent cover of sagebrush was measured a second time (as described above) at these sites a few weeks later (30 June-15 July) when damage from the *Aroga* moth larvae was largely complete for the year. Along with estimates of sagebrush cover, flowering

understory plant species richness and cover of these understory plants and bare ground were determined. These 13 sites were sampled again in early August 2012 to measure sagebrush canopy (as done in 2009).

Topographical Measures. Elevation was recorded at ground level at each of the 38 permanent sites using a GPS unit (Trimble Geoexplorer 3, Trimble Navigation Limited, Sunnyvale, CA). The slope at each site was determined using a clinometer, or vertical angle gauge (Suunto PM-5, Suunto, Vantaa, Finland); measurements were taken facing directly up slope. Aspect was measured at the plot center using a handheld compass (Suunto Silva Polaris, Suunto, Vantaa, Finland) and taken in the direction of the steepest down-slope direction.

Measurements of slope and aspect were used together to determine the incident solar radiation at each site according to Keating et al.'s (2007) simple solar radiation index (SRI). Calculating the varying amounts of solar radiation received by different sites within a mountainous region is challenging. Aspect and/or computer-generated hillshade values (as computed using a digital elevation model [DEM] and ARCGis) are used often to estimate solar radiation, but such approaches fail to account for effects of slope and latitude (Keating et al. 2007). The SRI integrates effects of slope, aspect, and latitude to estimate the amount of solar radiation theoretically striking a plot surface at a given site during the hour surrounding solar noon on the equinox (Keating et al. 2007). The value of the index is determined as:

$$SRI = \cos(latitude)*\cos(slope) + \sin(latitude)*\sin(slope)*\cos(aspect**)$$

where *aspect*** = 180° - aspect (i.e., south is 0° and north 180^0; southerly aspects range from + 270° through 0° to + 90°, and northerly aspects range between + 90° through + 270°). The index varies in value from - 1 to 1, but not all values are possible everywhere because of the effect of latitude (in the present study, latitude did not influence variation in SRI among the permanent sites given that all occurred at the same latitude).

Data Analyses. Data analyses were performed using SAS 9.3 (SAS Institute 2011). Topographic variables (elevation, slope, aspect, and SRI) were examined for correlation using linear and logistic models. Vegetation variables, including abundance of sagebrush cover and forb richness and cover, were compared across topography.

Peak larval abundances of the *Aroga* moth were compared across years. The peak abundance of larvae was determined as the average among sites of the number of larvae per stem (15 cm) that was recorded at each site during the weekly census for that site that coincided with second stadium peak. This occurred when 180 to 280 degree-days had accumulated since 1 January (Chapter 4). It is during this time that almost all larvae present are first or second instars (because first instars appear over an extended period, it is not until roughly all individuals have become second instars that the abundance of larvae on the host plant foliage peaks; Chapter 4). The calendar date of peak abundance at individual sites typically varied up to one week among years. Peak larval data were transformed by log (N+1) and then analyzed against elevation and SRI by curvilinear and linear regression, and against aspect and year by two-way ANOVA.

Survivorship of moths during their larval development (from first instar to pupation) was examined using census data collected approximately weekly in 2009 (16

censuses conducted at 4-10 day intervals, 24 April-5 August) from the 13 focal sites at which intensive vegetation sampling was conducted also (as described above). This set of 13 sites represented the full range of elevation and values of SRI of local moth habitats across Henefer-Echo WMA. Estimates of larval survivorship were calculated for each of the 13 sites using the Kiritani-Natmsuji-Manly (KNM) Method (Kiritani and Nakasuji 1967, Manly 1976, Manly 1997, Aubry et al. 2010) for naturally structured populations with overlapping life-stages. As in Aubry et al. (2010), this method was particularly useful for the present study because stage classes overlapped greatly over time and the interval between successive samples varied. Data were arcsine transformed, and then analyzed by regression analyses and a TTEST (survivorship as a function of elevation, SRI, or north versus south aspect).

Results

Temporal and Spatial Patterns of Sagebrush and Insect Abundance over 2008-2012. Physical attributes (elevation, slope, aspect, and solar radiation index [SRI]) varied widely among the study sites across Henefer-Echo WMA (Table 2.1). Among the 38 sites, elevation was not correlated with slope (r = - 0.06, df = 36, P = 0.70), aspect (χ^2 = 0.07, df = 1, P = 0.79), or SRI (r = 0.019, df= 36, P = 0.91). In contributing together to SRI, slope and aspect were strongly related among the study sites. Overall, sites with north-facing aspect had steeper slopes than sites with south-facing aspect (χ^2 = 16.8, df = 1, P < 0.0001).

Total sagebrush canopy cover (live and undamaged, defoliated, and dead cover combined as measured in 2009) also varied greatly among individual study sites, ranging

from 7.6% to 43.9%. Overall, total sagebrush cover declined among study sites with increasing elevation (Fig. 2.2a; $R^2 = 0.32$, df = 36, $P < 0.001$). Sagebrush cover did not differ overall in plots with north-facing versus south-facing aspects (North, x = 0.31, SE $\pm$ 0.02; South, x = 0.27, SE $\pm$ 0.03, $t = 1.23$, df = 18, $P = 0.24$). Sites with slopes less than or equal to 15° typically had high cover of sagebrush. At sites with slopes greater than 15°, sagebrush cover varied more widely and was inversely related to SRI across sites (Fig. 2.2b: $R^2 = 0.52$, df = 23, $P < 0.0001$).

Mean defoliator larval abundance across sites was moderately high when the study commenced in 2008 and rose to higher levels in 2009 (Fig. 2.3). Thereafter, in 2010-2012, larval abundance subsided to low levels (one-way ANOVA effect of year: $F_{4,150} = 35.75$, $P < 0.0001$). Individual sites varied greatly in local abundance of the defoliator in any given year (e.g., during the outbreak year of 2009 the number of larvae per sagebrush stem sample varied among sites from 0.08 to 2.84).

The abundance of *Aroga* moth larvae at individual sites during the outbreak year (2009) was not correlated with their abundance at these sites in the previous year (2008, $r_s = 0.21$, df = 26, $P = 0.29$). As the moth populations subsided thereafter, their abundance at individual sites was positively correlated from one year to the next (2009 vs. 2010, $r_s = 0.58$, df = 36, $P < 0.0001$; 2010 vs 2011: $r_s = 0.61$, df = 36, $P < 0.0001$). Even by 2012, when moth numbers had declined to very low levels throughout Henefer-Echo WMA, relative abundances among local populations continued to be positively correlated with relative abundances at those sites during the outbreak year of 2009

(r = 0.73, df = 11, *P* = 0.006). Thus, individual sites had a characteristic, consistent

tendency throughout much of the study to support more or fewer defoliator larvae.

The larval abundance of *Aroga* moths was not correlated with the abundance of

sagebrush (canopy cover) at individual sites, as measured in 2009 (r = -0.01, df = 36,

P = 0.97) nor did it change linearly in simple fashion with increasing elevation. Instead,

defoliator densities at individual sites showed a weak tendency to be higher at mid-level

rather than lower or higher elevations. This curvilinear pattern of abundance with

increasing elevation was observed consistently among years (Fig. 2.4a-d). The pattern

was not very strongly expressed, and high variance in larval abundance occurred at any

given elevation range. Indeed, the curvilinear regressions were significant only in two of

the four years (Table 2.2). Thus, neither sagebrush cover nor elevation was a strong

predictor of larval density, with elevation in particular accounting for little of the

variation in larval density in any given year.

The SRI of a site, which integrates the effects of both aspect and slope on incident

solar radiation, consistently among years affected the local abundance of moth larvae. In

each year, there was a significant linear decline in larval density associated with

increasing SRI among individual sites (Fig. 2.5a-d and Table 2.2). As with elevation,

SRI accounted for a modest fraction of the variation in larval density across space in any

given year.

To assess the importance of aspect on larval density, comparisons were made

between sites with south-facing versus north-facing aspects (higher SRI values are

associated with south-facing aspects than with north-facing aspects for a given slope and

latitude in the northern hemisphere). In each year of the study, the sagebrush defoliator's

larval abundance was higher at sites with north-facing aspect than at sites with south-

facing aspect (Fig. 2.3; two-way ANOVA: aspect, $F_{1, 145} = 20.24$, $P < 0.0001$; year,

$F_{4, 145} = 43.13$, $P < 00001$; aspect $\times$ year, $F_{4,145} = 3.26$, $P = 0.014$).

Because slope was correlated with aspect, the importance of slope in contributing

to defoliator larval abundance was evaluated separately for sites of north-facing and

south-facing aspect. In neither case was a significant relationship detected among sites

between slope and larval abundance of the moth in any of the five years of the study

(Table 2.3). Thus, the effect of SRI on moth larval abundance apparently arose primarily

from differences in aspect among study sites.

In 2009, the impact of the *Aroga* moth feeding on its host plant varied across

sites, with present year defoliation ranging from 0 to 43% across sites. Mean percentages

of defoliated and dead plant material at each site were positively correlated (Table 2.4;

r = 0.85, df = 36, $P = 0.005$). While elevation was not closely associated with

defoliation, SRI and slope were highly significantly correlated with defoliation

($P < 0.001$ for both). Defoliation and sagebrush mortality patterns across topography

were consistent with peak larval abundance, though more pronounced. Among steep

sloped areas, sites with northerly aspects had the most defoliated and dead plant material

in 2009 (Fig. 2.6; TTEST; defoliated $t = 3.76$, df = 18, $P = 0.002$; dead $t = 2.05$, df = 18,

$P = 0.06$).

Insect Performance and Plant Community Dynamics during an 'Irruptive'

Year. Survivorship of larvae varied widely among the 13 study sites sampled intensively

for vegetation during 2009; the estimated percent of hatching individuals that subsequently pupated ranged from 10% to 36%. Larval survivorship was positively correlated with peak larval density among these sites (r = 0. 83, df = 11, $P < 0.0001$). Larval survivorship was strongly associated with elevation and peaked at mid-elevations (Fig. 2.7a; curvilinear R^2 = 0.58, df = 11, P = 0.01). Larval survivorship also was negatively associated with SRI across the 13 sites (Fig. 2.7b; linear R^2 = 0.45, df = 11, P = 0.016) and was significantly higher at sites with north-facing versus south-facing aspects (x ± SE: 0.27 ± 0.02 versus 0.15 ± 0.02; t = 4.11, df = 11, P = 0.0017).

The impact of the defoliator on its host plant varied across sites: the mean percentage of sagebrush cover that was damaged on the individual shrubs intersecting the transect (i.e., including present year defoliation from larval feeding plus dead branches defoliated previously) ranged from 28-68% at any given site in 2009. As with larval survivorship, the percent sagebrush cover damaged increased among sites with decreasing SRI (Fig. 2.7c; linear R^2 = 0.68, df = 11, $P < 0.001$).

While north-facing sites sustained more damage from the moth, individual sagebrush plants also were taller and more voluminous than at south-facing sites (x ± SE for sagebrush plant height: 73.64 ± 1.67 cm versus; 59.08 ± 5.13 cm; TTEST, t = 2.86, df = 11, P = 0.02). Understory forbs also differed between north-facing versus south-facing sites, both in cover (x ± SE: north-facing sites, 14.4% ± 3.2% cover versus south-facing sites, 1.2% ± 0.5% cover; TTEST, t = 3.72, df = 11, P = 0.003), and in species richness

(x ± SE for species richness: north-facing sites, 16.97 ±1.41 species, versus south-facing sites, 10.57 ± 1.79, TTEST, $t = 2.88$, df = 11, $P = 0.02$).

Sites that had the most plant damage (defoliation + dead plant material) in 2009 were also those with the most damaged plant material in 2012 ($r = 0.80$, df = 11, $P < 0.0001$). Nonetheless, the overall amount of damaged and dead plant material was marginally less in 2012 than in 2009 (ANCOVA: effect of year, $F_{1,23} = 3.27$, $P = 0.08$) reflecting the subsidence of the *Aroga* moth populations as only traces of plant foliage could be found with larval webbing present. There was a tendency, though not significant, for potentially more recovery of sagebrush live cover from 2009 to 2012 at sites with lower SRI (Fig. 2.7c; ANCOVA SRI × year, $F_{1,23} = 0.80$, $P = 0.3818$) .

Discussion

The abundance of big sagebrush and the *Aroga* moth are tied closely to some physical attributes of the local habitat across the mountainous landscape studied here. The abundance (cover) of sagebrush decreased in linear fashion with increasing elevation at Henefer-Echo WMA. This could have arisen from habitat distribution of big sagebrush subspecies by elevation, as associated with soil composition and moisture availability (Cawker 1980, Schultz 1984, West 1988). Wyoming sagebrush (*A. tridentata wyomingensis* Beetle & Young) occurs at low-to-mid elevations on fine-textured soils. Basin sagebrush (*A. tridentata tridentata* Beetle & Young) is also found at low-to-mid elevations but on deep, well-developed soils. Mountain sagebrush (*A. tridentata vaseyana* Beetle), low in stature in comparison to the other two subspecies (Knight 1994)

is distributed from mid-to-high elevations where cooler temperatures, higher

precipitation, and developed soils are prevalent (Beetle 1960).

The *Aroga* moth feeds readily on all three big sagebrush subspecies (Henry 1961).

Elevation also affected the local abundance of the *Aroga* moth but in a different way.

Largest populations of the *Aroga* moth and greatest survival of larvae occurred at mid-

elevations. Hence the abundance of the moth was not strongly associated with the

abundance of the host plants across the elevational gradient at Henefer-Echo WMA.

The moth occurred in greater density and survived the larval period at higher rates

at sites with lower incident solar radiation as estimated by SRI. Of the two physical

attributes contributing to variation in SRI values among study sites at Henefer-Echo

WMA, aspect rather than slope was especially important in influencing both density and

survival of moth larvae. In particular, higher densities and survival rates of moth larvae,

and greater damage to sagebrush from these larvae, were recorded at north-facing sites

than at south-facing sites. Low values of SRI associated with north-facing sites

supporting sagebrush, thus, appear to reflect especially suitable local habitat for the

Aroga moth.

The microclimate an ectotherm experiences influences its physiological capacities

and its ecological performance (Huey 1991). The high suitability of north-facing sites for

the moth may result from favorable microclimate. North-facing sites with low SRI

fluctuate less in temperature throughout the day and the year than do south-facing sites,

and the deep snow cover at north-facing sites offers good insulation from winter cold.

North-facing slopes likely retain snowmelt longer into the summer, effectively reducing

the length of the dry season. This may explain both why sagebrush plants were more voluminous and the understory species richness and cover of forbs was greater on north-facing than on south-facing slopes. Prolonged snow-melt and associated greater soil moisture also may promote higher sagebrush recruitment rates (Cawker 1980, Perryman and Olson 2000).

The favorable microclimate of north-facing sites with low values of SRI may affect *Aroga* moth numbers directly and also indirectly, through effects on sagebrush productivity and performance. The persistence of moist conditions longer into the growing season may enhance larval survivorship directly. It may also enhance the nutritive quality of sagebrush foliage for moth larvae. Hsiao and Temte (1975) hypothesized that lack of moisture associated with high daily temperatures dehydrated sagebrush foliage, making it relatively unsuitable in early summer for late instars of the *Aroga* moth and thereby leading to high pupal mortality. The greater cover and species richness of forbs on north-facing slopes may result in greater nectar availability for moth adults in mid-summer, thereby promoting high egg production and foraging efficiency. These eggs in turn may escape best on north-facing slopes from incidental ingestion by ungulates. Areas with low SRI, where larval density of the *Aroga* moth tended to be highest, are likely little foraged upon by large ungulates during winter months. These herbivores (particularly mule deer) have been reported by Keating et al. (2007) to forage in areas with median SRI = 0.75. Houston (1982) concluded that mule deer are not well suited to forage in deep snow during winter. It is intriguing to consider that the *Aroga*

moth may evade inadvertent consumption by ungulates by occurring in greatest densities at north-facing sites with relatively deep snow cover during winter.

The importance of aspect in determining habitat suitability for the moth is likely reflected also in the fact that relative abundance of the moth changed little among sites even as absolute abundance changed greatly, as the moth population declined overall in its abundance from its peak in 2009 to very low levels in 2012. It is noteworthy in this regard, however, that there was no strong positive correlation for individual sites between years as moth numbers at Henefer-Echo WMA increased from 2008 to 2009. The high numbers of the moth recorded at Henefer-Echo WMA in 2009 likely reflect high moth survival as the result of high rainfall that provided favorable, moist conditions for larval growth and development (Chapter 4). Dry conditions during larval development, in contrast, may cause rapid deterioration in the food supply and low survival of moth larvae and pupae as a consequence (Hsiao 1984). It is possible that the favorable weather (intermediate temperatures and moist conditions) throughout the study area in 2009 promoted especially strong population growth at sites with relatively low population sizes at the outset (and, therefore, least drag on population growth from density dependence; e.g., Haynes et al. 2009). This may have weakened the correlation in numbers moth of individuals at individual sites in 2008 and 2009.

The epicenter hypothesis (Liebhold and McManus 1991, Royama 1992) predicts that local populations remain at endemic or persistent level until favorable weather increases larval survival, enabling the population to reach high density such that many individuals disperse into neighboring areas. Such epicenters are likely to have more

favorable habitat conditions perennially. Previous studies with mountain pine beetle and gypsy moth outbreaks have identified more homogenous tree stands of larger tree size and higher percentage canopy cover as epicenter habitats (Liebold et al. 1994, Chapman et al. 2012). The results of the present study suggest a similar dynamic may apply for *Aroga* moth populations at Henefer-Echo WMA, as sagebrush stands of high canopy cover and larger sized shrubs supported more abundant populations across years.

The tendency of sagebrush plants to recover to greater extent by 2012 at north-facing sites than at south-facing sites from moth-inflicted damage as measured in 2009 is also noteworthy. North-facing sites may well be more suitable for both sagebrush and moth alike. System persistence may hence be assured over the long term because the host plant has greatest capacity to recover from herbivore damage in the very same locations across the landscape where such damage is likely to be heaviest. The balance of varying damage and subsequent recovery across the landscape may account for the result in this study that no clear difference occurred in cover of sagebrush between north- and south-facing sites.

In summary, it appears that local habitats vary considerably in their suitability for the *Aroga* moth, as well as for sagebrush across mountainous landscapes. Local sites with north-facing aspect appear most suitable for both the moth and its host plant. This sets the stage for the interesting possibility that sagebrush may have more ability to recover from moth damage at the very sites where it is most likely to sustain more moth damage. The moth in turn is reasonably predictable in where it is likely to occur in greatest numbers across the landscape in any given year. Nonetheless, the population

dynamics of the moth over time vary among individual sites. In the present study, for example, local populations of the moth differed in the extent to which they grew in abundance from 2008 to 2009, even though thereafter they decreased at similar rates from 2009 through 2012. Further study is called for now especially to determine how environmental variables such as aspect that are fixed, and those such as rainfall that are not, interact to influence the spatial and temporal population dynamics of the *Aroga* moth and the sagebrush stands that it attacks.

LITERATURE CITED

Andresen, J. A., D. G. McCullough, D. B. E. Potter, C. N. Koller, L. S. Bauer, D. P. Lusche, and C. W. Ramm. 2001. Effects of winter temperatures on gypsy moth egg masses in the Great Lakes region of the United States. Agr. For. Meteorol. 110: 85-100.

Aubry, A., E. Becart, J. Davenport, and M. C. Emerson. 2010. Estimation of survival rate and extinction probability for stage-structured populations with overlapping life stages. Popul. Ecol. 52: 437-450.

Beetle, A. A. 1960. A study of sagebrush. The section Tridentatae of Artemisia. Bulletin of the Wyoming Agricultural Experiment Station 368.

Brewer, A. M., and K. J. Gaston. 2003. The geographical range structure of the holly leaf-miner demographic rates. J. Anim. Ecol. 72: 82-93.

Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. J. Forest. 39: 388-394.

Cawker, K. B. 1980. Evidence of climatic control from population age structure of Artemisia tridentata Nutt. in southern British Columbia. J. Biogeogr. 7: 237-248.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Wittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecol. Monogr. 77: 117-145.

Chapman, T. B., T. T. Veblen, and T. Schoennagel. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology. 93: 2175-2185.

Garrick, R. C. 2011. Montane refuges and topographic complexity generate and maintain invertebrate biodiversity: recurring themes across space and time. J. Insect Conserv. 15: 469-478.

Gates, D. H. 1964. Sagebrush infested by leaf defoliating moth. J. Range Manage. 17: 209-210.

Gripenberg S., and T. Roslin. 2007. Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. Oikos. 116: 181-188.

Hall, R. C. 1965. Sagebrush defoliator outbreak in Northern California. USDA Forest Service, Res. Note PSW-75.

Haynes, K. J., Liebhold, A. M., and Johnson, D. M. 2009. Spatial analysis of harmonic oscillation of gypsy moth outbreak intensity. Oecologia. 159: 249-256.

Henry, J. E. 1961. The biology of the sagebrush defoliator, *Aroga* websteri Clarke, in Idaho. M.S. thesis, University of Idaho, Moscow, ID.

Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and

community responses to altitude. Biol. Rev. 80: 489-513.

Houston, D. B. 1982. The Northern Yellowstone Elk: Ecology and Management.
Macmillan: New York.

Hsiao, T. H. 1984. Biology and demography of the sagebrush defoliator and its impacts
on big sagebrush. Pages 191-198 *in* E. D. McArthur and B. L. Welch, (eds.),
Proceedings, Symposium on the Biology of Artemisia and Chrysothamnus, 9-13
June 1984, Provo, UT. USDA Forest Service General Technical Report GTR-
INT-200.

Hsiao, T. H., and A. K. Temte. 1975. Demographic studies of sagebrush insects as
functions of various environmental factors. US/IBP Desert Biome Research
Memorandum. 76-23. Utah State University, Logan, UT.

Huey, R. B. 1991. Physiological consequences of habitat selection. Am Nat. 137: S91-
S115.

Irwin, J. T., and R. E. Lee. 2003. Cold winter microenvironments conserve energy and
improve overwintering survival and potential fecundity of the goldenrod gall fly,
Eurosta solidaginis. Oikos 100: 71-78.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat. 101: 233-
249.

Keating, K. A., P. J. P. Gogan, J. M. Vore, and L. R. Irby. 2007. A simple solar
radiation index for wildlife habitat studies. J. Wildlife Manage. 71: 1344-1348.

Kiritani, K., and F. Nakasuji. 1967. Estimation of the stage-specific survival rate in the
insect population with overlapping stages. Res. Popul. Ecol. 9: 143-152.

Kirkland, R. L. 1972. Ecology of *Aroga websteri* Clarke in Curlew Valley, Utah-Idaho. M.S. thesis, Utah State University, Logan, UT.

Knight, D. H. 1994. Mountains and plains: the ecology of Wyoming landscapes. Yale University Press, New Haven, CT.

Liebhold, A. M., G. A. Elmes, J. A. Halverson, and J. Quimby. 1994. Landscape characterization of forest susceptibility to gypsy moth defoliation. Forest Sci. 40: 18-29.

Liebhold, A. M., and M. J. McManus. 1991. Does larval dispersal cause the spread of gypsy moth outbreaks? North. J. Appl. For. 8: 95-98.

Manly, B. F. J. 1976. Extensions to Kiritani and Nakasuji's method for analyzing insect stage-frequency data. Res. Popul. Ecol. 17: 191-199.

Manly, B. F. J. 1997. A method for the estimation of parameters for natural stage-structured populations. Res. Popul. Ecol. 39: 101-11.

McCoy, E. D. 1990. The distribution of insects along elevational gradients. Oikos 58: 313-322.

Perryman, B. L., and R. A. Olson. 2000. Age-stem diameter relationships of big sagebrush and their management implications. J. Range Manage. 53: 342-346.

Root, T. 1988. Atlas of wintering North American birds. University of Chicago Press, Chicago.

Royama, T. 1992. Analytical population dynamics. Chapman & Hall, London, United Kingdom.

SAS Institute. 2011. PROC user's manual, version 6th ed. SAS Institute, Cary, NC.

Schulz, L. M. 1984. Taxonomic and geographic limits of Artemisia subgenus Tridentatae (Beetle), pp 20-27. *In* E. D. McArthur, B.Welch (eds.), Proceedings of the Symposium on the Biology Artemisia and Chrysothamnus. Techinal Report INT-200. U.S. Forest Service, Intermountain Research Station, Provo, UT.

Straw, N. A., J. E. L. Timms, and S. R. Leather. 2009. Variation in the abundance of invertebrate predators of the green spruce aphid Elatobium abietinum (Walker) (Homoptera: Aphididae) along an altitudinal transect. Forest Ecol. Manage. 258: 1-10.

Temte, A. K. 1977. The demography of the sagebrush defoliator, *Aroga websteri* Clarke (Lepidoptera: Gelechiidae), and its impact on Artemisia tridentata. M.S. thesis, Utah State University, Logan, UT.

Thomas, C. D. and W. E. Kunin. 1999. The spatial structure of populations. J. Anim. Ecol. 68: 647-657.

West, N. E. 1983. Western intermountain sagebrush steppe, p. 351-369. *In* N. E. West (ed.), Ecosystems of the world 5: temperate deserts and semi-deserts. Elsevier Scientific Publishing Company, New York.

West, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands. *In* M.G. Barbour and W. D. Billings (eds.), North American terrestrial vegetation. Cambridge University Press, Cambridge, United Kingdom.

West, N. E., and J. A. Young. 2000. Intermountain valleys and lower mountain slopes. *In* M. G. Barbour, and W. D. Billings, (eds.), North American Terrestrial Vegetation. Cambridge University Press, New York.

Wisdom, M., Rowland, M. Suring, L. Shueck, L. Meinke, C., and Knick, S. 2005.
Evaluating species of conservation concern at regional scales, pp. 289-307. *In* M.
Wisdom, M. Rowland and L. Suring (eds.). Habitat threats in the sagebrush
ecosystem: Methods of regional assessment and applications in the Great Basin.
Alliance Communications Group, Lawrence, KS.

Table 2.1. Descriptive statistics for topographic variables and for sagebrush canopy cover as measured in 2009 across the 38 permanent study sites at Henefer-Echo WMA.

	$\bar{x}$	SD	Range
Elevation (m)	1885	159	1658 - 2286
Slope^{o}	20°	10°	5 - 38°
SRI	0.65	0.22	0.23 - 0.94
%Sagebrush canopy cover	28%	9%	8 – 44%

Table 2.2. Summary of regression showing the relationship of elevation and SRI on *Aroga* larval abundance across years. See Figs. 2.4 and 2.5 for corresponding data.

	Mean	SD	2008[1]	2009[2]	2010	2011
(1) Elevation (m)	1885	159				
y			$-3E\text{-}08x^2+$ $0.0005x$ - 1.47	$-2E\text{-}06x^2 +$ $0.0077x -$ 7.25	$-4E\text{-}08x^2+$ $0.0005x$ - 1.49	$-4E\text{-}08x^2 +$ $0.0005x$ - 1.50
R^2			0.22	0.23**	0.13	0.29**
(2) SRI	0.65	0.22				
y			$-0.18x+ 0.38$	$-0.28x + 0.38$	$-0.22x + 0.27$	$-0.11x + 0.16$
R^2			0.06	0.29***	0.22**	0.11*

[1]N=28 for 2008 and [2]N=38 for 2009-2011)
*$p<0.05$, **$p<0.01$*** $p<0.001$

Table 2.3. Summary of linear regression analyses showing the relationship of slope on *Aroga* larval abundance with northerly and southerly aspects controlled across years.

Site Aspect	(2008)			(2009)			(2010)			(2011)		
	r^2	*slope*	*p*	r^2	*slope*	*p*	r^2	*slope*	*p*	r^2	*slope*	*p*
Northerly[1]	0.02	0.05	0.70	0.14	0.00	0.12	0.00	0.00	0.99	0.00	-0.00	0.93
Southerly	0.09	0.16	0.25	0.02	0.00	0.55	0.01	0.03	0.63	0.05	0.04	.33

[1]Northerly 2008, N=13& 2009-2011, N=19; Southerly: 2008, N=15& 2009-2011, N=19
*p<0.05, **p<0.01, *** p<0.001

Table 2.4. Correlation matrix for biotic and abiotic variables potentially impacting defoliated and dead sagebrush canopy across Henefer-Echo WMU (2009).

	Dead Sage 2009	Defoliated Sage 2009	Peak Larvae 2009	Elevation (m)	Slope°	SRI
Dead Sage 2009	1	0.85***	0.26	0.09	0.62***	0.54***
Defoliated Sage 2009		1	0.45**	0.09	0.70***	0.69***
Peak Larvae 2009			1	0.02	0.49**	0.54***
Elevation (m)				1	0.06	0.02
Slope °					1	0.73***
SRI						1

*$p<0.05$, **$p<0.01$, *** $p<0.001$

Fig. 2.1. Distribution of permanent field sites at Henefer-Echo WMA (outlined by red hexagon). Long-term field sites are designated by green circles.
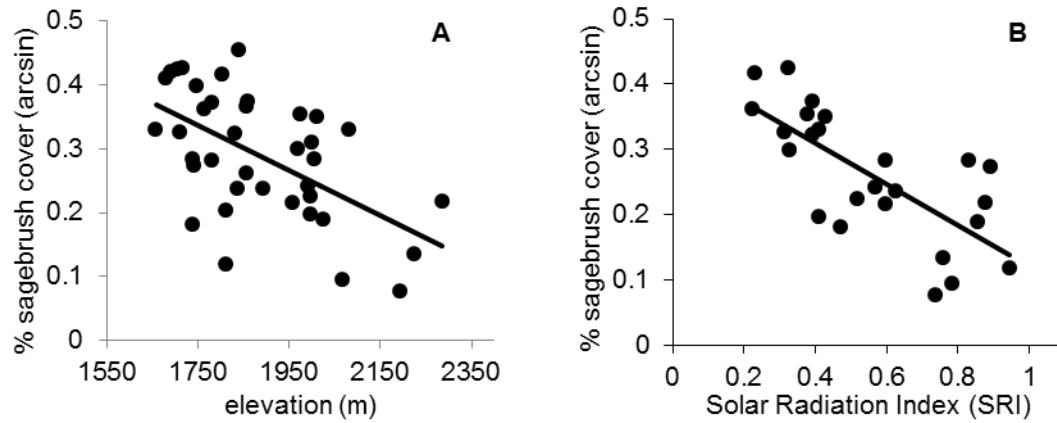
Fig. 2.2. (A) Mean total sagebrush cover canopy measured across transects decreased with increasing elevation across all 38 field sites in 2009. **(B)** Mean total sagebrush cover canopy measured across transects decreased with increasing SRI across all field sites with slopes > 15° (N=25) in 2009. Sagebrush cover values are arcsine transformed.
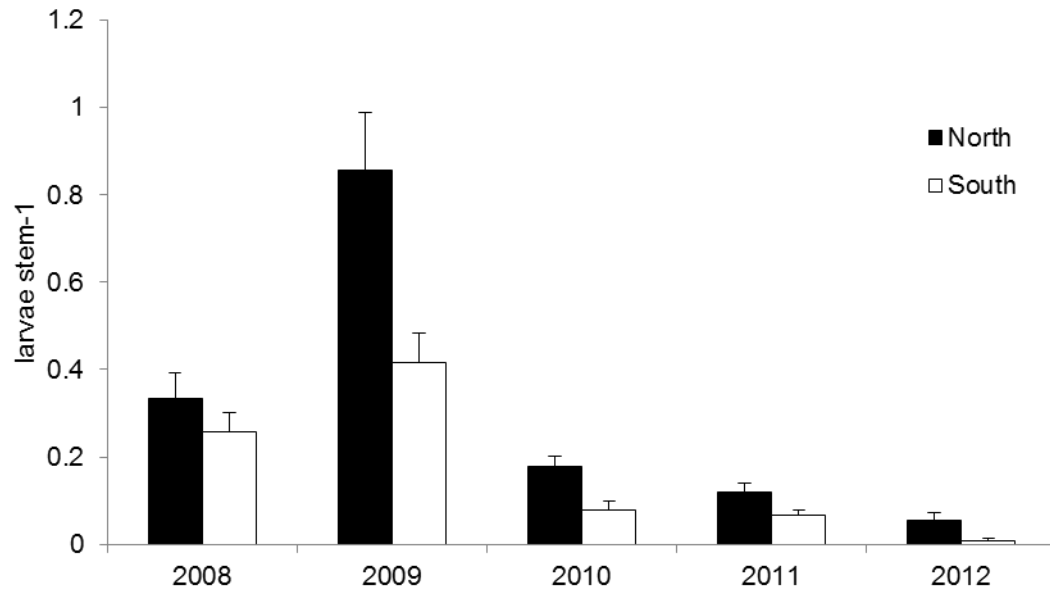
Fig. 2.3. Mean peak larval abundances at sites with northerly and southerly aspects across all years of the study (2008-2012).
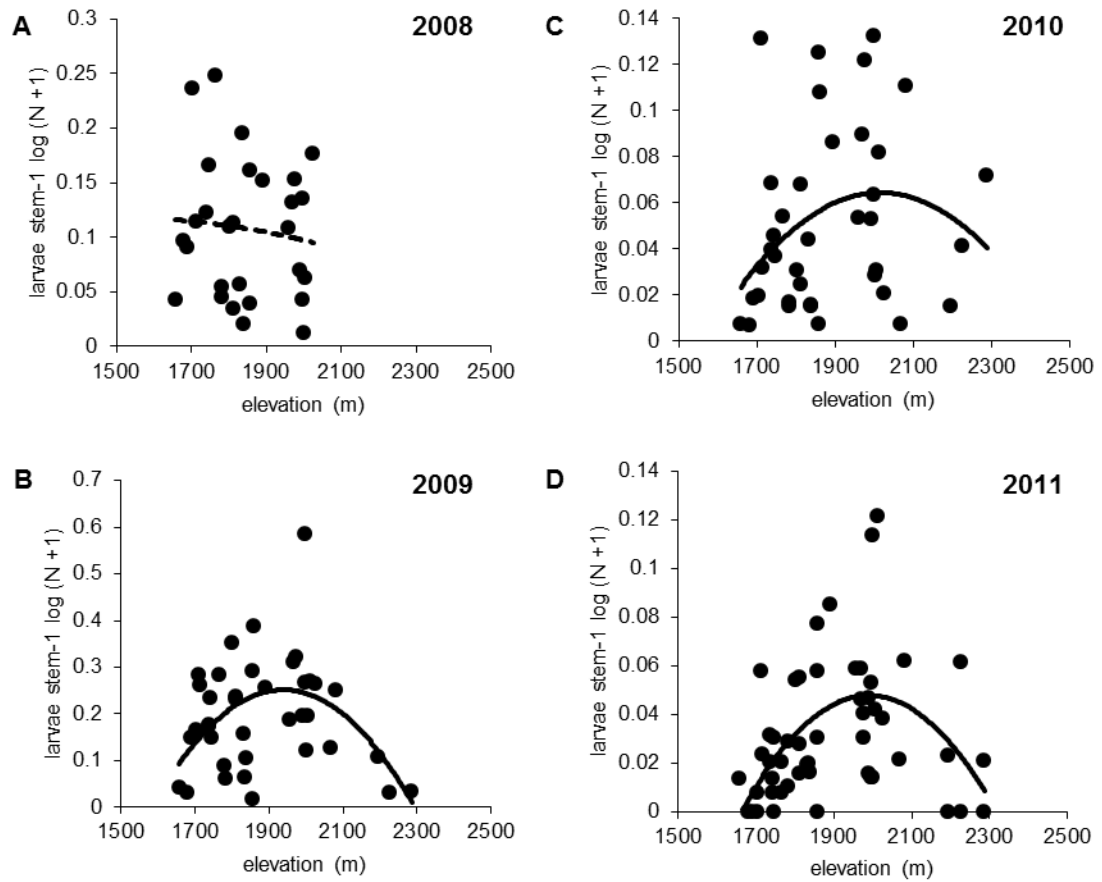
Fig. 2.4. Peak larval abundances across an elevation gradient at Henefer-Echo WMU sites across years **(A)** 2008, **(B)** 2009, **(C)** 2010, and **(D)** 2011. Larval abundance values are Log(N+1) transformed. See Table 2.2 for corresponding analyses.
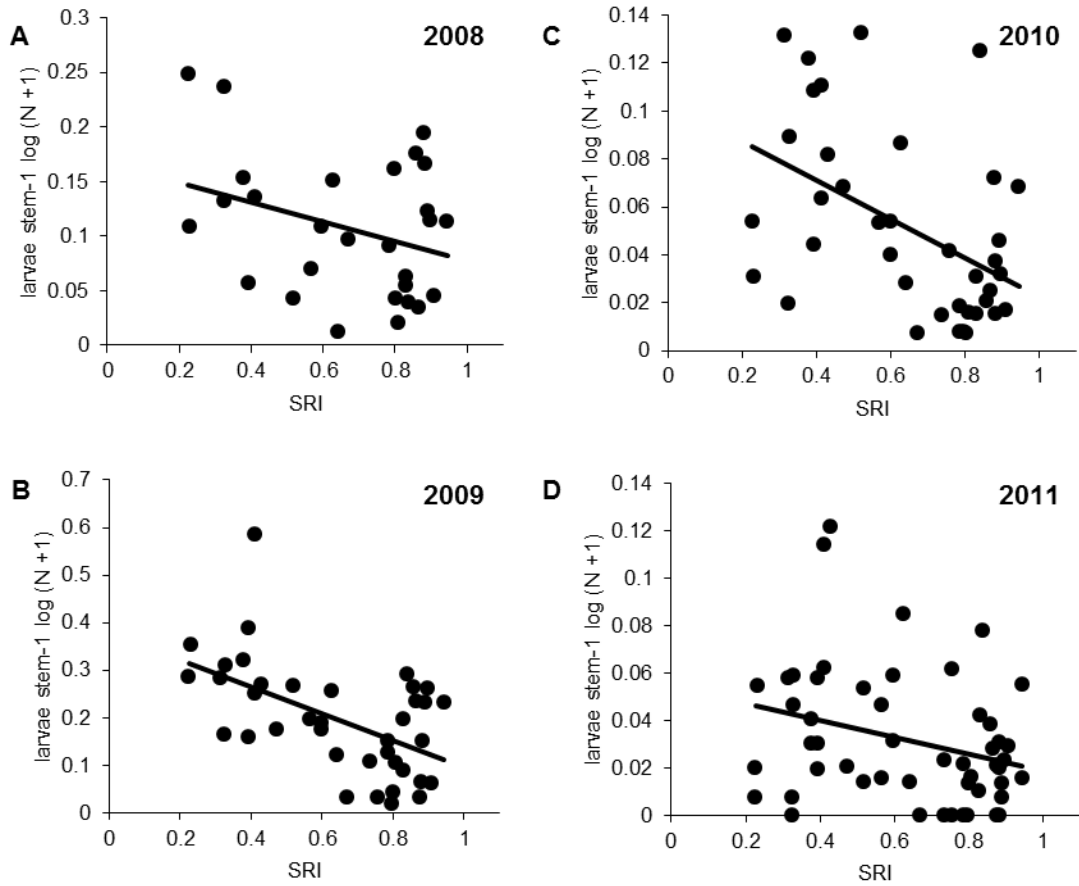
Fig. 2.5. Peak larval abundances across the range of SRI at Henefer-Echo WMU across years **(A)** 2008, **(B)** 2009, **(C)** 2010, and **(D)** 2011. Larval abundance values are Log(N+1) transformed. See Table 2.2 for corresponding analyses
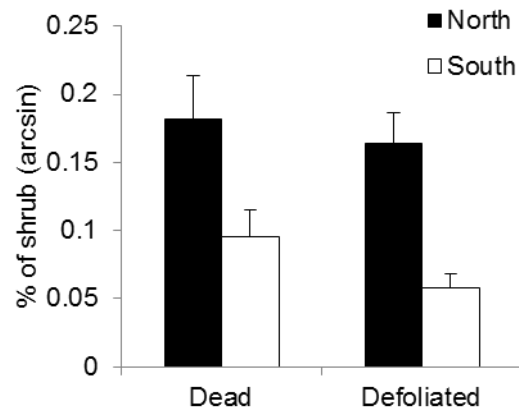
Fig. 2.6. Mean percentage of dead and defoliated plant material measured on individual sagebrush shrubs across sites with northerly and southerly aspects in 2009.
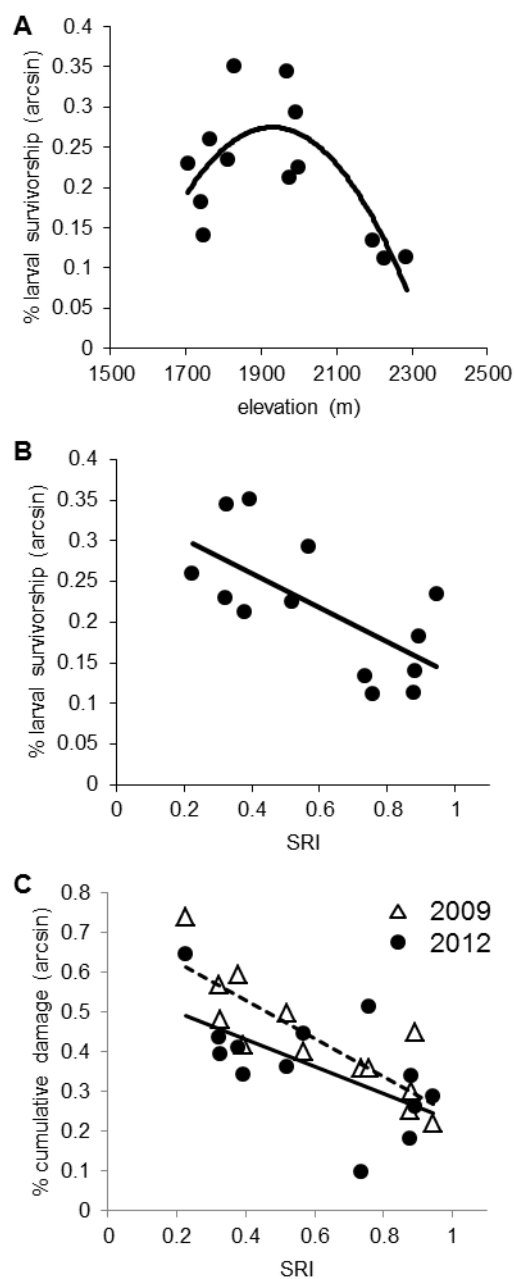
Fig. 2.7. (A) Survivorship of *Aroga* moth larvae from the second to the fifth stadium across sites of varying elevation in 2009. **(B)** Survivorship of *Aroga* moth larvae from the second to the fifth stadium across sites with varying SRI in 2009. **(C)** The percent sagebrush damage (including both defoliated and dead plant material) across sites of varying SRI in 2009 and 2012. Larval survivorship is arcsine transformed. Percent sagebrush damage is arcsine transformed.

CHAPTER 3

EFFECTS OF PARASITOID AND FLORAL DIVERSITY

ON PARASITISM OF A SAGEBRUSH DEFOLIATING MOTH

ACROSS A MONTANE LANDSCAPE[2]

ABSTRACT

Species diversity of natural enemies is hypothesized often to promote suppression of insect herbivores. I examined patterns of abundance along an altitudinal gradient for a sagebrush defoliator, the *Aroga* moth (*Aroga websteri* Clarke; Lepidoptera: Gelechiidae), and for the group of parasitoid species in the guild attacking the moth and the community of flowering understory plants that may provide critical food (nectar) for these parasitoids. The study was conducted at sites located throughout a 5700 hectare wildlife management area in a sagebrush steppe ecosystem dominated by the shrub *Artemesia tridentata*, big sagebrush. Over the course of four years (2008-2011), I found three major parasitoid species to differ strongly and predictably in attacking the moth along elevation clines, with greatest overall parasitism occurring when all three species were present. The species richness of the understory floral community also increased strongly from low to high elevation and was correlated with rates of parasitism by two major parasitoid species. Over a more limited range of mid to high elevation, parasitism of the moth was correlated with floral species richness, but neither parasitism nor floral species richness was correlated with elevation. Field experiments revealed that the two species of pupal parasitoids responded differently to provision of floral resources and methyl salicylate

(an herbivore-induced plant volatile). Even as the presence of all major parasitoids together led to greatest parasitism rates, individual species of parasitoids differed substantially and complemented one another in their patterns of attack among local populations of the *Aroga* moth across the montane landscape. Overall, the results of this study support the general hypothesis that over large scales of space and time, species diversity of natural enemies promotes suppression of insect herbivores.

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INTRODUCTION

With increasing global threats to biodiversity (Wilson 1989, Ehrlich 1991, Pimm et al. 1995, Barnosky et al. 2011), understanding the functional consequences of native diversity has never been more important for conservation efforts (Chapin et al. 2000, Schwartz et al. 2000). Biodiversity may increase and stabilize many ecosystem functions (Frank and McNaughton 1992, Tilman et al. 2006) by directly and indirectly influencing complex aspects of communities such as food web interactions (Worm and Duffy 2003). Food web interactions in diverse communities can differ widely across landscapes as population sizes of individual species vary over space and time in response to abiotic and biotic factors (Landis et al. 2000, Rand et al. 2006, Rand et al. 2012, Tscharntke et al. 2012). Collectively, these local food web interactions may act to stabilize population size (e.g., prevent eruptions) of abundant, widespread species over large scales of space and

time (Lawton and Brown 1994, Tylianakis et al. 2006, Veddeler et al. 2010, Tscharntke et al. 2012).

This study addresses these issues as they apply to a sagebrush defoliator, the *Aroga* moth (*Aroga websteri*, Lepidoptera: Gelechiidae), an insect herbivore of major importance in the sagebrush-steppe of the Great Basin in western North America. At high densities, the *Aroga* moth can kill large stands of big sagebrush (*Artemisia tridentata*) over a short period of time (Henry 1961, Gates 1964, Fillmore 1965, Hsiao 1984, Miller 2005; see also Calhoun 1964 as cited in Fillmore 1965). The *Aroga* moth is at the center of a food web that includes both its host plant sagebrush and associated vegetation, and the natural enemies that in turn attack it. Chief among these natural enemies are parasitoid insects. High rates of parasitism of both larval and pupal stages by Hymenopteran parasitoids in particular have been reported for the *Aroga* moth (Fillmore 1965). These co-evolved natural enemies of the defoliator may naturally limit its potential for outbreaks by reducing its numbers over time and space.

As is the case for the *Aroga* moth, multiple species of parasitoids often simultaneously attack a single species of insect herbivore (Godfray 1994, Borer et al. 2003, Amarareskare 2007, Hackett-Jones et al. 2009). These natural enemies play an important yet variable role in affecting the abundance of insect herbivore populations (Altieri 1999, Schmidt et al. 2003). Along with local host density, numerous factors can account for variable parasitism rates in heterogeneous environments (Walde and Murdoch 1988, Bellows and Fisher 1999). In particular, there has been much recent interest in the role of parasitoid diversity in promoting high rates of parasitism (e.g.,

Tylianakis et al. 2006, Veddeler et al. 2010). In addition, the rate of parasitism may depend on physical and biological attributes of the habitat. Elevation is one such central physical attribute that is linked with many other features in a montane setting such as that studied here. A major biological attribute could be the availability of floral resources that serve as sources of nutrition for foraging adult parasitoids (Root 1973, Evans 1994, Isaacs et al. 2008). Indeed, the maintenance of parasitoid diversity (and ultimately the overall rate of host parasitism) may depend on floral resource diversity (Hooper et al. 2005, Thebault and Loreau 2005, Veddeler et al. 2010). The strength of such linkages may vary across landscape gradients and habitat types (Tylianakis et al. 2006, Tscharntke et al. 2012).

The importance of natural enemy diversity for suppression of insect herbivores is addressed in this study. Such importance cannot simply be inferred, but instead needs to be assessed carefully for individual cases. On purely theoretical grounds, increasing diversity of natural enemies may be linked to increasing, decreasing, or unchanged herbivore mortality, depending on how these species combine and interact with each other in their effects on prey numbers (Ives et al. 2005, Cardinale et al. 2006, Schmitz 2007, Letourneau et al. 2009). Experimental studies have manipulated carefully the diversity and collective number or biomass of natural enemies in laboratory or field cages. These studies have provided examples for each of these theoretical outcomes (e.g., Bográn et al. 2002, Cardinale et al. 2002, 2003; Finke and Denno 2004, Rodriguez and Hawkins 2000, Straub et al. 2008).

Field investigations provide an important additional approach to understanding the importance and implications of natural enemy diversity for herbivore suppression. The precision gained from experimental manipulation of key variables in ecological studies often comes at a cost in terms of the broad applicability and robustness of conclusions drawn (Letourneau et al. 2009). Although field investigations are necessarily much less incisive in demonstrating causal mechanisms, they provide important opportunities to assess the outcomes of interactions among multiple species under natural conditions over large scales of space and time.

In this study, I have investigated the role of natural enemy diversity in determining the intensity of parasitism in natural populations of the *Aroga* moth at multiple local sites over a 4-year period across a varied landscape filled by sagebrush. I have included field experiments with these observational studies to further evaluate the significance of parasitoid diversity. I addressed whether the intensity of attack by individual parasitoid species varied with host density, elevation, or floral diversity across the landscape, and whether the combined attack of these parasitoids as a guild resulted in greater suppression of the *Aroga* moth through parasitism both locally and globally (i.e., collectively across the landscape) than the suppression resulting from any one species of parasitoid alone.

MATERIALS AND METHODS

Study system

The study was conducted at the Utah Division of Wildlife Resources (UDWR) Henefer-Echo Wildlife Management Area (WMA), in north central Utah, USA

(41.024°N, 111.444°W). Henefer-Echo WMA lies on the eastern edge of the Great Basin in the western foothills of the Wasatch Mountain Range in a sagebrush steppe ecosystem dominated by the shrub *Artemisia tridentata* (big sagebrush). All plots were located within the management area of 5700 hectares of brush and grasslands ranging from 1615 m to 2500 m elevation. This area is simultaneously managed to provide critical winter range for wildlife (e.g. elk and mule deer), and spring – late summer forage to cattle livestock.

Eggs of the *Aroga* moth overwinter in the cracks of sagebrush stems and hatch in early spring. Larvae feed on sagebrush foliage by clipping the stems and spinning the leaves into larval tubes. During years of high abundance, sagebrush stands (covering up to thousands of hectares) have experienced significant losses (Gates 1964, Miller 2005). Pupation commences typically in late June to early July. By the end of July adults begin to emerge, and they mate and oviposit over the next several weeks to complete a single life cycle each year.

Three species of Hymenoptera were found to be the major parasitoids attacking the *Aroga* moth during the present study: *Copidisoma* sp. (Encyrtidae), *Phaeogenes arogae* (Gittens & Henry) Ichneumonidae:Cryptinae), and *Conura* sp. (Chalcididae). These three species were found also in previous studies to be the most abundant parasitoids associated with the *Aroga* moth in southern Idaho and northern California (Henry 1961, Fillmore 1965). For simplicity, these three species of parasitoids are referred to hereafter only by genus.

The most widespread and abundant parasitoid, *Copidisoma*, is a polyembryonic, larval parasitoid. It is a generalist that attacks the *Aroga* moth, as well as other rangeland insects (Fillmore 1965, as identified as *Copidisoma bakeri* Howard). It is believed that this species oviposits in the eggs of *Aroga* during late summer, but that the embryos do not begin to develop until the host enters the fifth (and final) stadium the following summer. *Aroga* moth eggs parasitized by *Copidisoma* hatch and the host develops up to the mid-fifth instar at which point it stops feeding. Within two to three days thereafter, the host body hardens and *Copidisoma* pupal cases within the host's body become visible (Fillmore 1965).

The endo-pupal parasitoid *Phaeogenes* is believed to be a specialist, as it is known only from rearings of the *Aroga* moth in Idaho (Fillmore 1965). During the brief period when *Aroga* moth pupae occur on sagebrush, *Phaeogenes* females parasitize the host by laying a single egg in a pupa. Among field-collected individuals of the *Aroga* moth in this study, adults of *Phaeogenes* emerged from *Aroga* moth pupae a few days after unparasitized moths emerged in the laboratory when moth pupae were held at ambient temperature and natural lighting. This emergence of the parasitoid in the laboratory typically occurred near the end of July through the beginning of August (i.e., approximately 2 weeks after the egg had been laid in the host pupa).

Conura (previously identified as *Spilochalcis leptis* [Burks] by Fillmore (1965)) is an endo-pupal parasitoid and a confirmed generalist reared also from other species of Lepidoptera and Coleoptera (Fillmore 1965). Similar to *Phaeogenes* in its life history, *Conura* emerged in the lab as an adult from field collected *Aroga* pupal cases

approximately two weeks after estimated oviposition during peak moth emergence, consistent with Fillmore's (1965) findings. The emergence period of the adult parasitoid in the lab overlapped with that of *Phaeogenes,* but also continued for up to five weeks after the egg likely had been laid in the host pupa.

Study sites

Aroga moth and parasitoid populations along with communities of understory flowering plants were sampled in 38 permanent 100x50 m plots in 2008-2011 located in sagebrush stands stratified by elevation (1615 m-2286 m) and levels of moth infestation (i.e., varying levels of present and past defoliation as indicated by the amount of larval webbing and dead/barren sagebrush stems present at the time the site was selected for study). Adjacent sites were situated approximately 200-to-1600 m away from each other. Field data were obtained from 38 sites that were visited weekly from April through August each year; 27 of these sites were sampled all four years, and an additional 11 sites were sampled starting in 2009 through 2011. The degree of moth larval and pupal parasitism at these study sites was assessed in each year (2008-2011).

Parasitoid emergence

Field-collected host samples were reared in the lab. Host individuals were collected for rearing as larvae of all ages and as pupae in 2008, and thereafter (2009-2011) only as fourth and fifth instars and pupae. It was difficult to rear first and second instars, and most died in the lab. Moth larvae and pupae were reared by placing them singly on filter paper in vented Petri dishes (diameter: 35 mm). In 2008, half of the

larvae were provided water with dissolved sugar and the other half were provided with

sagebrush foliage. In subsequent years, during which only older instars were reared, the

larvae were provided with sugar water. The Petri dishes were kept in an incubator (at

23^0C, 16:08 L:D) in 2008 and 2009. The dishes were kept on the lab bench at ambient

temperature and photoperiod in 2010 and 2011.

Petri dishes were checked for emerging parasitoid adults every 1-2 days. Adults

that emerged were recorded as assigned initially to OTUs (operational taxonomic units).

They were placed in alcohol until they could be sent for identification to the Systematic

Entomology Laboratory, Agricultural Research Service, US Department of Agriculture,

and the American Entomological Institute. Voucher specimens are currently held in the

Utah State University Insect Collection.

Rates of parasitism were estimated for individual study sites each year. Larval

and pupal rates of parasitism were estimated only from site collections in a given year

consisting of a minimum, respectively, of eight larvae yielding either moth pupae or

larval parasitoids, or of eight moth pupae yielding either adult moths or pupal parasitoids.

With *Aroga* moth abundance very low across all sites in 2011, the rate of parasitism

could be estimated for only a single site. In other years, the number of sites for which the

rate of parasitism could be estimated ranged from 13 to 27.

Rates of larval parasitism by *Copidosoma* were calculated as the number of larvae

from which the wasp emerged, divided by the total of this number plus the number of

larvae that survived to pupate. Larvae that died before parasitoids could emerge were not

included in these estimates. Rates of parasitism by the two pupal parasitoids were

calculated using the number of hosts, collected in the field as pupae, from which one or the other pupal parasitoid emerged as an adult. This number was divided by the number of field-collected pupae from which an adult moth or an adult of either pupal parasitoid species emerged. Pupae that failed to yield either moth or parasitoid adults were not included in estimating rates of pupal parasitism. The overall rate of parasitism for a moth population was calculated as [1 - (the proportion of larvae escaping parasitism $\times$ the proportion of pupae escaping parasitism)].

Species richness of floral resources

All flowering plants in bloom (i.e., including both the understory herbaceous flora and flowering shrubs [e.g. Utah serviceberry, *Amelanchier utahensis* Koehne; chokecherry *Prunus virginiana* L.; elderberry, *Sambucus glauca* Nutt.]) were sampled weekly from May through mid-July at each study site in 2008 and 2009. They were sampled also for five weeks from mid-June through mid-July 2010 and 2011 (i.e., the five-week period during which parasitoid adults were likely active at the study sites). Floral species richness was measured as the number of nectar-producing plant species (primarily forbs and shrubs) that were found in flower at each site during each weekly survey. At each site, all such species occurring within the 50×100 m marked plot were recorded. An overall weekly mean for flowering species richness was calculated for each year at each study site.

In 2009, more detailed measurements of the floral understory community were taken at a limited number of sites to confirm the accuracy of whole plot visual estimates of floral species richness. Sites that had been censused in 2008 were selected based on

their elevations and accessibility by foot (i.e., they were located within 5 km of paved road), as June rains in 2009 made dirt 'roads' used by motor vehicle prone to washout. Of the ten plots selected for these detailed floral censuses, three were 'lower' elevation sites (~1615-1740 m), four were 'mid' elevations sites (~1745-1860 m), and three were 'high' elevation sites (~1968-2050 m). Measurements were taken along four random 50 m transects through each of these 10 permanent plots. The total number of species that were blooming within 0.5 m of the four transects combined in each of the 10 plots was determined. All measurements were taken during the first week and last week of June (two transects were censused at each plot during each of the two sampling periods). Total species richness along the transects in the plots was confirmed as positively correlated with whole plot flowering species richness estimates (r = 0.75, df = 9, $P <$ 0.0001). Voucher specimens were collected in the field and later identified using the Intermountain Herbarium, Utah State University, Logan, UT (see Appendix A Table A-1 for floral species identification).

Field experiment I (sugar provisioning)

In an initial experiment 12 plots, each 7×7 m, with 50 m between adjacent plots, were paired in a 6×2 grid across several hectares on a hillside at mid-elevation (approximately 1880-1920 m) at Henefer-Echo WMA. One plot of each pair was randomly chosen to be sprayed with sugar once weekly during the summer of 2009; the other plot served as a control. Spraying began on 2 July, when the majority of individuals of the *Aroga* moth had entered the final larval instar. Spraying ended on 7 August, approximately one week after pupal parasitoid emergence was estimated to have

occurred in the field, as based on such emergence among laboratory reared individuals and field collection at nearby sites. Sugar plots were sprayed on each occasion with 1 L per plot of a fine mist of sugar spray (150 g sucrose/1 L water) using a hand pump spray (Evans and Richards 1997). Control plots were sprayed similarly with 1 L of water. All vegetation within each plot, including grasses and understory forbs as well as sagebrush, was sprayed.

Larvae and pupae of the *Aroga* moth in the plots were left undisturbed in 2009; collection of moth larvae and pupae from the plots was postponed until the summer of 2010. This maximized the number of moths emerging in the plots to lay eggs during late summer, which in turn maximized the number of moth eggs in the plot available for parasitism by *Copidosoma* as occurred in late summer. This parasitism becomes apparent and can be scored the following summer once host larvae become fifth instars (at which time, host larval development is terminated as *Copidisoma* pupates inside the host and emerges as an adult). The experiment was designed to test whether sugar provision might enhance adult numbers and persistence of the generalist *Copidisoma* during the summer within treated plots (e.g., by promoting survival), thus enabling this parasitoid to attack greater percentages of *Aroga* moth eggs in late summer when the eggs became available.

Moth pupae parasitized by *Phaeogenes* and *Conura* in the plots in 2009 yielded adults of these wasp species that potentially could remain in the local area to parasitize the next generation of moth pupae. Pupal parasitism in 2010 might therefore be higher in

plots sprayed with sugar versus only with water in 2009 if these pupal parasitoids

attacked the host especially intensively in sugar sprayed plots in 2009.

In 2010, both larvae (as fourth and fifth instars) and pupae of the *Aroga* moth

were collected on three occasions (23, 28 July and 5 August) from the plots. Larvae were

reared in the lab (as described above) to score for parasitism by *Copidosoma*, and pupae

were held to score for parasitism by *Phaeogenes* and *Conura*. Percent parasitism and

parasitoid diversity were then calculated for individual experimental plots.

Field experiment II (addition of floral nectar and MeSA lures)

In a second experiment, two treatments (addition of flowering plants [common

buckwheat, *Fagopyrium esculentum*], and provisioning with lures of Methyl Salicylate

[MeSA; Predalure©), were applied in 2×2 factorial fashion to plots across the landscape

in a randomized design during June-August 2010. Common buckwheat is used

frequently to provide floral nectar in field experiments (Heimpel and Jervis 2005, Lee

and Heimpel 2005) because it matures quickly from seed to the flowering stage and

because its nectar is readily accessible to parasitoids (Patt et al. 1997). MeSA, also

known as oil of wintergreen, is a volatile chemical synthesized by a number of plants

when infested with herbivores; it may function as an herbivore induced plant volatile

(HIPV) or airborne signal that attracts parasitoids to such plants (Kessler and Baldwin

2001, Lee 2010). Floral nectar (as provided by buckwheat) and MeSA represent two

very different resources that can influence where parasitoids choose to forage in a habitat.

Each of the four combinations of the two treatments (including the control

without either treatment) was applied to a randomly selected 20×20 m (400 m^2) plot for a

total of 20 plots dispersed over several hectares within a relatively narrow range of 1850-1950 m in elevation, with adjacent plots 100 m apart. Plots assigned as control plots were left undisturbed.

In plots assigned to receive buckwheat (with or without MeSA), 18 flowering buckwheat plants (growing as groups of three in each of six 9.58 liter pots) were placed in the center of each plot on June 30. These plants were replaced every other day through August 5. Each set of six pots of potted buckwheat plants was arranged in 2×3 fashion with adjacent pots within 15 cm of each other. The pots were set in a shallow pit (15 cm deep) to prevent the wind from knocking them over. The potted-plants were grown in the greenhouse, and were placed in the field once they had begun flowering profusely approximately 4 weeks after seeding.

In plots designated to receive MeSA (with or without buckwheat added), the lures were attached initially (on 30 June) to a wooden post in the center of the plot. In response to disturbance from animals at the site, the lures were relocated subsequently and attached instead to the interior of the sagebrush plant nearest to the center of the plot. Lures were replaced every 2.5 weeks.

Host pupae were collected twice from all plots, on 28 July and 5 August 2010. They were reared in the lab to score for parasitism by *Phaeogenes* and *Conura* as described above.

Data analyses

Data analyses were performed using SAS 9.3 (SAS Institute 2011). Model residuals were tested for adherence to a normal distribution and homogeneity of variances and response variables were transformed when necessary.

Rates of parasitism at individual sites by individual species of parasitoids, and by all species combined, were tested for correlation with local host density in a given year (as measured when the area-wide density of *Aroga* moth larvae peaked each year), and with local host density in the previous year (to test for possible lag effect). Associations of rates of parasitism by different parasitoids at individual sites in individual years were tested also by correlation.

The effects of elevation and local floral species richness on parasitism by individual parasitoid species, and by all species combined, were examined among years by ANCOVA (Type III sums of squares). ANCOVA was applied similarly to examine the effects among years of parasitoid species richness on parasitism by all parasitoid species combined. The rates of parasitism by larval (*Copidisoma*) and pupal (*Phaeogenes* and *Conura*) parasitoids, both individually and combined, were arcsine transformed prior to the analyses to meet assumptions of parametric tests. For each analysis, ANCOVA was carried out first by including in the model the interaction between year and elevation, floral species richness, or parasitoid species richness. In all cases except for the interaction of elevation and year for parasitism by *Phaeogenes*, the interaction term was not significant ($P > 0.05$). Therefore, in all cases with this one exception, the data were analyzed again by ANCOVA with the interaction term removed

from the model; the results are given below. In the single case of parasitism by *Phaeogenes* the significant interaction of the effects of elevation and year was retained in the model (McDonald 2009) and individual slopes for each year of the study were fit to describe the relationship between rate of parasitism and elevation.

The effect of elevation on floral richness (square-root transformed) across years was tested using similar ANCOVA procedures. Thus, a model was fit first by including the interaction of elevation with year. Because this interaction proved to be not significant, a second ANCOVA was applied with the interaction term removed, and the results of this second analysis are presented below.

Analyses by multiple regression for the full set of study sites were conducted to examine in a single model the effects on rates of parasitism of elevation and local floral species richness, which were highly correlated with each other. The analyses did not isolate a significant effect of floral species richness on patterns of parasitism beyond the effect that could be accounted for by elevation. To address the confounding influence of elevation on floral species richness, simple linear regressions were conducted for a subset of study sites over a narrower range of elevation. In particular, the dependence of local floral species richness and rates of parasitism on elevation was assessed with restriction to only the seven mid-to-high elevation sites that were sampled intensively for floral species richness in 2009. Additionally, simple linear regressions were conducted to assess the dependence of rates of parasitism on local floral species richness at these seven sites.

For the results of the first field experiment, the percent parasitism of larval and pupal hosts was compared by paired TTEST (following arcsine transformation) for sugar sprayed versus paired control plots. It was hypothesized that parasitism by each of the three parasitoid species would be increased) by the provision of sugar. Sufficient numbers of pupae (a minimum of eight per plot) to determine the rate of parasitism were collected from four pairs of plots, and only these four pairs of plots were compared by paired TTESTs for parasitism of both pupal parasitoids combined, and for the three species (*Copidisoma*, *Phaeogenes*, and *Conura*) individually.

To analyze the differences in parasitism among treatments in the second field experiment, mean percent parasitism was compared among treatment groups using a two-way ANOVA (Proc GLM), after percent parasitism was arcsine transformed. Only 17 of the original 20 plots were included in analyses, as three sites (one plot each with flowers or MeSA added, and one plot with both flowers and MeSA added) failed to yield the minimum number of required pupae (i.e., eight pupae). As this study addressed only pupal parasitism as measured in the same year that the treatments were applied (2010), the effects of different treatment combinations (No Flower, No MeSA; No Flower, MeSA; Flower, No MeSA; and Flower, MeSA) were tested for the responses of the pupal parasitoids *Phaeogenes* and *Conura* together and individually.

RESULTS

Yearly patterns of parasitoid abundance

The *Aroga* moth was moderately abundant throughout the Henefer-Echo WMA in 2008 when the study began, and became very abundant in 2009 before dropping to low levels thereafter (Table 3.1; see also Chapter 2). Adults of moths and parasitoids were reared from nearly 2300 field-collected larvae and pupae during 2008-2011, with the majority collected in 2008 and 2009. The two generalist parasitoids, *Copidisoma* and *Conura,* and the specialist *Phaeogenes* accounted together for ~99% of moth parasitism in 2008 and 2009. In 2010 (with greatly reduced sample size), additional parasitoid species played a greater, but still relatively minor, role (Table 3.1**).** The population of the *Aroga* moth had reached such low numbers by 2011 that only one of the 38 study sites yielded enough individuals to estimate parasitism and only the three major parasitoid species were recorded.

The overall yearly rate of parasitism of the *Aroga* moth across the Henefer-Echo WMA (i.e., the yearly mean rate of parasitism among study sites) was high throughout 2008-2011. It increased from nearly half of individuals parasitized in 2008 to nearly three-quarters of individuals parasitized in 2010, before dropping slightly in 2011. The larval parasitoid *Copidisoma* accounted for the majority of parasitism in each year. Its rate of parasitism was especially high in 2010 (52%), almost doubling that in 2008-2009. Pupal parasitism by *Phaeogenes* was greater than by *Conura* in 2008-2010 (especially so in 2009-2010, during which the rate of parasitism by *Phaeogenes* increased markedly

from 2008). However, at the single site from which moths could be collected in

sufficient number in 2011, pupal parasitism by *Conura* was much higher than pupal

parasitism by *Phaeogenes* (Table 3.1).

Parasitoid responses to factors varying naturally over space

Host density. Parasitism (both by individual species and by all species combined)

varied greatly from site to site during 2008-2010. However, it was neither clearly nor

consistently related to local host density. The overall rate of parasitism (i.e., parasitism

by all species combined) was not correlated with peak host density at individual sites

during the years of observation: 2008-2010 ($P > 0.70$ in all cases). Similar results were

obtained for each of the three major species of parasitoids considered individually during

2008-2010 ($P > 0.05$ in all cases). There was no evidence for lag-effects wherein the rate

of parasitism at a site was positively correlated with the density of the host in the

previous year ($P > 0.05$ in all cases for comparisons between the same field sites

successive years).

Spatial associations among parasitoid species. In 2009, when large numbers of

Aroga moth were present throughout the Henefer-Echo WMA, the rate of parasitism by

pupal parasitoids (*Conura* and *Phaeogenes* combined) was positively correlated with the

rate of larval parasitism by *Copidisoma* among individual sites when both larval and

pupal parasitoids were present (r $= 0.50$, df $= 14$, $P = 0.05$). In other years when fewer

larvae of the *Aroga* moth were present throughout the area, rates of larval and pupal

parasitism were not correlated with each other (2008: r $= 0.02$, df $= 25$, $P = 0.90$; 2010:

r = 0.31, df = 5, P = 0.50). In both 2008 and 2009, the rates of parasitism by the two

species of pupal parasitoids (*Conura* and *Phaeogenes*) were negatively correlated with

each other among individual sites (2008: r = -0.47, df = 18, P < 0.05; 2009: r = - 0.67,

df = 14, P < 0.01). The correlation was also negative in 2010 among the relatively few

sites sampled that year, but not significantly so (r = -0.54, df = 5, P = 0.21).

 Elevation. The study sites spanned a large range in elevation throughout the

Henefer-Echo WMA. All three major species of parasitoids contributed significantly to

parasitism of the defoliator throughout the general area (Table 3.1). They differed,

however, in the intensities with which they attacked the host along the elevation gradient

(Fig. 3.1). The larval parasitoid *Copidisoma* was present at all elevations. The

percentage parasitism by this species, however, tended to be higher at higher elevations

(Fig. 1a; ANCOVA, effect of elevation: $F_{1, 57}$ = 14.64, P < 0.001; effect of year:

$F_{2, 57}$ = 11.37, P < 0.0001). The intensity of pupal parasitism by *Phaeogenes* and *Conura*

varied in opposite pattern to each other across elevation gradients. Greatest rates of

Phaeogenes parasitism occurred at high elevations (Fig. 3.1b showing regression lines

with varying slope; ANCOVA, effect of elevation: $F_{1, 46}$ = 17.97, P = 0.0001; effect of

year: $F_{2, 46}$ = 5.15, P = 0.0098; interaction of elevation x year: $F_{2, 46}$ = 6.35, p = 0.0038).

Highest rates of *Conura* parasitism in contrast occurred at low elevations (Fig. 3.1c;

ANCOVA, effect of elevation: $F_{1, 46}$ = 23.78, P < 0.0001; effect of year: $F_{2, 46}$ = 2.57,

P = 0.09). Combining the impact of all three species, the overall rate of parasitism of

Aroga increased as elevation increased (Fig. 3.1d). There were significant differences in

rates among years, with greatest rates of parasitism at any given elevation occurring in

2010 and lowest rates in 2008 (ANCOVA, effect of elevation: $F_{1, 46}$ = 13.93, P = 0.0005; effect of year: $F_{2, 46}$ = 13.51, $P < 0.0001$).

Floral species richness. In all years of the study, floral species richness at individual sites was greater at higher than at lower elevations (Fig. 3.2; ANCOVA, effect of elevation: $F_{1, 148}$ = 112.32, $P < 0.0001$; effect of year: $F_{3, 148}$ = 17.12, $P < 0.0001$). Associations of larval and pupal parasitism with floral species richness among study sites were therefore similar to those of parasitism with elevation.

The rate of parasitism by *Copidisoma* increased with increasing floral species richness at individual sites (Appendix Fig. B-1a; ANCOVA, effect of floral richness: $F_{1, 57}$ = 5.76, P = 0.02; effect of year: $F_{2, 57}$ = 12.07, $P < 0.0001$). The rate of parasitism by *Phaeogenes* also increased with increasing floral species richness (Fig. B-1b; ANCOVA, effect of floral richness: $F_{1, 46}$ = 6.88, P = 0.01; effect of year: $F_{2,46}$ = 1.80, P = 0.18). The rate of parasitism by *Conura* decreased with increasing floral species richness (Fig. B-1c; ANCOVA, effect of floral richness: $F_{1, 46}$ = 6.55, P = 0.01; effect of year: $F_{2, 46}$ = 3.78, P = 0.03). The overall rate of parasitism (i.e., the combined rates of the three major species) tended to increase (but not significantly so) with increasing floral species richness at individual sites (Fig. B-1d; ANCOVA, effect of floral richness: $F_{1, 46}$ = 3.05, P = 0.09; effect of year: $F_{2, 46}$ = 5.25, P = 0.009).

The seven mid-to-high elevation sites that were sampled intensively for floral richness in 2009 supported particularly high numbers of the parasitoids *Copidisoma.*and *Phaeogenes.* In contrast to results for floral richness across the elevations spanned by the full set of 38 plots, floral richness did not increase with elevation within this restricted set

of seven sites ($R^2 = 0.22$, df = 5, $P = 0.28$). Rates of parasitism also did not vary

significantly with elevation within this restricted set of sites for either *Copidisoma*

($R^2 = 0.33$, df = 5, $P = 0.18$) or *Phaeogenes* ($R^2 = 0.36$, df = 5, $P = 0.15$), or for overall

parasitism by the two parasitoid species combined ($R^2 = 0.38$, df = 5, $P = 0.14$). Overall

parasitism by these two species combined, however, did increase strongly with floral

species richness among these sites (Fig. 3.3; $R^2 = 0.64$, df = 5, $P = 0.03$); similar results

were apparent for single species rates of parasitism by *Copidisoma* ($R^2 = 0.51$, df = 5,

$P = 0.07$) and *Phaeogenes* ($R^2 = 0.59$, df = 5, $P = 0.04$).

Parasitoid responses to experimental treatments

Field experiment I. The rate of larval parasitism by *Copidisoma* in 2010 did not

differ between plots sprayed with sugar the previous year (in 2009) or sprayed with water

as controls (Fig. 3.4; paired TTEST, $t = 0.58$, df = 5, $P = 0.59$). In contrast, more pupal

parasitism occurred in 2010 in plots that had been sprayed with sugar in 2009 than in

control plots (Fig. 3.4; paired TTEST, *Phaeogenes* + *Conura*, $t = -5.19$, df = 3, $P = 0.01$;

Phaeogenes, $t = -7.27$, df = 3, $P = 0.005$; *Conura*, $t = -2.25$, df = 3, $P = 0.10$).

Field experiment II. An interaction occurred in the responses of the pupal

parasitoids as a group (*Phaeogenes* and *Conura* combined) to experimental treatments

(addition of experimental flowers and/or MeSA; two-way ANOVA: flower, $P = 0.02$;

MeSA, $P = 0.6437$; and flower×MeSA, $P = 0.05$). Pupal parasitism increased when

experimental flowers were added, but only when MeSA was absent. When MeSA was

added, the overall pattern was weak, with combined pupal parasitism tending to increase

when experimental flowers were absent, but decrease when flowers were added.

Parasitism by *Phaeogenes* in particular increased strongly when experimental flowers were added especially when MeSA was absent yet to some degree also (though less strongly so) when it was added (Fig. 3.5). Parasitism by *Phaeogenes* did not increase when MeSA was added (two-way ANOVA: flower, $P = 0.01$; MeSA, $P = 0.40$; and flower×MeSA, $P = 0.28$). Parasitism by *Conura*, in contrast, was not affected clearly by the addition of flowers, but did increase with the addition of MeSA, especially in the absence of experimental flowers (Fig. 3.5; two-way ANOVA: flower, $P = 0.75$; MeSA, $P = 0.01$; and flower×MeSA, $P = 0.04$).

Effects of parasitoid richness on overall parasitism

The three parasitoids differed widely from each other in the degree to which they parasitized the *Aroga* moth at individual sites. Indeed, at nearly one fifth of all sites sampled in all years, only a single species of parasitoid was responsible for the parasitism recorded: *Copidisoma* was the sole parasitoid recorded at 10% of all site-years, while *Phaeogenes* and *Conura* were the sole parasitoid recorded at 6% and 2%, respectively, of all site-years.

The overall rate of parasitism at an individual study site increased with the species richness of major parasitoids at that site (that is, with the occurrence of one, two, or all three of the major parasitoid species) (Fig. 3.6). The positive effect of parasitoid species richness was consistent among years (2008-2010) while the overall rate of parasitism varied among years (ANCOVA, effect of richness: $F_{1,46} = 35.56$, $P < 0.0001$; effect of year: $F_{2,46} = 7.41$, $P = 0.0004$). Results were similar when all parasitoid species were considered (i.e., including parasitoid species present in very low numbers, with up to five

species in total co-occurring at an individual site in a given year; ANCOVA, effect of parasitoid richness: $F_{1,45} = 17.96$, $P < 0.0001$; effect of year: $F_{2,44} = 7.80$, $P = 0.0003$; richness $\times$ year $F_{2,43} = 1.40$, $P = NS$).

Among the species of parasitoids reared from the *Aroga* moth in this study, only one is known to be a hyperparasitoid. This species (*Zatropis* sp.*) was found only in the experiment II plots (with buckwheat and MeSA) in samples taken in 2010; it did not occur in samples from unaltered, long-term field plots in any of the years of the study. Hyperparasitism by *Zatropis* accounted for up to 12% of the parasitism recorded in 2010 in individual plots in experiment II.

DISCUSSION

Parasitism of the *Aroga* moth by multiple species

There has been great interest recently in the importance of parasitoid diversity in promoting high rates of parasitism of insect herbivores (e.g., Tylianakis et al. 2006, Veddeler et al. 2010). In this field study, three species of parasitoids attacked the immature stages of the *Aroga* moth with considerable intensity in each year of the study. Each of these three species responded in its own way to the varying resource of local *Aroga* moth populations across the large expanse of sagebrush habitat encompassed by the Henefer-Echo WMA.

None of the three species responded to local host density in their rates of attack. The overall rate of parasitism from all three species combined also was consistently independent of local host density in each year of the study. In contrast, rates of

parasitism were strongly correlated with another spatially varying attribute associated with local moth populations, elevation. Previous studies of parasitoids have identified elevation as a key factor influencing rates of parasitism (e.g., Hodkinson 2005, Moya-Raygoza et al. 2012). At Henefer-Echo WMA, the rates of parasitism by the larval parasitoid *Copidisoma* and the pupal parasitoid *Phaeogenes* increased with elevation, while the rate of parasitism by the pupal parasitoid *Conura* decreased.

The negative correlation between local rates of parasitism of the two pupal parasitoids across the elevation gradient could reflect interspecific competition for hosts between them (e.g., Bogran et al. 2002). However, it may also simply reflect that the two species differ in their abilities to thrive under the different conditions associated with low versus high elevation (e.g., Hodkinson 2005). Certainly, interspecific competition and habitat preference are not necessarily mutually exclusive (e.g., Takasu et al. 1998). Further studies are needed to distinguish between these two possibilities.

The increase in rates of parasitism with elevation by both *Phaeogenes* and *Copidisoma* may also reflect the importance of the floral community of the sagebrush understory. The species richness of this community increased with elevation. Flowering plants are often critical resources for adult parasitoids in providing carbohydrate food in the form of nectar (e.g., Fiedler and Landis 2007, Issacs et al. 2008). The availability of nectar to parasitoids may have increased with increasing floral species richness (and hence also with elevation) among the study sites. This hypothesis is supported by the positive relationship between floral species richness and parasitism among mid-to-high

elevation sites (among which no relationship was detected between elevation and parasitism).

The results of the field experiments also support the hypothesis that the local availability of floral nectar promotes parasitism of the *Aroga* moth by *Phaeogenes*. Thus the rate of parasitism by *Phaeogenes* was increased significantly by the application of sugar in the first experiment, and by the provision of flowering buckwheat in the second experiment. A similar increase in the rate of parasitism by *Copidisoma* was not observed with these experimental treatments. But whereas the treatments were applied at the time during the summer when *Phaeogenes* was laying its eggs, this was not the case for *Copidisoma*, which lays its eggs later in the summer (in the eggs of the host). This may account for the ineffectiveness of the experimental treatments in regard to parasitism by *Copidisoma*.

Parasitism by the pupal parasitoid *Conura* was not positively associated with local floral species richness of the sagebrush understory, and indeed was greatest at low elevations where such floral richness was often low. Consistent with this result, *Conura* responded less strongly than did *Phaeogenes* to additions of sugar and flowers in experimental plots. In contrast, *Conura* showed a stronger response to MeSA than did *Phaeogenes*. MeSA is a volatile released by many plants when under attack by insect herbivores and can serve as a signal in triggering induced defenses in plants (Ozawa et al. 2000, Chen et al. 2003, Schiestl 2010). The response of *Conura* to MeSA may indicate that the generalist *Conura* is more strongly influenced in its foraging behavior by volatile chemical cues from host plants signaling the presence of insect herbivores. While this

hypothesis requires further testing, the results of the field experiments more generally

reinforce those of the field censuses in indicating that the three parasitoid species differed

in their responses to cues and other spatial attributes in attacking local populations of the

Aroga moth.

The co-occurrence of the three parasitoids in attacking moth populations resulted

in greater overall parasitism locally. This, combined with the fact that the three species

differed in their presence and relative rates of attack among local moth populations (e.g.,

as associated with differing elevation), resulted in greater parasitism of the *Aroga* moth

across Henefer-Echo WMA as a whole, as the net outcome of their combined use of the

host. Interest in the potential benefits of biodiversity as applied to natural enemies and

biological control of insect herbivores (e.g., pest insects) is often tied to the concept of

complementarity. This is the concept that niche differences among natural enemies will

promote their differential use of a shared host over space and time, such that their

collective activities will result in greater overall mortality of the herbivore (Cardinale et

al. 2002, 2003, 2006; Perfecto et al. 2004, Snyder et al. 2005, Letourneau et al. 2009).

While complementarity is far from inevitable as the outcome of interactions of

natural enemies that compete for a shared host, it is reflected in this study in which the

overall rate of parasitism of a local moth population increased with increasing species

richness of the parasitoid guild. Similar results have been reported previously in other

field studies in which multiple species of parasitoids have been released for biological

control of insect pests (Dorn et al. 1999, Kirk et al. 2000, Brewer and Larkan 2005).

Thus, the degree to which the parasitoids in the present study may have interfered with

each other (e.g., through competition) or simply substituted for each other (e.g., in inflicting compensatory host mortality) was outweighed by their independent, complementary contributions to overall mortality.

Comparison with other studies of *Aroga* moth parasitism

Overall rates of parasitism of the *Aroga* moth at Henefer-Echo WMA were high throughout the study. This contrasts strongly with results from a previous intensive study of sagebrush defoliation by the *Aroga* moth. That study commenced in the 1970s at a highly disturbed site in Curlew Valley, ID, where the understory vegetation was dominated by cheatgrass, *B. tectorum* (Hsiao 1984). The *Aroga* moth experienced much lower rates of parasitism (less than 10 percent parasitism) than in the present study, in 4 of the 5 years (1971-1975) that the area was surveyed (Temte 1977). While the major parasitoids we describe here were present at the Curlew Valley sites, they were much less prominent (*Copidisoma* accounted for only 0.7 - 5.5% mortality). However, previous studies in natural sagebrush steppe (Henry 1961, Hall 1965, Fillmore 1965) found the three major species of parasitoids present at our studies to have rates of incidence similar to those reported here, with *Copidisoma* being the most abundant followed by *Phaeogenes* and then *Conura* (these studies were conducted in Idaho and northern California). The contrast in habitat characteristics and rates of parasitism particularly between the Curlew Valley and Henefer-Echo studies, combined with results among study sites and experimental plots in the present study, suggest the potential importance

of species rich floral understory communities of sagebrush in promoting *Aroga* moth parasitism.

Potential effects of grazing on parasitism of *Aroga* moth

There was a strong elevational gradient in floral understory species richness associated with sagebrush stands at Henefer-Echo WMA. Agricultural use (grazing) of the area may be responsible for this pattern, with consequences for parasitism of the *Aroga* moth. The diversity of sagebrush-steppe plant communities is at risk from the intensification of grazing (Mack 1986, Billings 1990, Whisenant 1990). These communities evolved with few large herbivores; use of these plant communities by domestic livestock is considered a deviation from the historical disturbance regime (Mack and Thompson 1982, Davies et al. 2009). With European settlement of western North America, large numbers of cattle and sheep were introduced in the mid-to-late 1800s (Oliphant 1968). These herbivores joined the *Aroga* moth in greatly affecting the sagebrush-steppe vegetation (Adler et al. 2001, 2005; Davies et al. 2009). It is estimated that over 40% of the current area of sagebrush is at moderate to high risk of displacement by *B. tectorum* in the next 30 years (Suring et al. 2005).

Cattle grazing often results in drastic alterations and reduced forb diversity in herbaceous understory plant communities (Milchunas and Lauenroth 1993, Jones 2000, Foley et al. 2005). It is well documented that cattle graze heavily in areas nearest watering troughs and natural bodies of water (e.g., ponds) in sagebrush-steppe as well as in other systems (e.g., Putfarken et al. 2008). Bailey (2005) emphasized that water is the

most critical component of livestock habitat and one of the most important factors determining the selection of feeding places by herbivores is the reduction of traveling distance to water (Bailey et al. 2004). To support annual grazing at Henefer-Echo WMA, permanent cattle troughs have been placed at the most accessible locations in the lowest elevations. Thus, just as species richness of the floral understory increased with elevation among the study sites, so too did it increase with distance from the nearest cattle trough (Appendix Fig. C-1). Future studies hence should address whether the altitudinal gradient in understory floral species richness arises from grazing.

Through their impact on the flowering vegetation (and ultimately on parasitoids), cattle and sheep could influence the population dynamics of the *Aroga* moth indirectly. The potential indirect influence of grazing on *Aroga* moth abundance highlights the potentially adverse effects of habitat alteration on biodiversity at multiple levels within food webs. The intensification of agriculture (including grazing) is a major disturbance and driver of biodiversity loss and related decline in ecosystem functioning (Foley et al. 2005, Gagic et al. 2012, Tscharntke et al. 2012). Loss of biodiversity associated with the intensification of agriculture can adversely affect food web interactions and related ecosystem services such as biological control (Bianchi et al. 2006). Adverse effects of agricultural intensification on food web interactions may unleash species such as the *Aroga* moth to erupt with both greater frequency and intensity.

Concluding remarks

The results of the present study indicate considerable potential for parasitoids, working as a diverse community of species acting in net complementary fashion, to limit

excessively severe outbreaks of the *Aroga* moth in sagebrush-steppe habitat such as that

of Henefer-Echo WMA. The results also suggest that promotion of a diverse community

of understory flowering herbs, as part of the food web centered on the moth, will in turn

promote parasitism. Further studies of grazing in particular may indicate good

management options for preserving and promoting such floral diversity, with the ultimate

aim of managing the *Aroga* moth as a sometimes serious pest of sagebrush.

LITERATURE CITED

Adler, P., D. Raff, and W. Lauenroth. 2001. The effect of grazing on the spatial

heterogeneity of vegetation. Oecologia **128**: 465-479.

Adler, P. B., D. G. Milchunas, O. E. Sala, I. C. Burke, and W. K. Lauenroth. 2005. Plant

traits and ecosystem grazing effects: comparison of US sagebrush steppe and

Patagonian dteppe. Ecological Applications **15**: 774-792.

Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems.Agriculture,

Ecosystems & Environment **74**: 19-31.

Amarasekare, P. 2007. Trade-offs, temporal variation, and species coexistence in

communities with intraguild predation. Ecology **88**: 2720-2728.

Bailey, D. W. 2005. Identification and creation of optimum habitat conditions for

livestock. Rangeland Ecology & Management **58**: 109-118.

Bailey, D. W., M. R. Keil, and L. R. Rittenhouse, 2004. Research observation: daily

movement patterns of hill climbing and bottom dwelling cows. Rangeland

Ecology & Management **57**: 20-28.

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. Wogan, B. Swartz, T. B. Quental, E. A.
Ferrer, and C. Marshall. 2011. Has the Earth/'s sixth mass extinction already
arrived? Nature **471**: 51-57.

Bellows, T. S., and T. W. Fisher. 1999. Handbook of Biological Control. Academic
Press, San Diego, California, USA.

Bianchi, F. J., C. J. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in
agricultural landscapes: a review on landscape composition, biodiversity and
natural pest control. Proceedings of the Royal Society B: Biological Sciences **273**:
1715-1727.

Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of impoverishment in the Great
Basin. Pages 301-322 *in* G. M. Woodell, editor. The earth in transition: patterns
and processes of biotic impoverishment. Cambridge University Press, Cambridge,
England.

Bográn, C. E., K. M. Heinz, and M. A. Ciomperlik. 2002. Interspecific competition
among insect parasitoids: field experiments with whiteflies as hosts in cotton.
Ecology **83**: 653-668.

Borer, E. T., C. J. Briggs, W. W. Murdoch, and S. L. Swarbrick, 2003. Testing intraguild
predation theory in a field system: does numerical dominance shift along a
gradient of productivity? Ecology Letters **6**: 929-935.

Brewer, M. T., and R. P. Larkin. 2005. Efficacy of several potential biocontrol organisms
against Rhizoctonia solani on potato. Crop Protection **24**: 939-950.

Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances

ecosystem functioning through interspecific facilitation. Nature **415**: 426-429.

Cardinale, B. J., C. T. Harvey, K. Gross, and A. R. Ives. 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. Ecology Letters **6**: 857-865.

Cardinale B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, and A. L. Downing. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature **443**: 989-92.

Chapin, F. S, III., E S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L Reynolds, D. U. Hooper, S. Lavore, O. E. Sala, S. H. Hobbie, M. C. Mack, and S. Diaz. 2000. Consequences of changing biodiversity. Nature **405**: 234-242.

Chen, F., J. C. D'Auria, D. Tholl, J. R. Ross, J. Gershenzon, J. P. Noel, J. P., and E. Pichersky. 2003. An *Arabidopsis thaliana* gene for methylsalicylate biosynthesis, identified by a biochemical genomics approach, has a role in defense. The Plant Journal **36**: 577-588.

Davies, K. W., T. J. Svejcar, and J. D. Bates. 2009. Interaction of historical and nonhistorical disturbances maintains native plant communities. Ecological Applications **19**: 1536-1545.

Dorn, S., P. Schumacher, C. Abivardi, and R. Meyhöfer. 1999. Global and regional pest insects and their antagonists in orchards: spatial dynamics. Agriculture, Ecosystems & Environment **73**: 111-118.

Ehrlich, P. R. 1991. Biodiversity studies: science and policy. Science **253**: 758-762.

Evans, E. W. 1994. Indirect interactions among phytophagous insects: aphids, honeydew

and natural enemies. Pages 287-297 *in* S. Leather, K. Walters, N. Mills, and A. Watt, editors. Individuals, populations, and patterns in ecology. Andover, Hampshire, England.

Evans, E. W., and D. R. Richards. 1997. Managing the dispersal of ladybird beetles (Col.: Coccinellidae): Use of artificial honeydew to manipulate spatial distributions. BioControl **42**: 93-102.

Fiedler, A. K., and D. A. Landis. 2007. Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. Environmental Entomology **36**: 751-765.

Fillmore, O. O. 1965. The parasitoids of *Aroga websteri* Clarke (Lepidoptera: Gelechiidae) in southern Idaho. Thesis. University of Idaho, Moscow, ID, USA.

Finke, D. L. and R. F. Denno. 2004. Predator diversity dampens trophic cascades. Nature **429**: 407-410.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. B. Bonan, S. R. Carpenter, R. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science **309**: 570–574.

Frank, D. A., and S. J. McNaughton. 1992. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. Ecology **73**: 2043-2058.

Gagic, V., S. Hänke, C. Thies, C. Scherber, Ž. Tomanović, and T. Tscharntke. 2012.

Agricultural intensification and cereal aphid–parasitoid–hyperparasitoid food webs: network complexity, temporal variability and parasitism rates. Oecologia **170**: 1099-1109.

Gates, D. H. 1964. Sagebrush infested by leaf defoliating moth. Journal of Range Management. **17**: 209-210.

Godfray, H. C. J. 1994. Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, New Jersey, USA

Hackett-Jones, E., C. Cobbold, and A. White. 2008. Coexistence of multiple parasitoids on a single host due to differences in parasitoid phenology. Theoretical Ecology **2**: 19-31.

Hall, R. C. 1965. Sagebrush defoliator outbreak in Northern California. U.S. Forest Service, Res. **Note PSW-75**.

Heimpel, G. E. and M. A. Jervis. 2005. An evaluation of the hypothesis that floral nectar improves biological control by parasitoids. Pages 267-304 *in* F. Wäckers, P. vanRijn, J. Bruin, editors. Plant-provided food for carnivorous insects: a protective mutualism and its applications. Cambridge University Press, Cambridge, England.

Henry, J. E. 1961. The biology of the sagebrush defoliator, *Aroga websteri* Clarke, in Idaho. Thesis. University of Idaho, Moscow, Idaho, USA.

Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews **80**: 489-513.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H.

Lawton, D. Lodge, M. Loreau, S. Naeem, B. Schmid, A. H. Setal, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs **75**: 3–35.

Hsiao, T. H. 1984. Biology and demography of the sagebrush defoliator and its impacts on big sagebrush. Pages 191-198 *in* E. D. McArthur and B. L. Welch, editors. Proceedings, Symposium on the Biology of *Artemisia* and *Chrysothamnus*, 9-13 June 1984, Provo, UT. USDA Forest Service General Technical Report **GTR-INT-200.**

Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2008. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. Frontiers in Ecology and the Environment **7**: 196-203.

Ives, A. R., B. J. Cardinale, and W. E. Snyder. 2005. A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. Ecology Letters **8**: 102-116.

Jones, A. 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. Western North American Naturalist **60**: 155-164.

Kessler, A., and I. T. Baldwin. 2001. Defensive function of herbivore-induced plant volatile emissions in nature. Science **291**: 2141-2144.

Kirk, A. A., L. A. Lacey, J. K. Brown, M. A. Ciomperlik, J. A. Goolsby, D. C. Vacek, L. E. Wendel, and B. Napompeth. 2000. Variation in the *Bemisia tabaci* s. species complex (Hemiptera: Aleyrodidae) and its natural enemies leading to successful

biological control of *Bemisia* biotype B in the USA. Bulletin of Entomological Research **90**: 317-328.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology **45**: 175–201.

Lawton, J. H., and V. K. Brown. 1994. Redundancy in ecosystems. Pages 255-268 *in* E. D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Springer, London, England.

Lee, J. C. 2010. Effect of methyl salicylate-based lures on beneficial and pest arthropods in strawberry. Environmental Entomology **39**: 653-660.

Lee, J. C., and G. E. Heimpel. 2005. Impact of flowering buckwheat on lepidopteran cabbage pests and their parasitoids at two spatial scales. Biological Control **34**: 290-301.

Letourneau, D. K., J. A. Jedlicka, S. G. Bothwell, and C. R. Moreno. 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics **40**: 573-592.

Mack, R. N. 1986. Alien plant invasions into the Intermountain West: a case history. Pages 192-213 *in* H. A. Mooney and J. Drake editors. Ecology of Biological Invasions in North America and Hawaii. Springer-Verlag, New York, New York, USA.

Mack R. N., and J. N. Thompson. 1982. Evolution in steppe with few large, hoofed

mammals. American Naturalist **119**: 757–773.

McDonald, J. H. 2009. Handbook of biological statistics (Vol. 2). Sparky House

Publishing: Baltimore, Maryland, USA.

Milchunas, D. G., and W. K. Lauenroth, 1993. Quantitative effects of grazing on

vegetation and soils over a global range of environments. Ecological

Monographs **63**: 327-366.

Miller, R. 2005. *Aroga* moth and sagebrush defoliation. The Grazier **325**: 2-3.

Extension Service. Oregon State University, Corvallis, Oregon, USA.

Moya-Raygoza, G., E. L. Albarracin, and E. G. Virla. 2012. Diversity of egg parasitoids

attacking *Dalbulus maidis* (Hemiptera: Cicadellidae) populations at low and high

elevation sites in Mexico and Argentina. Florida Entomologist **95**: 105-112.

Oliphant, J. O. 1968. On the Cattle Range of the Oregon Country. University of

Washington Press, Seattle, Washington, USA.

Ozawa, R., G. I. Arimura, J. Takabayashi, T. Shimoda, and T. Nishioka. 2000.

Involvement of jasmonate-and salicylate-related signaling pathways for the

production of specific herbivore-induced volatiles in plants. Plant and Cell

Physiology **41**: 391-398.

Patt, J. M., G. C. Hamilton, and J. H. Lashomb. 1997. Foraging success of parasitoid

wasps on flowers: interplay of floral architecture and searching behavior.

Entomological Experimental Applications **83**: 21–30.

Perfecto I., J. H. Vandermeer, G. L. Bautista, G. I. Nunez, and R. Greenberg. 2004.

Greater predation in shaded coffee farms: the role of resident neotropical birds. Ecology **85**: 2677-2681.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. Science **269**: 347-350.

Putfarken, D., J. Dengler, S. Lehmann, and W. Härdtle. 2008. Site use of grazing cattle and sheep in a large-scale pasture landscape: a GPS/GIS assessment. Applied Animal Behaviour Science **111**: 54-67.

Rand, T. A., J. M. Tylianakis, and T. Tscharntke. 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect predators into adjacent natural habitats. Ecology Letters **9**: 603–614.

Rand, T. A., F. J. Van Veen, and T. Tscharntke. 2012. Landscape complexity differentially benefits generalized fourth, over specialized third, trophic level natural enemies. Ecography **35**: 97-104.

Rodriguez, M. A., and B. A. Hawkins. 2000. Diversity, function and stability in parasitoid communities. Ecology Letters **3**: 35-40.

Root, R. B. 1973. Organization of plant-arthropod association in simple and diverse habitats: The fauna of collards (Brassica oleraceae). Ecological Monographs **43**: 95-124.

SAS Institute. 2011. PROC user's manual, version 6th ed. SAS Institute, Cary, North Carolina, USA.

Schiestl, F. P. 2010. The evolution of floral scent and insect chemical communication. Ecology Letters **13**: 643-656.

Schmidt, M. H., A. Lauer, T. Purtauf, C. Thies, M. Schaefer, and T. Tscharntke. 2003.

Relative importance of predators and parasitoids for cereal aphid

control. Proceedings of the Royal Society of London. Series B: Biological

Sciences **270**: 1905-1909.

Schmitz, O. J. 2007. Predator diversity and trophic interactions. Ecology **88**:2415-2426.

Schwartz, M. W., C. A. Brigham, J. D. Hoeksema, K. G. Lyons, M. H. Mills, and P. J.

Van Mantgem. 2000. Linking biodiversity to ecosystem function: implications for

conservation ecology. Oecologia **122**: 297-305.

Snyder W. E., G. C. Chang, and R. E. Prasad. 2006. Conservation biological control:

biodiversity influences the effectiveness of predators. Pages 324-343 i*n* P.

Barbosa and I. Castellanos, editors. Ecology of Predator-Prey Interactions. Oxford

University Press, New York, New York, USA.

Straub, C. S., D. L. Finke, and W. E. Snyder. 2008. Are the conservation of natural

enemy biodiversity and biological control compatible goals?. Biological

Control **45**: 225-237.

Takasu, K., Y. Hirose, and M. Takagi. 1998. Occasional interspecific competition and

within-plant microhabitat preference in egg parasitoids of the bean bug, *Riptortus*

clavatus (Hemiptera: Alydidae) in soybean. Applied Entomology and Zoology **33**:

391–399.

Temte, A. K. 1977. The demography of the sagebrush defoliator, *Aroga websteri*

Clarke (Lepidoptera: Gelechiidae), and its impact on Artemisia tridentata. Thesis.

Utah State University, Logan, Utah, USA.

Thébault, E., and M. Loreau. 2005. Trophic interactions and the relationship between species diversity and ecosystem stability. The American Naturalist **166**: 95-114.

Tilman, D., Reich, P. B., and Knops, J. M. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature **441**: 629-632.

Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batáry, and C. Westphal. 2012. Landscape moderation of biodiversity patterns and processes-eight hypotheses. Biological Reviews **87**: 661-685.

Tylianakis, J. M., T. Tscharntke, and A. M. Klein. 2006. Diversity, ecosystem function and stability of parasitoid-host interactions across a tropical habitat gradient. Ecology **87**: 3047–3057.

Veddeler, D., J. Tylianakis, T. Tscharntke, and A. M. Klein. 2010. Natural enemy diversity reduces temporal variability in wasp but not bee parasitism. Oecologia **162**: 755–762.

Walde, S. J., and W. W. Murdoch. 1988. Spatial density dependence in parasitoids. Annual Review of Entomology **33**: 441-466.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. Pages 4-10 *in* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller, editors. Proceedings: symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management. USDA General Technical Report INT-276, Ogden, Utah, USA.

Wilson, E. O. 1989. Threats to biodiversity. Scientific American **261**:108-116.

Worm, B., and J. E. Duffy. 2003. Biodiversity, productivity and stability in real food

webs. Trends in Ecology & Evolution **18**: 628-632.

Table 3.1. Mean proportion of *Aroga websteri* larvae and/or pupae parasitized per plot (range of parasitism ± SE) by *Copidosma*, *Phaeogenes*, *Conura*, various 'other' parasitoids and their cumulative parasitism across permanent plots and associated *Aroga* (host) density (range of peak larvae per stem with means ± SE), 2008-2011.

Year	Mean Host (range ± mean SE) *Aroga websteri* larvae stem-1	Mean Parasitism % (range ± mean SE) *Copidosma* sp. larval parasitism	*Phaeogenes* sp. pupal parasitism	*Conura* sp. pupal parasitism	Other (additional spp.) larv/pup parasitism	Parasitism combined	site N	reared N
2008	0.29 ± 0.007 (0.03 − 0.77)	28.18% ± 0.04 (0 - 0.63)	13.15% ± 0.03 (0 - 0.67)	12.30% ± 0.03 (0 - 0.5)	0.86% ± 0.002 (0 - 0.05)	46.35% ± 0.04 (0 - 0.64)	27	921
2009	0.63 ± 0.013 (0.04 − 2.84)	27.76% ± 0.03 (0 - 0.56)	25.22% ± 0.07 (0 - 1.00)	13.90% ± 0.05 (0 - 1.00)	1.16% ± 0.005 (0 - 0.1)	52.12% ± 0.07 (0 - 1.00)	27	1060
2010	0.13 ± 0.003 (0.02 − 0.36)	51.85% ± 0.09 (0 - 1.00)	37.44% ± 0.08 (0 - 1.00)	11.43% ± 0.03 (0 - 0.33)	8.11% ± 0.03 (0 - 0.21)	72.64% ± 0.07 (0 - 1.00)	13	144
2011	0.09 ± 0.002 (0 − 0.32)	42.85%	9.09%	36.36%	0%	68.83%	1	17
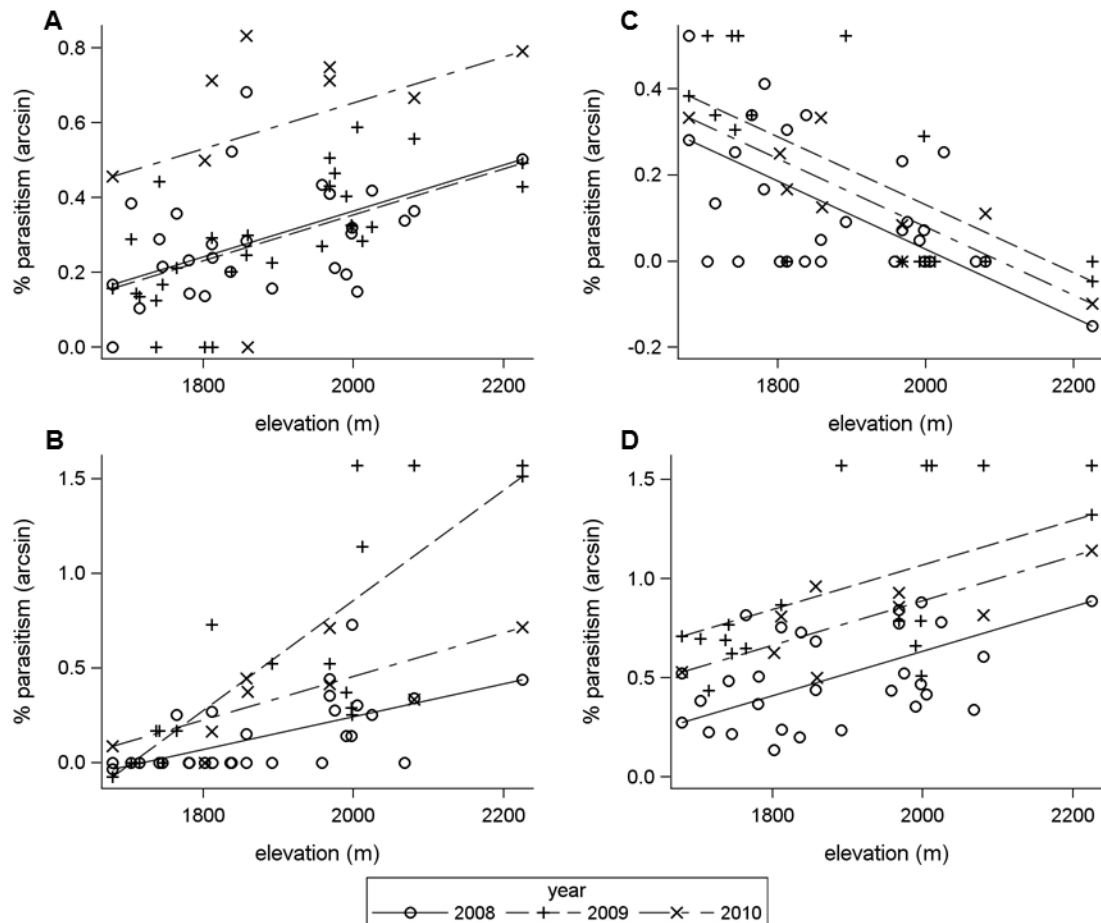
Figure 3.1. Relationship between individual parasitoid species' parasitism rate, elevation, and year. Rates of parasitism are shown for all three major parasitoid species considered individually **(A)** *Copidisoma*, **(B)** *Phaeogenes*, **(C)** *Conura*, and combined **(D)**. Elevation spans the spatial extent of field plots at Henefer-Echo WMA. Parasitism rates are the proportion of host larvae or pupae parasitized (arcsine transformed).
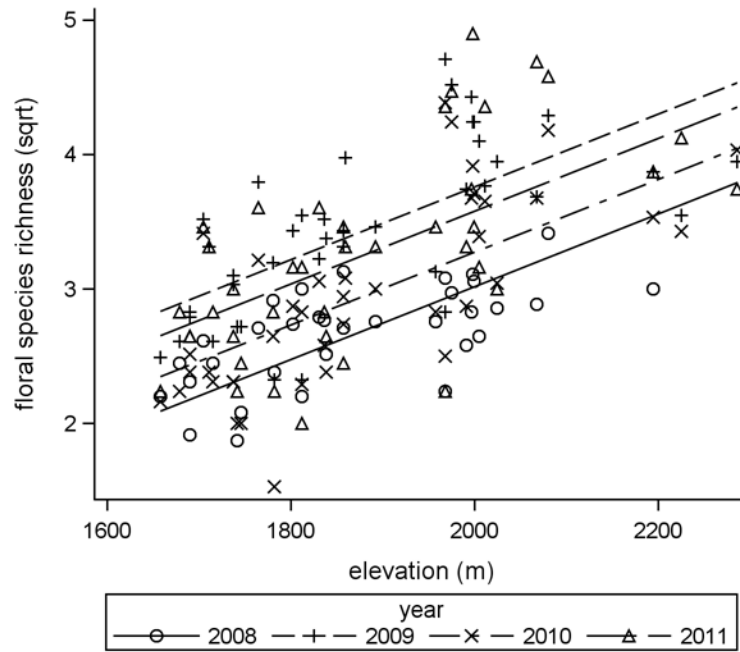
Figure 3.2. Relationship between flowering species richness, elevation, and year. Flowering species richness represents the mean number of blooming species per weekly visit (square-root transformed) across years.
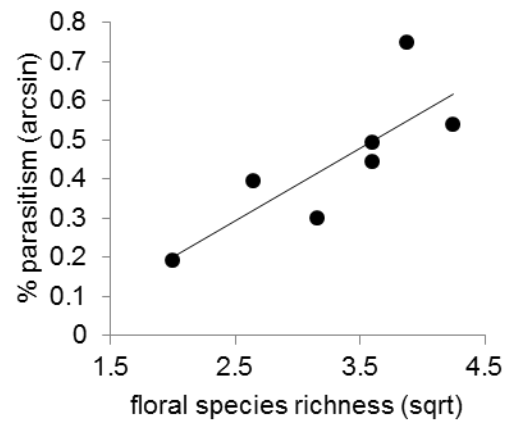
Figure 3.3. Combined parasitism by *Copidisoma* and *Phaeogenes* across a range of floral richness at mid-to-high elevation sites (see text).
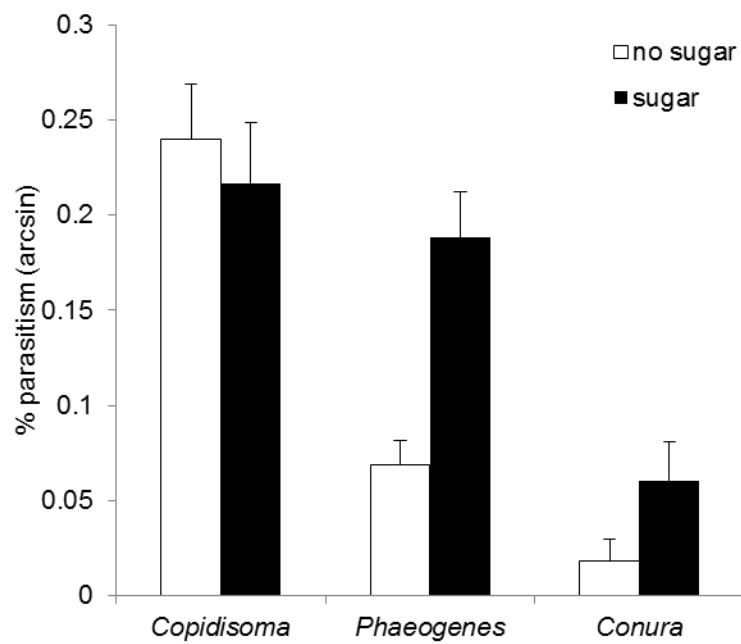
Figure 3.4. Response of three major parasitoid species to field plots with sugar and no sugar (experiment I).
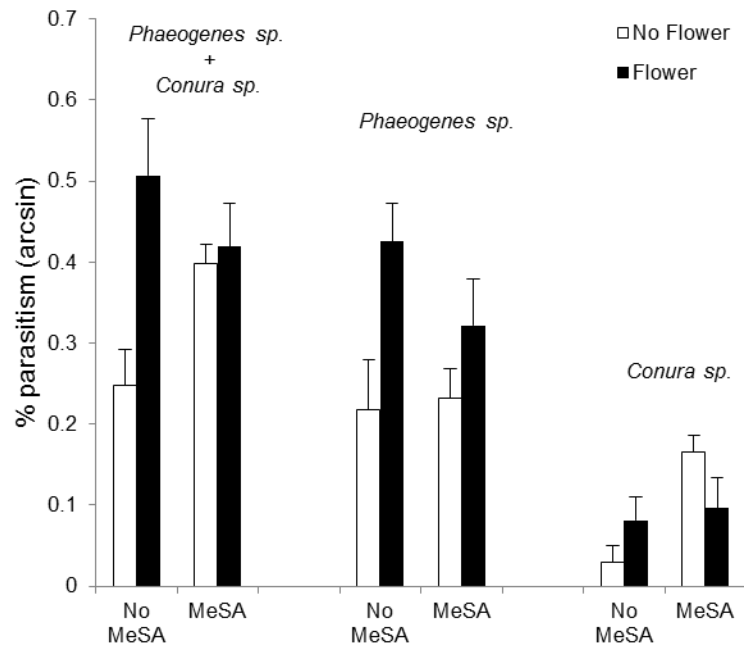
Figure 3.5. Rates of pupal parasitism by *Phaeogenes* and *Conura* combined and considered individually, in response to treatment combinations of provision of flowers and/or methyl salicylate (MeSA) (experiment II).
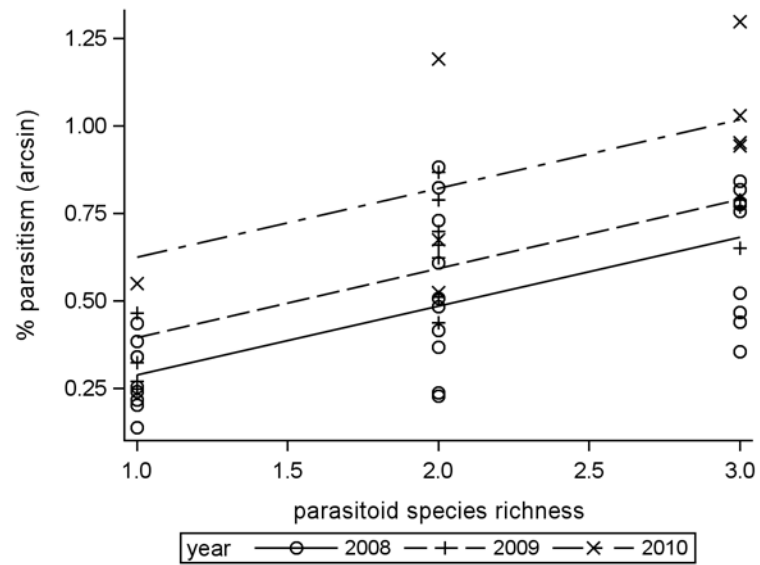
Figure 3.6. Effects of parasitoid species richness on overall parasitism per study site across years.

CHAPTER 4

**DEGREE-DAY MODELING OF PHENOLOGY OF THE SAGEBRUSH
DEFOLIATING MOTH *AROGA WEBSTERI* CLARKE (LEPIDOPTERA:
GELECHIIDAE), WITH APPLICATION TO MOTH OUTBREAKS[3]**

ABSTRACT Larval populations of the sagebrush defoliating *Aroga* moth (*Aroga websteri* Clarke; Lepidoptera: Gelechiidae) were sampled throughout the spring and summer in a montane stand of sagebrush in northern Utah during 2008-2010. Simple degree-day (°D) models were developed to describe the phenology of these field populations and populations studied previously (in 1972-1975) in a lowland valley stand of sagebrush on the Utah-Idaho border. Degree-days were calculated with the single-sine method, with base temperatures of 5°C, 8°C, and 10°C (and no upper cut-off). Least variation (lowest CV) among years in degree-day phenology resulted with the single-sine method using a base temperature of 5°C. Peak larval numbers (of mostly first and second instars) occurred on average at 239 degree-days (accumulated beginning 1 January), and peak numbers of fourth instars occurred on average at 482 degree-days. The degree-day model was used to compare °D accumulations associated with annual moth population estimates made during my studies at Henefer-Echo WMA (2008-2012) as well as previously in Curlew Valley, ID/UT during 1971-1975 and in Alturas, CA during 1962-1964. Patterns of fluctuating temperature and precipitation associated with key periods in *Aroga* moth development were compared among years with endemic (low) and outbreak levels of the *Aroga* moth. Years of historical outbreaks of the moth had characteristic

seasonal patterns of °D accumulation that were intermediate, when compared to accumulations in endemic years, during mid-May through mid-June (when early instars of the moth are developing). Outbreak years were also characterized by high precipitation in June and July during late stage larval development. Thus it appears that periodic outbreaks of the defoliator are due to favorable weather conditions. These conditions likely are associated with increased larval survivorship, and with high nutritional value and palatability of sagebrush foliage for the moth.

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[3] Co-author: Edward W. Evans. Written following *Annals of the Entomological Society of America* Journal specifications.

The *Aroga* moth, *Aroga websteri* Clarke (Lepidoptera: Gelechiidae), known also as the sagebrush defoliator, is a native North American insect that feeds on sagebrush, primarily big sagebrush (*Artemisia tridentata* Nuttall), throughout the Great Basin. Sagebrush steppe ecosystems are diverse and life-sustaining habitats for a variety of flora and fauna. At times the *Aroga* moth becomes a pest in these habitats, defoliating large expanses of its host plant. Such defoliation events have become even more of concern with the continuing acceleration of large-scale change to the sagebrush ecosystem that was triggered by European settlement. Agricultural practices and other human developments in particular have been estimated to have reduced the extent of sagebrush-steppe by nearly half (Welch 2005) with disturbed habitat prone to invasion by non-

native species such as cheatgrass, *Bromus tectorum* L. (Whisenant 1990, Chambers et al. 2007).

Varying degrees of *Aroga* moth defoliation and associated mortality of sagebrush have been reported from widespread areas throughout the Great Basin. These areas occur in Utah (Knowlton 1960, Kirkland 1972, Hsiao 1984), Idaho (Henry 1961), Oregon (Miller 2005), California (Hall 1965), Washington, Montana, and Nevada (Artz 1972, Bechtel 1972). Larvae of the *Aroga* moth begin to feed externally on sagebrush foliage in the spring, and develop to the pupal stage by mid-summer. In the process, they feed on sagebrush leaves enclosed in webbed silken tubes that the larvae construct along the terminal ends of the branches (Temte 1977); the bulk of this damage occurs in the latter instars of larval development. Feeding damage from large numbers of these larvae can kill sagebrush plants after a single year of complete defoliation (Hall 1965).

The potential of the *Aroga* moth to defoliate and kill sagebrush plants in large numbers over large areas of rangeland underscores the need for tools with which land managers can monitor populations of the moth. One such tool is a degree-day (°D) description of seasonal development of the moth. With this tool, the land manager can predict and anticipate when during a spring and summer the moth will occur in its different life stages, and when its numbers will peak. Degree-day models have been developed for many insects, including numerous species of Lepidoptera (e.g., Pitcairn et al. 1992, Spear-O'Mara and Allen 2007). These models have proved quite useful, as temperature directly influences physiological processes and hence the calendar timing of life cycles of ectothermic organisms such as insects. Thus, these models are valuable in

forecasting when particular events of interest may occur, such as peak periods in development associated with defoliation. Presently, no °D tools exist for the *Aroga* moth and scouting in the field for the moth correspondingly is hampered.

Degree-day modeling is an important tool for predicting not only how a population of insects will develop within a season, but also how a population may vary in size among years. Temperature plus precipitation regimes are key elements of weather and climate. Both environmental factors are generally believed to play important roles in determining when insect outbreaks occur on Great Basin rangelands. Though exact mechanisms are not well understood, temperature and precipitation can influence insect survivorship and reproduction both directly (through effects on insect metabolism and physiology; Huey and Kingsolver 1989, Kingsolver 1989, Huey 1991) and indirectly (e.g., by altering the abundance and/or nutritional quality of food plants for herbivorous insects; White 1976, 1978; Belovsky and Slade 1995). General patterns in the weather, including both temperature and precipitation, therefore may be associated with outbreaks of rangeland insects such as the *Aroga* moth.

The study presented here of the field biology of the *Aroga* moth had two objectives. First, a °D model was applied to field data to determine the number of °D associated with the seasonal peak in abundance of individual instars (larval stages) of the *Aroga* moth, and of all larvae (of varying instar) combined. Second, this model was then used to compare the accumulation of °D during spring and early summer in outbreak years (i.e., years of high moth numbers and extensive defoliation of sagebrush) versus endemic years with relatively low moth abundances in natural stands of sagebrush.

Seasonal patterns of precipitation were compared among years as well, to address

whether either a distinctive temperature and/or precipitation regime is associated with

outbreaks of the *Aroga* moth in particular years. To address these two objectives, field

data were collected at a study site in northern Utah from 2008 to 2012, and the data were

combined for analysis with similar data collected and published previously from another

site in northern Utah/southern Idaho during the 1970s and sites in northern California

during the 1960s.

Materials and Methods

Study Organism. The *Aroga* moth has one generation per year and passes

through five larval instars during a season (Henry 1961, Temte 1977). Adults emerge in

mid-summer (late July) and are active through late summer (September), and during this

period a female may lay 70-120 eggs or more (Henry 1961, Kirkland 1972). Females

deposit their eggs in the cracks and crevices of terminal sagebrush stems, where these

eggs are generally believed to overwinter before hatching the following spring (Kirkland

1972, Temte 1977; *Bolshakova unpublished data*). Upon hatching, larvae move to the

foliage. Young larvae (first and second instars) are difficult to find in the field and are

detected most easily upon magnification of host plant material in the laboratory; during

this phase little visible damage to the plant occurs. In contrast, older larvae (third, fourth,

and fifth instars) are readily detected in the field from the webbed tubes that they build on

the terminal stems of the sagebrush plant (Figs 1a-c), and it is this cohort of older larvae,

especially fourth and fifth instars, that significantly defoliates and damages the sagebrush

plant.

Only a few studies have been published on the biology of the *Aroga* moth. Henry (1960) was the first to give in-depth descriptions of the defoliator's biology and life history. Hall (1965) reported on *Aroga* moth population dynamics as well as relative damage to the sagebrush plant over multiple years of defoliation in northern California including an outbreak in 1964. Fillmore (1965) provided an inventory and account of the potential of parasitoids attacking the defoliator. Most recently, field studies of the demography and ecology of the *Aroga* moth were conducted in Curlew Valley, Utah-Idaho including during an outbreak in 1973 (a year of unusually high numbers of larvae as late as well as early instars, with heavy damage to sagebrush; Kirkland 1972, Temte 1977, Hsiao 1984).

Sampling *Aroga* Moth Populations. Populations of larvae and pupae of the *Aroga* moth were sampled from late April through early August in 2008-2010 at Henefer-Echo Wildlife Management Area (WMA). The 5700-hectare area, owned by the State of Utah and managed by the Division of Wildlife Resources, is in north central Utah, USA (41.024°N, 111.444°W), and is 56 km southeast of Ogden. The management unit lies on the eastern edge of the Great Basin in the western foothills of the Wasatch Mountain Range in a sagebrush-steppe ecosystem dominated by big sagebrush.

The initiation of sampling in the spring each year at Henefer-Echo WMA was determined by snowmelt and site accessibility (with 4-wheel drive) via dirt trails. The first opportunity to sample each spring occurred as *Aroga* moth eggs began hatching and first instars appeared on the sagebrush foliage. In each of the three years, repeated sampling was conducted at the same set of 38 permanent plots (each 50 x 100 meter)

spread widely across Henefer-Echo WMA (with adjacent plots separated by 200 to 1600 m, and located at elevations of 1615 to 2500 m). In 2008 and 2010, samples were taken at weekly intervals. In 2009, samples were taken every 4 to 5 days.

On each occasion when a site was sampled, approximately 70 randomly selected vegetative stems (terminal 15 cm) were clipped from sagebrush plants during a ten-minute sampling period at each site. A single stem was collected randomly from each shrub sampled. Sampling bias (especially of concern when the webbing was present on shrubs) was avoided by collecting stems along a zig-zagging transect in which a stem was collected from the nearest shrub approximately every ten meters along the transect. Stems were collected blindly from systematically alternating top, middle, and bottom portions of the shrubs encountered (without regard to shrub height or volume). All stems were hand-sorted in the laboratory for larvae, and then further processed in Berlese funnels for 96 hours. The population abundance at each site (the number of larvae per stem) and number of larvae in each instar (as identified by head capsule width; Henry 1961) were recorded.

Similar, but less extensive, sampling at Henefer-Echo WMA in 2011 and 2012 provided estimates of peak population size in those two years as well (Chapter 3). Previously published studies from a single study site in Curlew Valley, and from multiple study sites in northern California near Alturas, provide additional estimates of sizes of populations of *Aroga* moth larvae infesting stands of sagebrush in the Great Basin. These data are available for five years (1971-1975) at Curlew Valley (Kirkland 1972, Temte 1977, Hsiao 1984), and for an additional three years (1962-1964) at Alturas (Hall 1965).

The data from Curlew Valley (collected from sampling sagebrush within a single hectare plot) also include age structure of the populations as sampled repeatedly throughout the growing season for three years (1972, 1974, and 1975).

Weather and Moth Population Dynamics. Daily minimum and maximum temperatures as well as precipitation data were obtained for stations near the three sites (Henefer-Echo WMA, Curlew Valley, and Alturas) from the Climate Database Server maintained by the Utah Climate Center, an official repository for published climate data spanning decades. Data were obtained as recorded at weather stations maintained by the U.S. Weather Bureau (National Oceanic and Atmospheric Administration [NOAA]): (1) Echo Dam, UT (ID# USC00422385: 40.966, -111.435), (2) Snowville, UT Station (ID# U00427931: 41.9667, -112.717), and (3) Alturas, CA Stations (ID# USC00040161: 41.493,-120.533). Each of these three locations was close to (within 1.5-16 km of) the corresponding study site. Records from these locations were used to prepare climate profiles (including mean January and July temperatures and annual precipitation for all years on record (Table 4.1) for the three sites to give reference comparisons for the study years focused on here.

Daily accumulation of degree-days at each study site during each study year was determined from the temperature data obtained from the three NOAA weather stations. Using daily maximum and minimum temperatures from January 1 through August 1, degree days were calculated with the single-sine method, as is commonly used for insects (e.g., Beasley and Adams 1996). However, an upper horizontal cutoff was not applied since an upper threshold temperature for larval development is unknown for the *Aroga*

moth (for many organisms an upper threshold is not used because data are lacking to

obtain such an estimate). Degree-days were determined using the degree-day calculator

provided by UC-IPM Online for the single-sine method, with a base temperature of 5°C,

8°C, or 10°C (and no upper cut-off). The results obtained using these three alternative

base temperatures were compared to determine which base temperature produced the

lowest coefficient of variation (CV) in the number of °D associated with peaks in larval

abundance among years (Arnold 1959, Beasley and Adams 1996). The accumulated °D

from January 1 were determined for the calendar dates on which each of the five instars

peaked in abundance in each of the three study years at Henefer-Echo WMA and at

Curlew Valley.

Estimates of overall population size of the *Aroga* moth were available for a total

of 13 years at the three locations combined: Alturas (1962-1964), Curlew Valley (1971-

1975), and Henefer-Echo WMA (2008-2012). At each of the three locations, *Aroga* moth

populations were monitored directly via larval/adult moth counts and/or indirectly via

estimated amount of defoliation of sagebrush stands. At each location during the time

period studied, one year stood out as a year of high *Aroga* moth abundance, i.e., an

outbreak year: 1964 (Alturas), 1973 (Curlew Valley), and 2009 (Henefer-Echo). In 1964,

the majority of sagebrush stands near Alturas sustained between 70-100% defoliation, a

significant loss exceeding losses observed in 1962 and 1963 (and also in subsequent

years at Curlew Valley and Henefer-Echo WMA). In comparison with the other four

years during the Curlew Valley study, significantly greater numbers of *Aroga* moth adults

were caught in 1973; e.g., nearly 8x as many moths were caught per trap in 1973 as in

1975 (larval counts in 1973 are not available for comparison with other years). Highest

abundances were observed in 2009 at Henefer-Echo WMA; e.g., nearly 20x as many

larvae per terminal stem occurred in 2009 as in 2012 (Chapter 2).

The relative warmth of the spring and early summer during these three outbreak

years was compared with the other ten years by examining the rate with which °D

accumulated over the spring and early summer among these years. Precipitation regimes

were compared among years by determining the amount of precipitation occurring in

each month during the period of *Aroga* moth larval development (i.e, from April through

July). In particular, results for the three outbreak years were compared with results for

the ten years when fewer *Aroga* moths were present.

Data Analyses. All statistical analyses were completed in SAS 9.3 (SAS Institute

2011). Mean peak °D accumulations for each larval cohort were compared between

Henefer-Echo and Curlew Valley by TTEST. To analyze the difference in precipitation

among endemic and outbreak population cycles, mean precipitation was compared

among individual months using a two-way ANOVA (Proc GLM). This analysis was

followed by a series of one-way ANOVAs to test for differences between endemic and

outbreak years during individual months.

<div align="center">

Results

</div>

Larval Population Peaks and Degree-Days. Although generally similar in

climate, the three study areas differ to some extent (Table 4.1). The average annual

precipitation varies from 307 and 308 mm at the two drier sites (Curlew Valley and

Alturas) to 371 mm at the wettest site (Henefer-Echo WMU). Typical of the Great Basin region, most rainfall at each location occurs in the spring and fall with drought conditions predominating during the summer and snow covering the ground in the winter. Mean temperatures are fairly similar across all sites, although the Northern Utah sites are generally colder during the winter months than Alturas (Table 4.1). Over the course of any year, Alturas generally accumulates more than 100 °Ds (base 10°C as calculated by the Utah Climate Center long-term record) than the Curlew Valley and Henefer-Echo WMA sites.

As illustrated both at Curlew Valley and Henefer-Echo WMA sites, there was a distinct seasonal progression in the rise and fall of larval numbers of successive instars as the univoltine *Aroga* moth developed on its host plant (Figure 4.2, Appendix Figure E-1). Individuals apparently hatched over an extended period of a few weeks, and/or individuals differed in their rates of development upon hatching. Consequently, individuals of different stadia overlapped in their appearance during the spring and early summer, such that in 2009 for example all five instars were present on sagebrush at Henefer-Echo WMA in early June (Figure 4.2b). The peak abundance of *Aroga* moth larvae (all instars combined) occurred each year when most individuals were either first or second instars.

As determined from the single-sine method, there was considerable variation among years in the number of accumulated °D for census dates when peak numbers of each instar were sampled at Henefer-Echo WMA in 2008-2010 and at Curlew Valley in 1972-1975. Least variation (reflected in lowest CV) resulted with the single-sine method

using a base temperature of 5°C (Table 4.2). Similar but slightly more variation occurred

among years (as measured by CV) when the single-sine method was applied with a base

of 8 or 10°C (Appendix tables D-1 and D-2). For all three base temperatures, the most

variability in the °D accumulated at peak abundance was associated with peak numbers

of first instars, and of all instars combined (with CVs of 38% and 45%, respectively, for

base temperature 5°C; Table 4.2). Considerably less variability (with an average CV of

17% with base temperature 5°C) was associated with peak numbers of the second to fifth

instar (Table 4.2).

Estimates of °D accumulation at peak field density for individual instars were

similar at both Henefer-Echo and Curlew Valley sites, with no difference apparent

between the two areas in overall mean estimates among the years studied (Fig. 4.3;

TTEST: $P > 0.40$ for all comparisons except for the first instar peak comparison [$P =$

0.20]). Accumulations were most similar among years and between the two study

locations for the number of °D estimated on the date on which peak numbers of second

and fourth instars were sampled in the field (Table 4.2). In this regard (and consistently

across all instars), °D estimates for Curlew Valley in 1975 were unusually low in contrast

to the °D accumulations among the other five years of study (Table 4.2).

Overall (for the six years considered together), the number of second and fourth

instars peaked on the sagebrush plants at means of 254 and 482 °D, respectively. From

these °D calculations, the estimated time of the season at which the numbers of second

and fourth instars peaked occurred during the latter half of May (on average on JD 140

for second instars), and early June (on average on JD 162 for fourth instars) at the

Henefer-Echo WMU and Curlew Valley sites (Table 4.2). The total number of larvae on sagebrush (all instars combined, composed mostly of second instars plus some first instars, peaked in early to mid-May each year in the two study locations when 239 °D on average had accumulated (Table 4.2).

°D Accumulation and Precipitation in Outbreak Versus Other Years. The variation among years at both Henefer-Echo WMA and Curlew Valley in the estimated calendar dates on which numbers of second and fourth instars peaked reflects the considerable variability in the warmth of the springs and early summers in those years (and hence in the accumulation of degree-days). Thus, the mean daily temperatures during May and June varied substantially among years from 8.4 to 12.5 °C at Henefer-Echo and from 14.8 to 19.2°C at Curlew Valley.

In these and additional years at Henefer-Echo WMA (2008-2012), Curlew Valley (1971-1975), and in 1962-1964 in Alturas CA, the population size of *Aroga* moth larvae varied widely. At each of these three locations, the year with greatest *Aroga* abundance (1964 at Alturas, 1973 at Curlew Valley, and 2009 at Henefer-Echo) was distinctive in comparison with other years in its temperature regime during May and June. In particular, these three years with high larval abundance had intermediate accumulations of °D between 15 May and 15 June; in years with lower larval abundances, °D either accumulated relatively fast or relatively slow during this period (Fig. 4.4). The period of °D accumulation between 15 May and 15 June in the three outbreak periods corresponds with the period during which larval development of the *Aroga* moth from second to fourth instar occurred.

Precipitation patterns also differed in important ways with years of high moth abundance (outbreak years) having significantly greater precipitation than endemic years later but not early in the growing season (Fig. 4.5, two-way ANOVA [amount of precipitation $\times$ month]: amount $F_{1,\,51} = 2.46$, $P = 0.12$; month $F_{3,\,49} = 4.09$, $P = 0.01$; amount $\times$ month, $F_{4,\,49} = 24$, $P = 0.03$). In particular, the amount of precipitation did not differ between outbreak and endemic years in either April (one-way ANOVA:

$F_{1,\,11} = 0.34$, $P = 0.57$) or May (one-way ANOVA: $F_{1,\,11} = 0.02$, $P = 0.88$), but did differ significantly in both June (one-way ANOVA: $F_{1,\,11} = 18.14$, $P < 0.001$) and July (one-way ANOVA: $F_{1,\,11} = 5.07$, $P = 0.04$). Furthermore, for both June and July, more precipitation fell in each of the three outbreak years than in any of the ten endemic years. Thus, the sequence in weather of both intermediate temperatures from mid-May to June and the pulse of precipitation in June continuing into July differentiates outbreak years of the moth from endemic years.

Discussion

As demonstrated here, a °D description of the development of *Aroga* moth field populations yields relatively consistent estimates concerning larval phenology among years and geographic areas. In addition, the °D model used in this study reveals that historical outbreaks throughout the Great Basin have characteristic °D accumulations that are intermediate, when compared to accumulations in endemic years, during mid-May through mid-June when early instars of the moth are developing. Outbreak years are associated with not only distinctive temperature regimes at this time, but also with high

precipitation in June and July during late stage larval development. This link of high

Aroga moth populations with the pattern of intermediate °D accumulation followed by

ample precipitation supports the general hypothesis that meteorological factors are a

dominant force in insect population cycles (e.g. Myers 1998, Baltensweiler et al. 2008).

Although the °D model presented here (a single-sine model with base temperature

of 5°C and no upper cut-off) provided fairly consistent estimates of °D accumulation at

peak field density for individual instars, these estimates nonetheless varied among years

and between the two areas studied (Henefer-Echo WMA and Curlew Valley). This

variation reflects in part the logistical difficulty of pinpointing the precise timing of

biological events in the field unlike in controlled experiments in the laboratory.

Sampling dates often depend on limiting external factors such as weather and access to

field sites (including at the beginning of the season, when access to montane field sites

can be limited by snow depth, snowmelt, and road conditions). Furthermore, the number

of larvae collected during individual field censuses (and hence the determination of when

peak numbers occur) also can depend on weather, such as significant rain events (Brazzel

and Martin 1959, Beasley and Adams 1996) or wind events. In addition, the frequency

with which it is feasible to sample in the field each year also limits the ability to

accurately estimate peak abundances. Just as undersampling can overestimate the high

frequency of rare species (Coddington et al. 2009), it can also underestimate a

population's peak abundance if such abundance occurs between two successive sampling

occasions.

Even with inevitable error imposed by such limitations, sampling conducted approximately weekly at both Henefer-Echo (2008-2012) and Curlew Valley (1971-1975) yielded generally well-characterized seasonal patterns in the rise and fall of numbers of each larval instar of the *Aroga* moth on the host plant. The variation in estimates of °D accumulation at peak field density for individual instars as drawn from such sampling was similar at both sites, with no difference apparent between the two areas in overall mean estimates among the years studied. Thus climatic differences between the two study areas (high elevation-montane versus lowland-valley) as well as differences in the areas sampled (a 5700 hectare area at Henefer-Echo WMA versus a one hectare plot at Curlew Valley) seemingly contributed little to the differences among all study years in the estimates for °D accumulation at peak field densities. Of interest is that because fewer °D accumulated on a daily basis at higher elevation, the numerical rise and fall of individual instars was extended over a greater timespan on a calendar basis at Henefer-Echo WMA than at Curlew Valley. It is unclear at present whether the considerable variation that was apparent at both study areas in estimates of °D accumulation at peak densities of each instar is primarily a reflection of sampling limitations, or a reflection also of significant modifications of life cycle timing in the *Aroga* moth in response to yearly conditions. Additional, intensive field scouting is needed to address this question.

The °D model reveals an intriguing difference in heat accumulation for outbreak versus endemic years during the time of development of early larval stages (second to fourth instars). The pattern of °D accumulation in late spring and early summer (15 May-

15 June, 135-166 JD) was distinctive for all three outbreak years in comparison with endemic population years. In particular, outbreak years were moderate (intermediate) in °D accumulation whereas years of lower moth numbers had either less or more rapid °D accumulation (i.e., they were years with cooler or warmer late springs and early summers). Mortality is often closely allied with more extreme temperatures (i.e., with slow or rapid °D accumulation) for other defoliating insects, (e.g. mountain pine beetle, pink bollworm, bronze birch borer; Bentz et al. 1991, Beasley and Adams 1996). *Aroga* moth is known to occur throughout much of the Great Basin with a wide range of weather and climatic conditions. As a result, its response to temperature may be more generalized than for more geographically and seasonally restricted species that are more specialized for particular temperature conditions (Jones et al. 1987). While extreme temperatures occur often in desert biomes, populations of insects such as the *Aroga* moth may thrive best in moderate years that are neither too cool nor too warm.

The contrast in °D accumulation during late spring and early summer in outbreak versus endemic years suggests that intermediate temperatures throughout early larval development may be critical for the *Aroga* moth's survivorship. Because insects are ectotherms, performance and fitness generally increase with temperature, plateau at an optimal level and then decline rapidly near the upper maximum (or lethal temperature) (Huey and Kingsolver 1993). Within a population, there will be variability among individuals in tolerance to extreme heat or cold. Intermediate °D accumulation may enable a greater breadth of individuals to survive (i.e., both individuals especially tolerant of cool temperatures and individuals especially tolerant of warm temperatures), whereas

fewer individuals may be able to survive under unusually cool or warm conditions. In

laboratory experiments with *Drosophila,* Huey and Kingsolver (1993) found that thermal

sensitivity responds rapidly under both natural and artificial selection and tolerance of

extreme high temperature appears genetically correlated with performance at

intermediate temperature. This too may be the case for the *Aroga* moth, especially during

its early larval development (and could have major implications with climate warming).

However, when the larvae were older (fourth and fifth) instars, outbreak and endemic

years did not differ consistently in °D accumulation from mid-June on for the *Aroga*

moth. These older instars may be less sensitive in any case to patterns of °D

accumulation, as they may be able to modify their microclimate sufficiently by building

tubular domiciles with clipped sagebrush foliage.

During this latter period of larval development in June and July (when severe

defoliation can occur), outbreak years were distinctive in the unusually large amounts of

precipitation recorded. High rainfall at this time of year may promote high survivorship

of late instar larvae of the *Aroga* moth, for example through effects on nutritional aspects

of sagebrush foliage. Hsiao (1984) hypothesized that periodic outbreaks of the defoliator

were probably due to favorable weather conditions, with unfavorably high temperatures

and low precipitation reducing the water content and nutritional quality of sagebrush

vegetative foliage and thereby causing 'drastic decreases in defoliator populations.'

Hsiao and Temte (1975) found small size and high mortality in field-collected pupae

when the moths as larvae fed on low quality foliage (dehydrated), leading to major

reductions in adult population size and reproductive success. Similar observations have

been made for forest defoliating insects, such as the gypsy moth that is closely associated in its population dynamics with June precipitation pulses and oak masting (Peltononen et al. 2002). Supplemental watering of sagebrush during the growing season led to increased production of reproductive tissue in late June (Evans and Black 1993). A June-July flush in sagebrush floral tissues may provide late instar larvae of the *Aroga* moth with highly nutritious food in wet years, thereby promoting high survivorship.

The performance of an animal depends on many factors in the environment and not only on its thermal physiology. Ambient temperatures and precipitation also may affect all larval stages of the *Aroga* moth by influencing seasonal patterns in the defensive components of sagebrush foliage. The defensive and nutritional chemistry of big sagebrush fundamentally influences habitat selection and population dynamics of herbivores (Frye et al. 2013). The production of secondary metabolites, which often defend against herbivory, is strongly related to abiotic stresses (Sudha and Ravishankar 2002, Vinocur and Altman 2005). Cedarleaf et al. (1983) found lowest levels of monoterpenoids in big sagebrush vegetative foliage in May and highest levels in July. Sanford and Huntly (2010) found a general decline in arthropod diversity and abundance on big sagebrush from May to August, coinciding with the increased seasonal production of secondary metabolites. Wiens et al. (1991) found a strong positive association between varying monoterpene production among sagebrush plants and the abundance of chewing insects that included the *Aroga* moth. Other species of insects feeding on foliage with high terpene content suffer increased mortality and reduced growth when compared to feeding on low terpene foliage (Larsson et al. 1986). Additional study is

needed to determine whether variation in secondary metabolite production in sagebrush may play a role in the link between weather and *Aroga* moth outbreaks.

This study provides a °D model for the seasonal development of field populations of the *Aroga* moth. In addition, the study provides data supporting the hypothesis that across multiple areas throughout the Great Basin, patterns of temperature accumulation and precipitation during the growing season influence larval survivorship of the *Aroga* moth. The °D model combined with the apparent link between patterns of °D accumulationand precipitation, and *Aroga* moth density provides a useful tool for range managers. Managers can use this tool to sample efficiently and anticipate potentially devastating instances of sagebrush defoliation. Systematic monitoring of the *Aroga* moth throughout the Great Basin as supported by the °D model will provide more information concerning the biology of the moth and the ways in which its population cycles are driven by weather and other factors.

LITERATURE CITED

Arnold, C. Y. 1959. The determination and significance of the base temperature in a linear heat unit system. P. Am. Soc. Hort. Sci. 74: 430-445

Artz, J. L. 1972. The sagebrush defoliator. Range. News 4: 1-2.

Baltensweiler, W., U. M. Weber, and P. Cherubini. 2008. Tracing the influence of larch-bud-moth insect outbreaks and weather conditions on larch tree-ring growth in Engadine (Switzerland). Oikos 117: 161-172.

Beasley, C. A., and C. J. Adams. 1996. Field-based, degree-day model for pink

bollworm (Lepidoptera: Gelechiidae) development. J. Econ. Entomol. 89: 881-890.

Bechtel, R. C. 1972. Nevada cooperative economic insect report. Nev. Dept. Agr. Circ. 876.

Belovsky, G. S., and J. B. Slade. 1995. Dynamics of two Montana grasshopper populations: relationships among weather, food abundance and intraspecific competition. Oecologia 101:383-396.

Bentz B. J., J. A. Logan, and G. D. Amman. 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. Can. Entomol. 123:1083-1094.

Brazzel, J. R., and D. P. Martin. 1959. Winter survival and tiem of emergence of diapausing pink bollworm. J. Econ. Entomol. 52:305-308.

Cedarleaf, J. D., B. L. Welch, and J. D. Brotherson. 1983. Seasonal variation of monoterpenoids in big sagebrush [Artemisia tridentata]. J. Range Manage. 36: 492-494.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Wittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by Bromus tectorum? Ecol. Monogr. 77:117-145.

Coddington, J. A., I. Agnarsson, J. A. Miller, M. Kuntner, and G. Hormiga. 2009. Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. J. Anim. Ecol. 78: 573-584.

Evans, R. D., and R. A. Black. 1993. Growth, photosynthesis, and resource investment

for vegetative and reproductive modules of Artemisia tridentate. Ecology 74:1516-1528.

Fillmore, O. O. 1965. The parasitoids of *Aroga websteri* Clarke (Lepidoptera: Gelechiidae) in southern Idaho. M.S. thesis. University of Idaho, Moscow, ID.

Frye, G. G., J. W. Connelly, D. D. Musil, and J. S. Forbey. 2013. Phytochemistry predicts habitat selection by an avian herbivore at multiple spatial scales. Ecology 94: 308-314.

Hall, R. C. 1965. Sagebrush defoliator outbreak in Northern California. USDA Forest Serv. Res. Note PSW-75.

Henry, J. E. 1961. The biology of the sagebrush defoliator, *Aroga* websteri Clarke, in Idaho. M.S. thesis, University of Idaho, Moscow, ID.

Hsiao, T. H. 1984. Biology and demography of the sagebrush defoliator and its impacts on big sagebrush, pp. 191-198. *In* E. D. McArthur and B. L. Welch (eds.), Proceedings, Symposium on the Biology of Artemisia and Chrysothamnus, 9-13 June 1984, Provo, UT. USDA, Forest Service Gen. Tech. Report INT-200. Ogden, UT.

Hsiao, T. H., and A. K. Temte. 1975. Demographic studies of sagebrush insects as functions of various environmental factors. US/IBP Desert Biome Research Memorandum. 76-83. Utah State University, Logan, UT.

Huey, R. B. 1991. Physiological consequences of habitat selection. Am. Nat. S91-S115.

Huey, R. B. and J. G. Kingsolver. 1989. Evolution of thermal sensitivity of ectotherm performance. Trends Ecol. Evol. 4:131–135.

Huey, R. B., and J. G. Kingsolver. 1993. Evolution of resistance to high temperature in ectotherms. Am. Nat. S21-S46.

Jones, R. E., V. G. Nealis, P. M. Ives, and E. Scheermeyer. 1987. Seasonal and spatial variation in juvenile survival of the cabbage butterfly *Pieris rapae*: evidence for patchy density-dependence. J. Anim. Ecol. 56: 723–737.

Kingsolver, J. G., 1989. Weather and the population dynamics of insects: integrating physiological and population ecology. Physiol. Zool. 62: 314-334.

Kingsolver, J. G. 2000. Feeding, growth, and the thermal environment of cabbage white caterpillars, Pieris rapae L. Physiol. Biochem. Zool. 73: 621-628.

Kingsolver, J. G., and R. B. Huey. 1998. Selection and evolution of morphological and physiological plasticity in thermally varying environments. Am. Zoo. 38:545–560.

Kirkland, R. L. 1972. Ecology of *Aroga* websteri Clarke in Curlew Valley, Utah-Idaho. M.S. thesis, Utah State University, Logan, UT.

Knowlton, G. F. 1960. Insects: a range problem. Utah Ext. Mim. Ser. 175.

Larsson, S., C. Björkman, and R. Gref. 1986. Responses of *Neodiprion sertifer* (Hym., Diprionidae) larvae to variation in needle resin acid concentration in Scots pine. Oecologia 70: 77-84.

Miller, R. 2005. *Aroga* moth and sagebrush defoliation. Extension Service. Oregon State University, Corvallis, OR. Grazier 325: 2-3.

Myers, J. H. 1998. Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran effect. Ecology 79:1111-1117.

Peltonen, M., A. M. Liebhold, O. N. Bjørnstad, and D. W. Williams. (2002). Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. Ecology 83: 3120-3129.

Pitcairn, M. J., F. G. Zalom, and R. E. Rice. 1992. Degree-day forecasting of generation time of *Cydia pomonella* (Lepidoptera: Tortricidae) populations in California. Environ. Entomol. 21: 441-446.

Sanford, M. P., and N. J. Huntly. 2010. Seasonal patterns of arthropod diversity and abundance on big sagebrush, *Artemisia tridentata*. West. N. Am. Nat. 70: 67-76.

SAS Institute. 2011. PROC user's manual, version 6th ed. SAS Institute, Cary, NC.

Spear-O'Mara, J., and D. C. Allen. 2007. Monitoring populations of saddled prominent (Lepidoptera: Notodontidae) with pheromone-baited traps. J. Econ. Entomol. 100: 335-342.

Sudha, G., and G. A. Ravishankar. 2002. Involvement and interaction of various signaling compounds on the plant metabolic events during defense response, resistance to stress factors, formation of secondary metabolites and their molecular aspects. Plant Cell Tiss. Org. 71: 181-212.

Temte, A. K. 1977. The demography of the sagebrush defoliator, *Aroga websteri* Clarke (Lepidoptera: Gelechiidae), and its impact on Artemisia tridentata. M.S. thesis, Utah State University, Logan.

Vinocur, B., and A. Altman. 2005. Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. Curr. Opin. Biotech. 16: 123-132.

Wiens J. A., R. G. Cates, J. T. Rotenberry, N. Cobb, B. Van Horne, and R. A.

Redak. 1991. Arthropod dynamics on sagebrush (Artemisia tridentate): effects of plant chemistry and avian predation. Ecol. Monogr. 61: 299-321.

Welch, B. L. 2005. Big sagebrush: a sea fragmented into lakes, ponds, and puddles. Gen. Tech. Rep. RMRS-GTR-144 U.S. D.A. Forest Serv. Fort Collins, CO.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications, pp. 4-10. *In* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller, (eds.). Proceedings: symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management. USDA GTR INT-276, Ogden, Utah.

White, T. C. R. 1976. Weather, food and plagues of locusts. Oecologia 22: 119-134.

White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia 33: 71-86.

Williams, D. W. 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. Ecology 83: 3120-3129.

Table 4.1. Climate profiles for *Aroga* moth study site locations, including mean January and July temperatures and annual precipitation.

	Field Location		
	Henefer-Echo, UT	Curlew Valley, ID/UT	Alturas, CA
Latitutde, Longitude	40.97, -111.43	41.97, -112.92	41.49,-120.55
Years on record	1940-2013	1893-1991	1905-2013
January Mean Temp (°C)	-5.2	-5.8	-1.5
Std dev	6	9.5	5.8
July Mean Temp (°C)	20.3	21	19
Std dev	2.3	5.6	3.2
January Min Temp (°C)	-11.8	-12.4	-8.4
Std dev	7.4	13	7.8
July Max Temp (°C)	31.1	32.2	31.2
Std dev	2.9	6.6	4.2
Annual Precip (mm)	370.54	307.1	308.2
Annual Growing DD (based on 10◦C)	1194	1103	1287
Aroga population data	2008-2012	1971-1975	1962-1964
Aroga moth outbreak years	*2009*	*1973*	*1964*

Table 4.2. Julian dates (JD) and associated accumulated degree-days at larval peak abundances for first-fifth instars of the *Aroga* moth, and for all larvae combined, at field sites at Henefer-Echo and Curlew Valley.

Sine Model (5°C Lower Threshold)[1]						Life stages					
1st Instar peak		2nd Instar peak		3rd Instar peak		4th Instar peak		5th Instar peak		Combined peak	
Location (year)											
JD	°D	JD	°D	JD	°D	JD	°D	JD	°D	JD	°D
Hen-Echo, UT (2008)											
141	215	148	248	169	405	172	590	183	602	141	215
Hen-Echo, UT (2009)											
133	238	133	238	149	382	155	449	182	718	133	238
Hen-Echo, UT (2010)											
130	183	146	260	155	340	169	478	174	531	155	340
Cur Val UT/ID (1972)											
113	182	132	291	141	374	154	496	161	585	141	374
Cur Val UT/ID (1974)											
117	187	131	295	155	514	155	514	164	607	117	187
Cur Val UT/ID (1975)											
111	48	147	190	158	289	165	362	171	416	126	78
Mean	124	176	140	254	155	384	162	482	173	577	136	239
SE	5	27	3	16	4	31	3	31	4	41	5	44
CV (%)	10	38	6	15	6	20	5	16	5	17	10	45

[1]Degree-days were calculated using a single-sine method with lower development thresholds 5 and no upper horizontal cut-off. Model (base 5°C) displayed above had lowest CV.
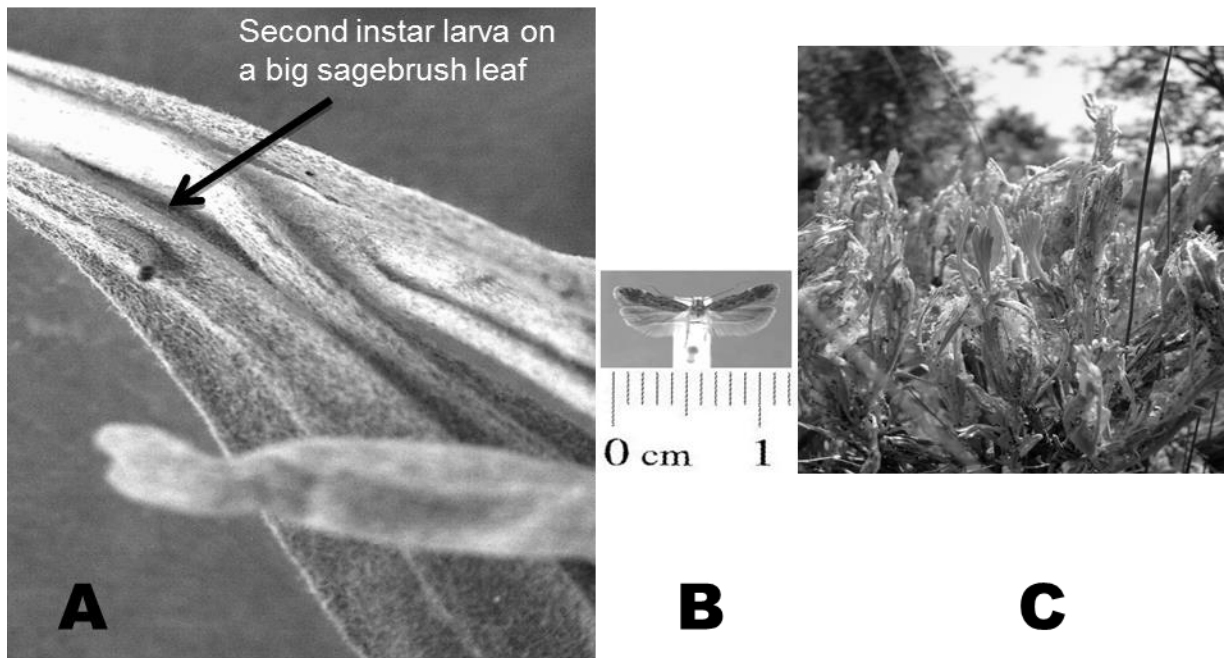
Figure 4.1. A second instar of *Aroga websteri* on a big sagebrush, *Artemesia tridentata* **(A),** adult *Aroga* moth **(B),** and signature webbed tubes and subsequent defoliation of sagebrush plant by older instars (4th & 5th) of the *Aroga* moth **(C).**
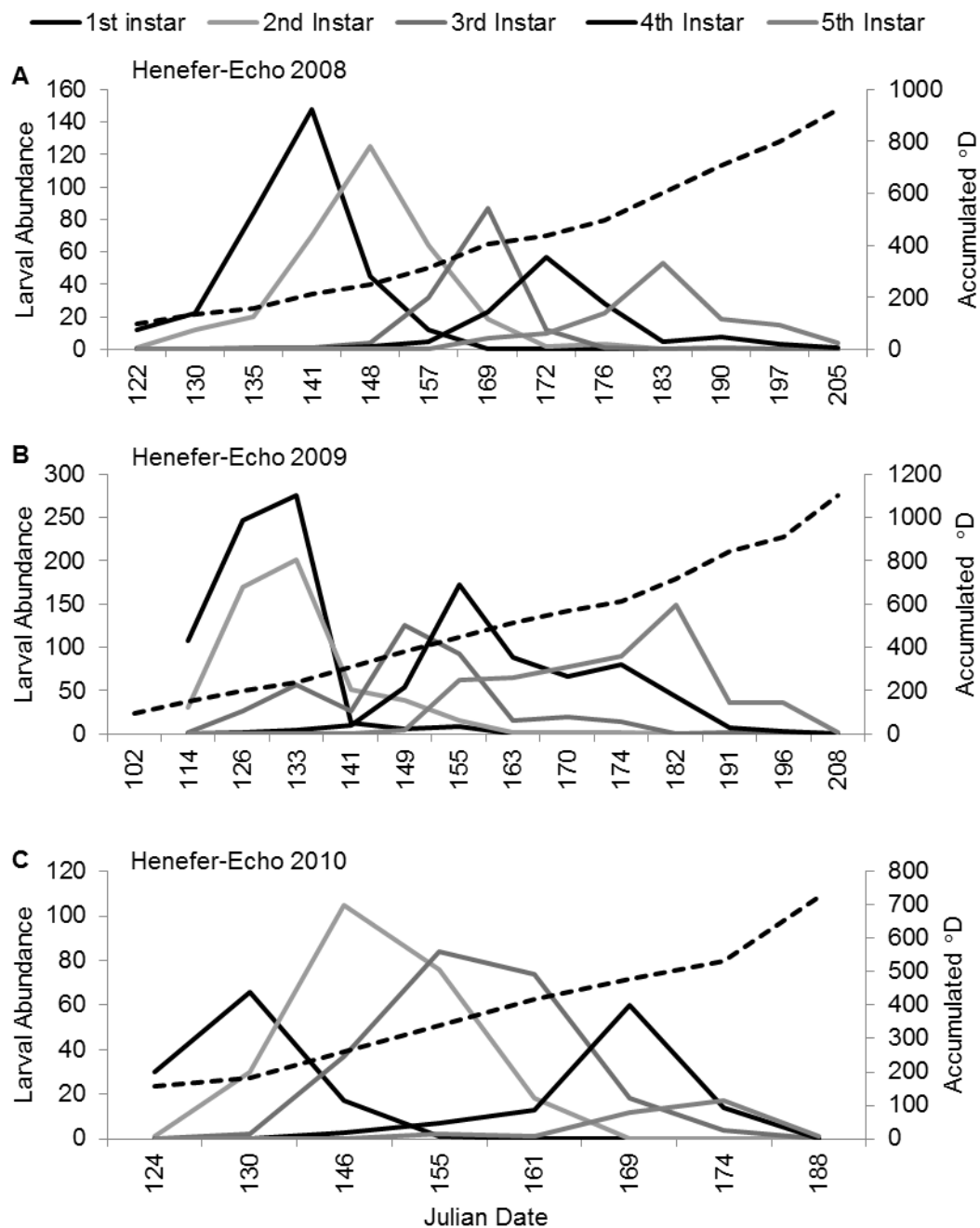
Figure 4.2. Age structure and population density of *Aroga* (solid lines) and accumulated DD (dotted line) versus Julian calendar date (120 JD corresponds ~1 May) **(A)** Henefer-Echo 2008, **(B)** Henefer-Echo 2009, and **(C)** Henefer-Echo 2010.
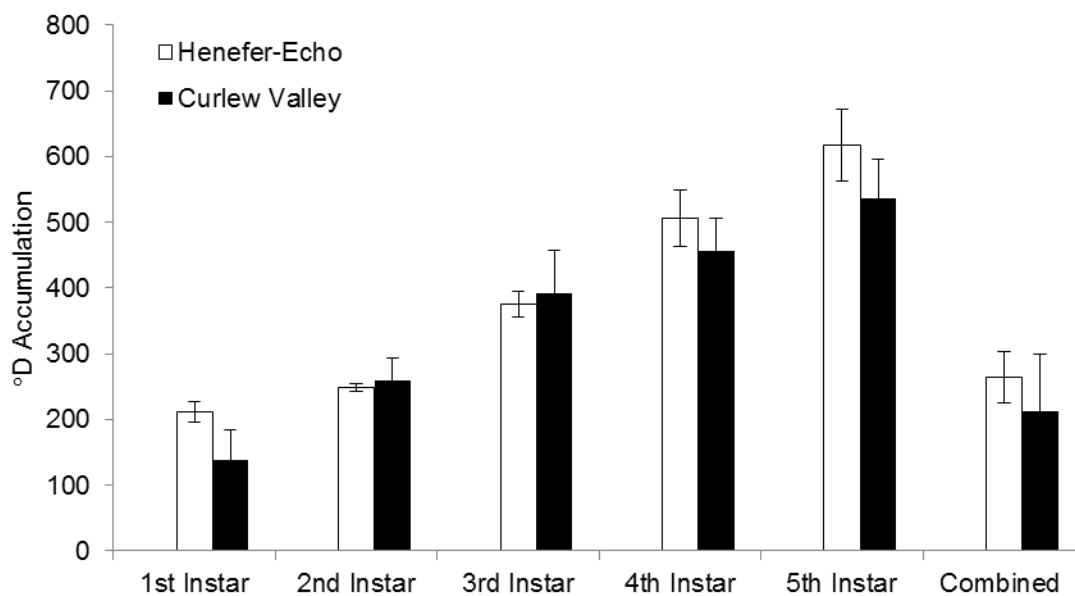
Figure 4.3. Mean estimate of °D accumulation at peak *Aroga* larval abundance for individual instars and for all larvae combined at Henefer-Echo and Curlew Valley field sites.
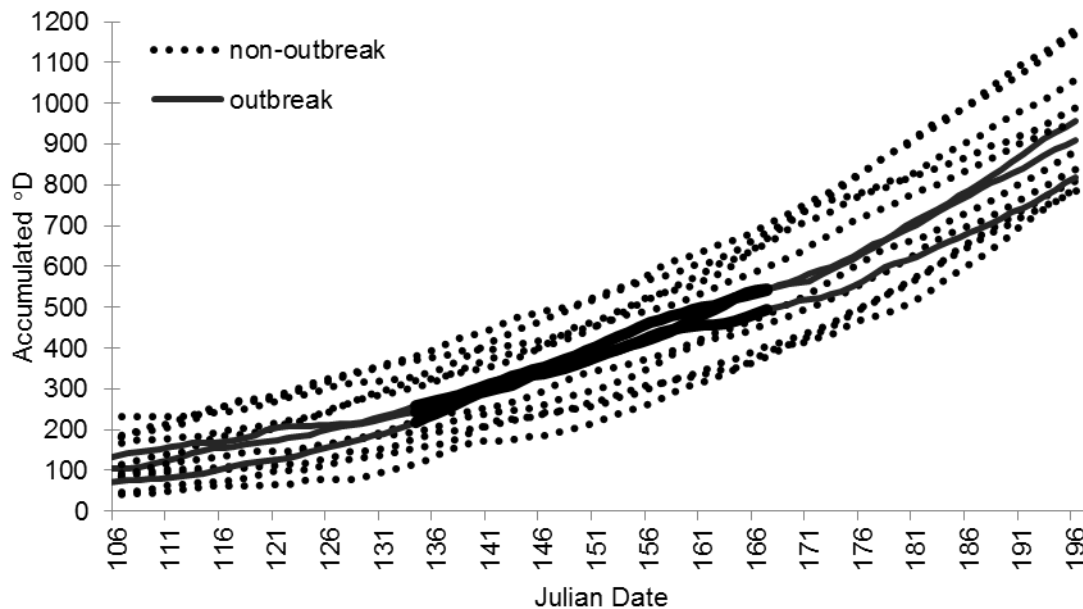
Figure 4.4. Degree-day accumulation versus Julian date (for 15 April-15 July) during the 13 study years on record for Henefer-Echo, Curlew Valley and Alturas. Thickened lines indicate for outbreak years the degree-day accumulation during the critical period (15 May-15 June) when young *Aroga* moth larvae are present.
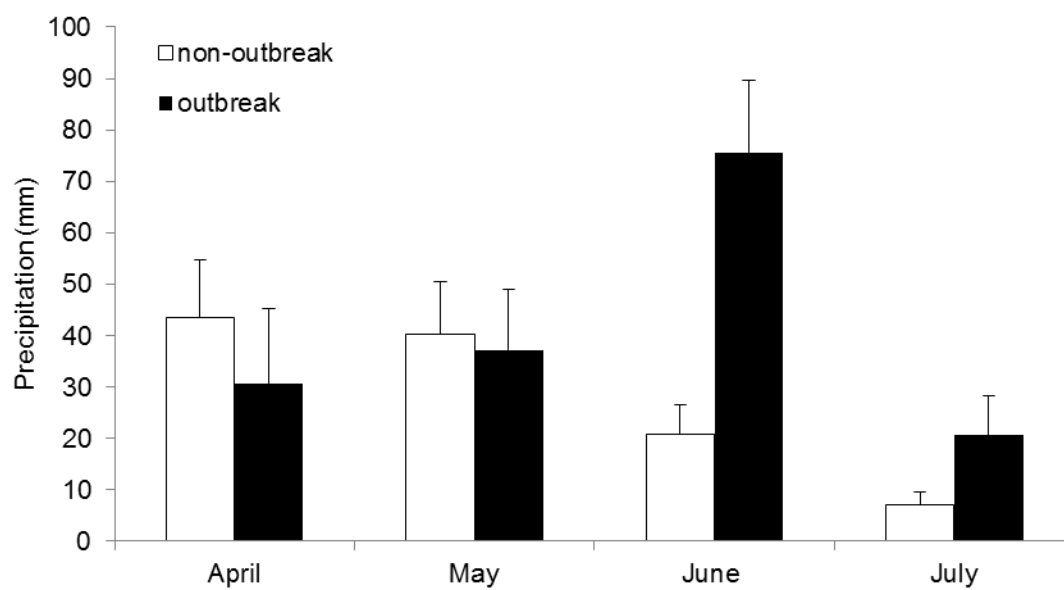
Figure 4.5. Mean monthly precipitation for Henefer-Echo, Curlew Valley, and Alturas during outbreak versus endemic population years (N=13).

CHAPTER 5

SUMMARY AND CONCLUSION

Big sagebrush (*Artemisia tridentata* Nuttall) shrub steppe is the largest vegetation type in the western United States (Miller et al. 2011). Most recent estimates suggest that only 50-67% of the original sagebrush cover remains (Schroeder et al. 2004, Welch 2005, Miller et al. 2011). Because of its historically expansive range and its importance for all other organisms in the region (Braun et al. 1976), big sagebrush serves the role of keystone species throughout this region (Khanina 1998). Large-scale declines in sagebrush distribution associated with biotic and abiotic forces, including human disturbance (agriculture and development), herbivory, pathogens, wildfire, and climatically related events, have contributed to the imperiled status that it now shares with the many other species of flora and fauna that it supports as a keystone species.

The studies presented here focused on one serious ecological and economic threat to sagebrush rangeland, the sagebrush defoliator or *Aroga* moth (*Aroga websteri* Clarke; Lepidoptera: Gelechiidae). In Chapter 2, I examined how the moth's abundance and impact on its host plant over space and time is related to local habitat characteristics. In Chapter 3, I investigated how the intensity of parasitism of the *Aroga* moth varied with physical (elevation) and biological (parasitoid and floral diversity) attributes in a montane setting. Lastly, in Chapter 4 I developed a degree-day (°D) model and compared seasonal patterns of temperature and precipitation with annual moth population estimates from three regions within the intermountain west. Together, the three chapters illuminate both abiotic and biotic factors affecting *Aroga* moth population dynamics.

In Chapter 2, patterns of sagebrush and *Aroga* moth abundance across a varied landscape were examined. *Aroga* moth abundance was not strongly associated with sagebrush cover across the elevation gradient at Henefer-Echo WMA. However, sagebrush cover and moth abundance were found most abundantly in areas with lower values of the solar radiation index (SRI) as developed by Keating et al. (2007). When one accounts for individual effects of aspect and slope as component variables of the SRI, aspect rather than slope contributed most significantly to spatial variation in moth density and survivorship. Both sagebrush and the *Aroga* moth were most abundant on north-facing slopes. For the moth, this likely reflects the effects of microclimate and a habitat relatively rich in resources (large host shrubs with high canopy cover). Sagebrush growing at these favorable north-facing sites tended to have the greatest capacity to recover from the defoliation sustained during an irruptive episode of the defoliator in 2009.

In Chapter 3, field experiments and observational studies were conducted to evaluate the role of natural enemies in *Aroga* moth population dynamics. During each year of the study, three key parasitoid species accounted for most of the parasitism of the moth: two generalists, *Copidisoma* sp. (Hymenoptera: Encyrtidae) and *Conura* sp. (Hymenoptera: Chalcididae), and one specialist, *Phaeogenes* sp. (Hymenoptera: Ichneumonidae). Overall rates of parasitism were high throughout the study. Rates of parasitism by individual species varied with elevation, with the two pupal parasitoids (*Conura* sp. and *Phaeogenes* sp.) having maximum densities at opposite ends of the elevation gradient (*Conura* sp. parasitism was greatest at low elevation and *Phaeogenes*

sp. parasitism was greatest at high elevation). Floral species richness was tightly

correlated with elevation across years, with greatest diversity found in areas of highest

elevation (and furthest away from cattle watering troughs). Field experiments were

conducted to test the influence of floral provisions (sugar sprays and buckwheat plant

treatments) and herbivore induced plant volatiles (MeSA lures) on rates of parasitism.

The specialist parasitoid (*Phaeogenes* sp.) responded strongly to both sugar sprays and

the buckwheat treatments, while the generalist parasitoid (*Conura* sp.) responded most

strongly to MeSA lures. The generalist *Copidisoma* sp. (examined only in the first

experiment) did not respond clearly to sugar spray. At local stands of sagebrush across

the Henefer-Echo WMA, greatest overall parasitism occurred when all three major

parasitoid species were present. Conflict and competition between heterospecifics may

have been reduced by differential use of resources along the elevation gradient.

In Chapter 4, a °D model was developed and applied to the phenology of field

populations of the *Aroga* moth. I determined the number of °D associated with the

seasonal peak in abundance of individual instars (larval stages) and of all larvae

combined. Despite the limitations to estimating peak abundances of field populations of

insects, the model provided relatively consistent estimates among years. Using this

model, I found that years of historical outbreaks of the moth throughout the Great Basin

had characteristic seasonal patterns of °D accumulation that were intermediate, when

compared to accumulations in endemic years, during mid-May through mid-June (when

early instars of the moth are developing). Outbreak years were also characterized by high

precipitation in June and July during late stage larval development. As Hsiao (1984) had

hypothesized, it appears that periodic outbreaks of the defoliator are due to favorable weather conditions. These conditions likely are associated with increased larval survivorship, and with high nutritional value and palatability of sagebrush foliage for the moth.

Landscapes as filled with biological communities result from ecological processes and events operating on different scales of space and time. Studies along natural gradients of abiotic and biotic factors (e.g., those in mountainous regions such as Henefer-Echo WMA), allow one to examine several biologically important environmental variables. Study of these variables across a montane landscape may elucidate the role of heterogeneity as it affects populations and biotic communities.

Like other indigenous, eruptive insect groups (e.g., bark beetles), the *Aroga* moth is a native insect with potential to kill its host plant in large numbers across an endangered landscape. It is a specialist herbivore of a long-lived, native plant, and has coexisted with its host plant throughout the Great Basin for many thousands of years. Previous work has demonstrated that native insect outbreaks could promote species richness and plant coexistence (Carson and Root 2000). Yet, cumulative effects of outbreak and non-outbreak levels likely play a role in regulating plant communities that include long-lived, keystone species (big sagebrush). Defoliation of high resource areas with high sagebrush cover and taller plants may in turn decrease competition for understory herbaceous plants, such as forbs. These forbs in turn may enhance the parasitoid community and their ability to suppress eruptive episodes of the moth. Long-term experiments over broad spatial scales are required to more critically evaluate the

role of defoliator herbivory under outbreak and non-outbreak conditions in regulating plant communities and mediating tritrophic interactions.

The potential consequences of biodiversity loss for ecosystem functioning and services (e.g. parasitism) has received much attention over the last several years (Loreau et al. 2003). Diversity in tritrophic interactions studied here across a heterogeneous landscape at Henefer-Echo WMA between plant resource, herbivore, and parasitoid guild appears to offer spatial insurance to buffer the potential impacts of an irruptive insect. It is unsettling to think that this relationship of long-term stability may now be upset in a landscape experiencing great change from human activities. Pristine patches of sagebrush steppe habitat are becoming more and more discontinuous as understory plant communities become less and less diverse.

The studies presented in this dissertation provide insight into factors that make sagebrush stands susceptible to outbreaks of the *Aroga* moth and to the damaging effects of these outbreaks, as well as understanding into factors that make sagebrush stands resilient to and buffered from such episodic attacks. For example, parasitism of *Aroga* moth populations was high at the Henefer-Echo WMA (a site with abundant floral diversity). A high rate of parasitism during the outbreak year of 2009 may have contributed strongly to the substantial reduction in moth numbers by the following year. In contrast, the community of parasitoids associated with the *Aroga* moth at Curlew Valley as studied by Hsaio and colleagues during the 1970s (with cheatgrass as the dominant understory plant; Hsiao 1984) was relatively ineffective (with low rates of parasitism), and abiotic factors likely were the most important factors in influencing the

population dynamics of the moth. Careful management of sagebrush habitat to promote

diverse communities of understory flowering plants and parasitoids may minimize the

potential for large and sustained irruptions of the defoliator when weather conditions

trigger an outbreak. Baseline work on the population dynamics of the *Aroga* moth across

a varied landscape is essential for comparison with other out-breaking insects (both

native and non-native), as well as for developing rangeland management plans to address

ever complicated ecological, climatic, and social issues. As the late Robert MacArthur

(1955) insightfully wrote, "Efficiency enables individual animals to out compete others,

but stability allows individual communities to out-service less stable ones."

LITERATURE CITED

Braun, C. E., M. F. Baker, R. L. Eng, J. S. Gashwiler, and M. H. Schroeder. 1976.

    Conservation committee report on effects of alteration of sagebrush communities

    on the associated avifauna. Wilson Bulletin **88**: 165-171.

Carson, W. P., and R. B. Root. 2000. Herbivory and plant species coexistence:

    community regulation by an outbreaking phytophagous insect. Ecological

    Monographs **70**: 73-99.

Hsiao, T. H. 1984. Biology and demography of the sagebrush defoliator and its impacts

    on big sagebrush. Pages 191-198 *in* E. D. McArthur and B. L. Welch, editors.

    Proceedings, Symposium on the Biology of Artemisia and Chrysothamnus, 9-13

    June 1984, Provo, UT. USDA Forest Service General Technical Report **GTR-**

    INT-200.

Keating, K. A., P. J. P. Gogan, J. M. Vore, and L. R. Irby. 2007. A simple solar
   radiation index for wildlife habitat studies. Journal of Wildlife Management. **71**:
   1344-1348.

Khanina, L. 1998. Determining keystone species. Conservation Ecology **2**(2): R2.

Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in
   heterogeneous landscapes. Proceedings of the National Academy of Sciences **100**:
   12765-12770.

MacArthur, R. H. 1955. Fluctuations of animal populations, and a measure of community
   stability. Ecology **36**: 533-536.

Miller, R. F., S. T. Knick, D. A. Pyke, C. W. Meinke, S. E. Hanser, M. J. Wisdom,
   and A. L. Hild. 2011. Characteristics of sagebrush habitats and limitations to
   long-term conservation. Pages 145-184 *in* S. T. Knick and J. W. Connelly editors.
   Greater sage-grouse: ecology and conservation of a landscape species and its
   habitats. University of California Press. Berkeley, California, USA.

Schroeder, M. A., C. L. Aldridge, A. D. Apa, J. R. Bohne, C. E. Braun, S. D.
   Bunnell, J. W. Connelly, P. A. Deibert, S. C. Gardern, M. A. Hilliard, G. D.
   Kobrider, S. M. McAdam, C. W. McCarthy, J. J. McCarthy, D. L. Mitchell, E. V.
   Riderson, and S. J. Stiver. 2004. Distribution of sage-grouse in North America.
   The Condor **106**: 363-376.

Welch, B. L. 2005. Big sagebrush: a sea fragmented into lakes, ponds, and puddles.
   General Technical Report **RMRS-GTR-144**.

APPENDICES

APPENDIX A

Flowering species list for Chapter 3

Table A-1 Flowering species list identified from Henefer-Echo WMU field plots referenced in Chapter 3:

Bloom ID	Genus species	Common name
F24	*Achillea millefolium*	Yarrow
F88	*Agastache urticifolia*	Horsemint
F35	*Agoseris glauca*	Mountain Dandelion
F44	*Allium acuminatum*	Tapertip Onion
F44.2	*Allium parvum*	Dwarf Onion
F27	*Amelanchier utahensis*	Serviceberry
F02	*Astralagus utahensis*	Utah Milkvetch or Locoweed
F02.2	*Astralagus whitneyi*	Whitney's Locoweed
F89	*Balsamorhiza macrophylla*	Cutleaf Balsamroot
F40	*Balsamorhiza sagittata*	Arrow leaf, Balsamroot
F70	*Verbascum thapsus*	Common Mullein
F29	*Berberis aquifolium*	Creeping Oregon Grape
F74	*Brodiaea douglasii*	Douglas Brodiaea or Wild Hyacinth
F63	*Calochortus bruneaunis*	Sego Lily
F92	*Camassia quamash*	Camas Lily
F64	*Campanula rotundifolia*	Round Leaf Harbell
F59	*Carduus nutans*	Musk Thistle
F01	*Castilleja applegatei*	Wavy-Leaved Paintbrush
F01.1	*Castilleja miniata*	Great Red Paintbrush
F86	*Chaenactis stevioides*	Stevia Dusty-Maiden
F57	*Chrysanthamnus nauseosus*	Rubber Rabbitbrush
F78	*Chrysanthemum leucanthemum*	Oxeye Daisy
F58	*Cirsium arvense (L.) Scop*	Canada Thistle
F58.2	*Cirsium vulgare*	Bull Thistle
F05	*Comandra umbellatum*	Bastard Toadflax
F75	*Convolvulus arvensis*	Morning Glory, Bindweed
F18	*Crepis acuminata*	Hawksbeard
F18.2	*Crepis modocensis*	Low Hawksbeard
F37	*Cryptantha cinerea*	James' Cryptanth
F15	*Cymopterus terebinthinus*	Spring Parsley

F04	*Delphinium nuttallianum*	Low Larkspur
F52	*Echium vulgare*	Viper's Bugloss
F30	*Ephedra virdis*	Mormon Tea
F42	*Erigeron speciosus*	Showy Daisy, Fleabane
F54.2	*Eriiogonum ovalifolium*	Oval-Leaf Buckwheat
F54	*Eriogonum umbellatum*	Sulfur Buckwheat
F39	*Erodium cicutarium*	Filaree
F34	*Erysimum asperum*	Western Wallflower
F12	*Erythronium grandiflorum*	Glacier Lily
F67	*Euphorbia myrsinites*	Blue Spurge
F10	*Frasera speciosa*	Green Gentium or Monument Plant
F84	*Fritillaria atropurpurea*	Leopard Lily or Purple Spot Fritillaria
F20	*Fritillaria pudica*	Yellowbell or Yellow Fritilary
F93	*Gentiana calycosa*	Explorer's Gentian
F38	*Geranium viscosissimum*	Silky Geranium
F79	*Geum triflorum*	Prairie Smoke, Old Man's Whisk
F94	*Grindelia squarrosa*	Curly-Cup Gumweed
F28	*Hackelia patens*	Pale Stickseed
F48	*Hedysarum boreale*	Northern Sweetvetch
F68	*Helianthus annus*	Common Sunflower
F07	*Hydrophyllum capitatum*	Ballhead Waterleaf
F90	*Ipomopsis aggregata*	Scarlet Gilia
F09	*Lathyrus pauciflorus*	Utah Sweet Pea
F46	*Linum lewisii*	Wild Blue Flax or Lewis Flax
F65	*Lithophragma parviflorum*	Woodland Star
F15.1	*Lomatium austinae*	Desert Parsley
F15.2	*Lomatium dissectum*	Fern-Leaf
F49	*Lupinus argenteus*	Silvery Lupine
F95	*Melilotus alba*	White Sweet Clover
F55	*Mentha arvensis*	Horsemint
F33	*Mertensia brevistyla*	Wasatch Bluebell, Short-Styled Bluebell
F62	*Mertensia ciliata*	Mountain Bluebell
F96	*Microsteris gracilis*	Slender Phlox

F47	*Oenothera caespitosa*	Primrose
F60	*Opuntia polycantha*	Prickly Pear Cactus
F51	*Penstemon cyananthus*	Wasatch Beardtongue
F76	*Penstemon eatonii Gray*	Eaton Penstemon, Firecracker
F77	*Penstemon utahensis*	Utah Penstemon
F71	*Phlox hoodii*	Cushion Phlox
F71.2	*Phlox longifolia*	Long-Leaf Phlox
F91	*Polygonum bistortoides*	Western Bistort
F97	*Potentilla fruticosa*	Shrubby Cinquefoil
F26.2	*Prunus emarginata*	Bitter Cherry
F26	*Prunus virginiana*	Chokecherry
F82	*Purshia mexicana*	Cliff-Rose
F25	*Purshia tridentata*	Bitterbrush, Antelope Bitterbrush
F98	*Ribes cereum*	Wax Currant
F83	*Rosa woodsii*	Wood's Rose
F99	*Sambucus glauca*	Blue Elderberry
F66	*Senecio douglasii*	Thread-Leaf Groundsel
F11	*Senecio serra*	Saw Groundsel or Butterweed
F69	*Sidalcea oregana*	Oregon Checkermallow
F45	*Sphaeralcea munroana*	Globe Mallow
F72	*Symphoricarpos oreophilus*	Mountain Snowberry
F31	*Taraxacum officinale*	Common Dandelion
F61.2	*Tragopogon dubius*	Yellow Salsify
F61	*Trapopogon pratensis*	Meadow Salsify
F100	*Trifolium kingii*	Shasta Clover
F73.2	*Vicia americana*	Peavine
F03	*Viola purpurea*	Mountain Violet
F41	*Wyethia amplixicaulis*	Northern Mule Ears
F13	*Zigadenus paniculatus*	Sand Corm

APPENDIX B

ANCOVA figures for Chapter 3
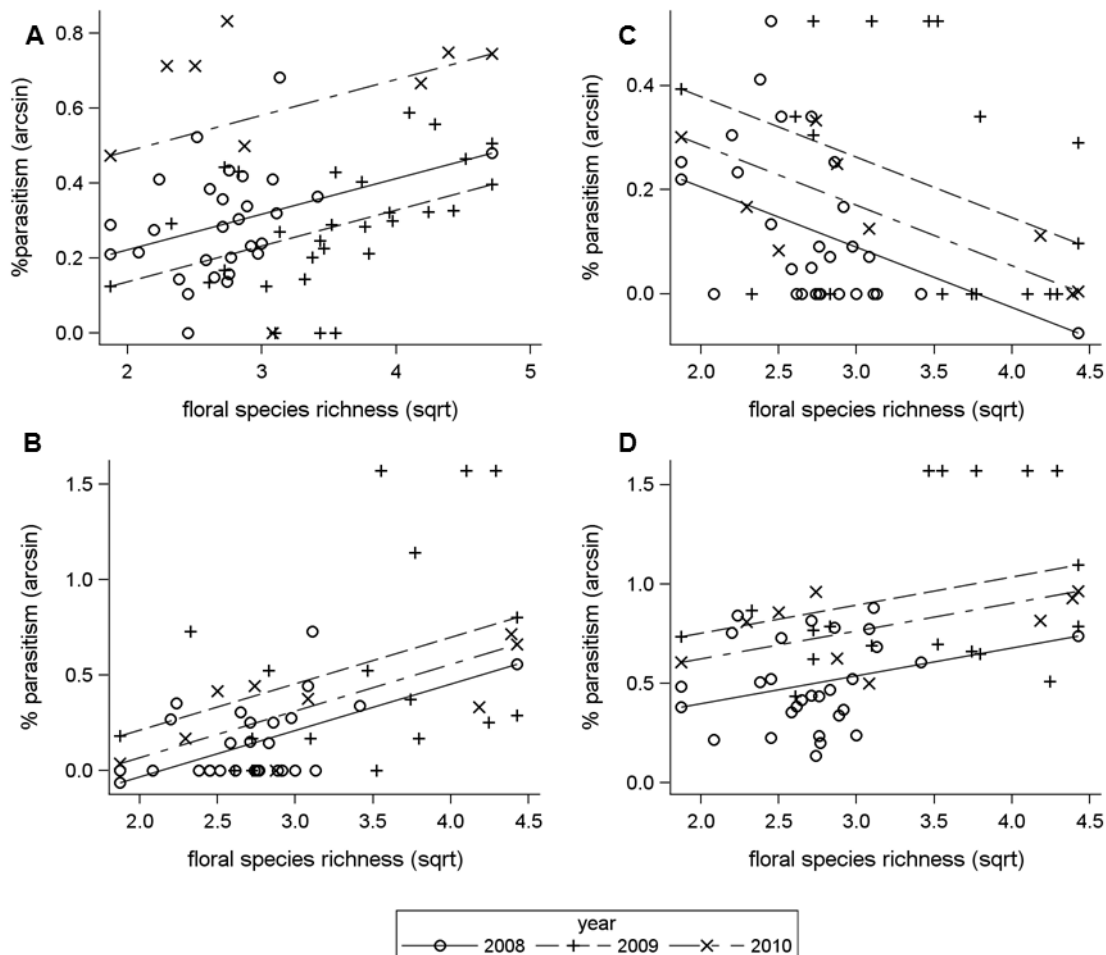
Figure B-1. Relationship between individual parasitoid species' parasitism rate, floral species richness, and year. Rates of parasitism are shown for all three major parasitoid species considered individually **(A)** *Copidisoma*, **(B)** *Phaeogenes*, **(C)** *Conura*, and combined **(D)**. Floral species richness spans the spatial extent of field plots at Henefer-Echo WMA. Parasitism rates are the proportion of host larvae or pupae parasitized (arcsine transformed).

APPENDIX C

Supplemental text and ANCOVA figures for Chapter 3

Cattle grazing

At HEWMA, permanent cattle troughs were placed at the most accessible locations in the lowest elevations. The impact of cattle grazing was indirectly measured based on distance from nearest cattle trough or watering source using GPS coordinates (distances from trough ranged from 106-3030 m).

Floral richness was greater at increasing distance from the nearest cattle trough (Fig. 2b; ANCOVA, effect of distance from trough: $F_{1, 137}=81.49$, $p<0.0001$; effect of year: $F_{3,137}=5.15$, $p=0.002$; interaction of trough x year: $F_{2,137}=2.17$, $p=0.09$).

Copidisoma was present at all distances from the trough; overall, the percentage parasitism by this species increased with increasing distance from the nearest trough (Table 3; ANCOVA, effect of distance from trough: $F_{1, 57}=6.20$, $p=0.02$; effect of year: $F_{2,57}=9.42$, $p<0.001$; interaction of elevation x year: $F_{2,55}=0.59$ $p=0.56$).

The intensities of pupal parasitism by *Phaeogenes* and *Conura* varied in opposite pattern to each other across varied distances from the nearest cattle trough. Highest rates of Phaeogenes parasitism generally occurred at furthest distances away from the cattle trough; this was especially evident in 2009 (ANCOVA, effect of distance from trough: $F_{1,43}=10.13$, $p=0.003$; effect of year: $F_{2,43}=0.45$, $p=0.64$; interaction of trough distance x year: $F_{2,43}=5.40$, $p=0.008$). Highest rates of *Conura* parasitism occurred at locations nearest to the cattle trough (ANCOVA, effect of distance from trough: $F_{1,45}=24.25$, $p<0.0001$; effect of year: $F_{2,45}=2.05$, $p=0.14$; interaction of elevation x year: $F_{2,43}=1.43$, $p=0.25$).

Combining the impact of all three species, the overall rate of parasitism of *Aroga* generally increased as distance from the cattle trough increased, with differences in rates among years but no significant interaction of year with cattle trough distance (ANCOVA, effect of distance from trough: $F_{1,45}=5.79$, $p=0.02$; effect of year: $F_{2,45}=12.26$, $p<0.0001$; interaction of elevation x year: $F_{2,43}=1.80$, $p=0.18$).
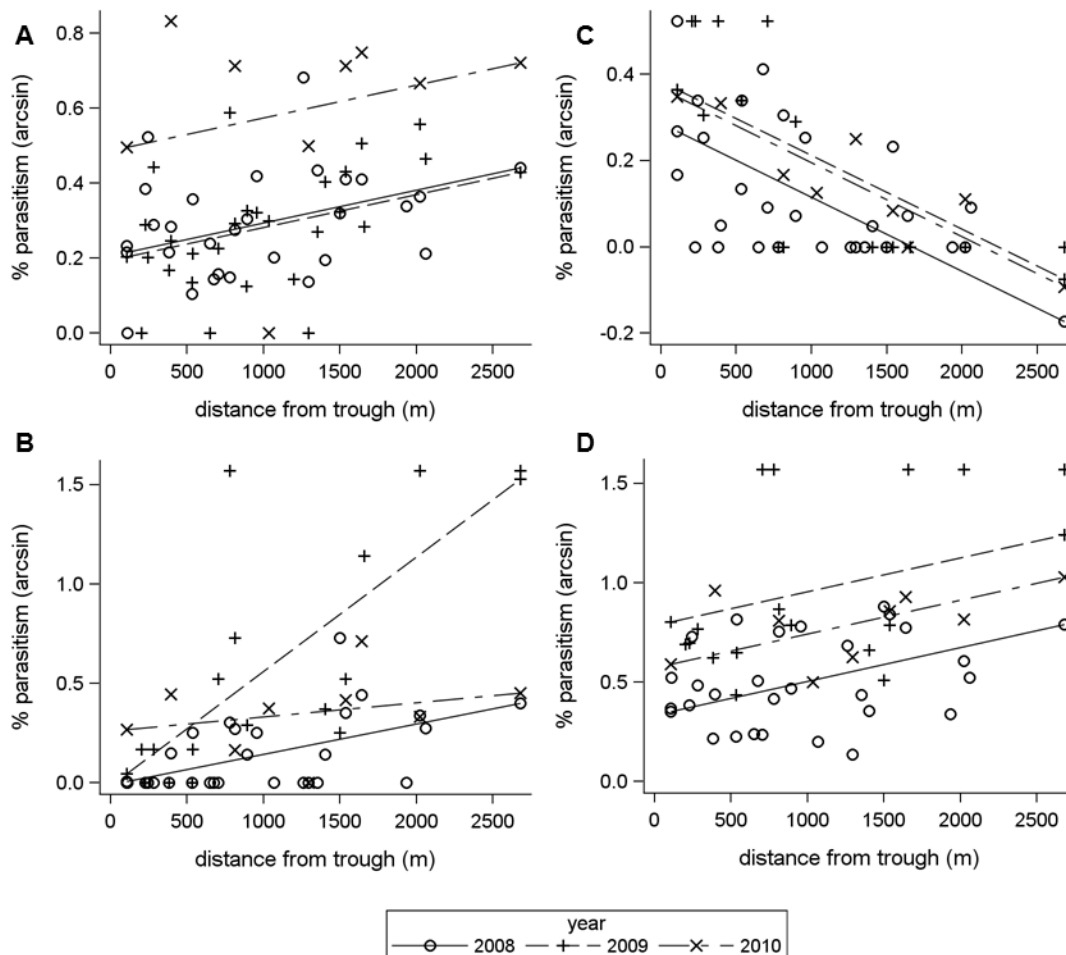
Figure C-1. Relationship between individual parasitoid species' parasitism rate, distance from cattle trough (m), and year. Rates of parasitism are shown for all three major parasitoid species considered individually **(A)** *Copidisoma*, **(B)** *Phaeogenes*, **(C)** *Conura*, and combined **(D)**. Distance from the cattle trough spans the spatial extent of field plots at Henefer-Echo WMA. Parasitism rates are the proportion of host larvae or pupae parasitized (arcsine transformed).

APPENDIX D

Julian dates and degree-days for Chapter 4

Table D-1. Julian dates (JD) and associated accumulated degree-days at larval peak abundances for first-fifth instars of the *Aroga* moth, and for all larvae combined, at field sites at Henefer-Echo and Curlew Valley.

Sine Model (8∘C Lower Threshold)[1]		Life stages									
		1st Instar peak		2nd Instar peak		3rd Instar peak		4th Instar peak		5th Instar peak		Combined peak
Location (year)	JD DD	JD DD	JD DD	JD DD	JD DD	JD DD
HEWMA, UT (2008)	141 133	148 154	169 267	172 294	183 424	141 133
HEWMA, UT (2009)	133 138	133 138	149 244	155 294	182 490	133 138
HEWMA, UT (2010)	130 102	146 149	155 206	169 307	174 347	155 206
Cur Val UT/ID (1972)	113 102	132 176	141 239	154 331	161 400	141 239
Cur Val UT/ID (1974)	117 105	131 183	155 347	155 347	164 419	117 105
Cur Val UT/ID (1975)	111 15	147 108	158 182	165 238	171 277	126 31
Mean	124 99	140 151	155 247	162 302	173 393	136 142
SE	5 18	3 11	4 23	3 15	4 30	5 30
CV (%)	10 45	6 18	6 23	5 12	5 19	98 52

[1]Degree-days were calculated using a single-sine method with a lower threshold of 8∘C and no upper horizontal cut-off.

Table D-2. Julian dates (JD) and associated accumulated degree-days at larval peak abundances for first-fifth instars of the *Aroga* moth, and for all larvae combined, at field sites at Henefer-Echo and Curlew Valley.

Sine Model (10°C Lower Threshold)[1]		Life stages									
1st Instar peak		2nd Instar peak		3rd Instar peak		4th Instar peak		5th Instar peak		Combined peak	
JD	DD	JD	DD	JD	DD	JD	DD	JD	DD	JD	DD
Location (year)											
HEWMA, UT (2008)											
141	97	148	112	169	199	172	222	183	331	141	97
HEWMA, UT (2009)											
133	92	133	92	149	176	155	216	182	371	133	92
HEWMA, UT (2010)											
130	66	146	98	155	142	169	221	174	255	155	142
Cur Val UT/ID (1972)											
113	63	132	116	141	164	154	234	161	293	141	164
Cur Val UT/ID (1974)											
117	67	131	128	155	261	155	261	164	320	117	67
Cur Val UT/ID (1975)											
111	6	147	74	158	134	165	181	171	216	126	16
Mean	124	65	140	103	155	179	162	223	173	298	136	96
SE	5	13	3	8	4	19	3	11	4	23	5	22
CV (%)	10	50	6	19	6	26	5	12	5	19	10	55

[1]Degree-days were calculated using a single-sine method with a lower threshold of 10°C and no upper horizontal cut-off.

APPENDIX E
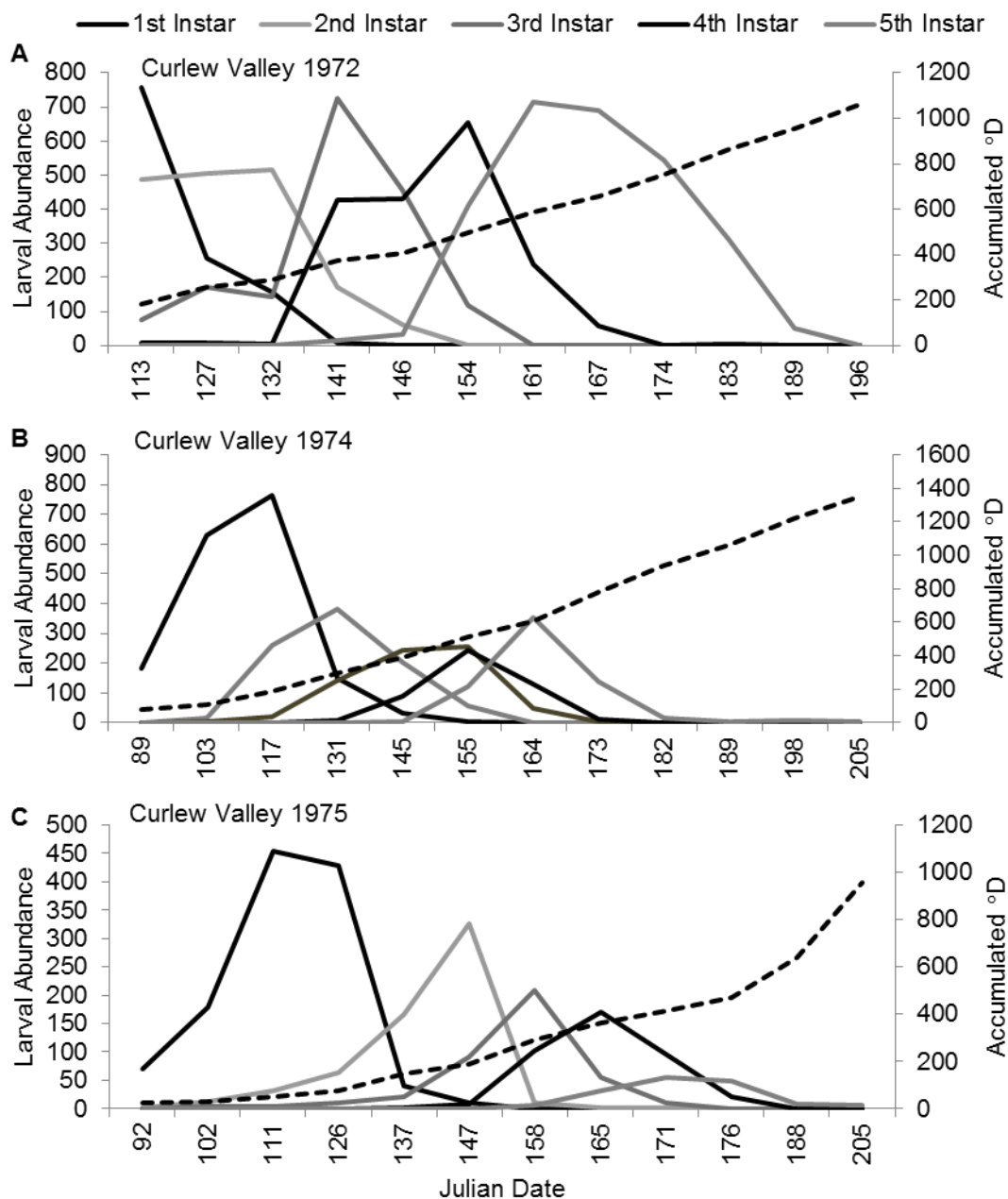
Age structure and population density for Chapter 4

Figure E-1. Age structure and population density of *Aroga* (solid lines) and accumulated DD (dotted line) versus Julian calendar date (120 JD corresponds ~1 May) **(A)** Curlew Valley 1972, **(B)** Curlew Valley 1974, and **(C)** Curlew Valley 1975.

CURRICULUM VITAE

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Education

PhD	**Utah State University**, Logan UT, Insect Ecology, 2013 Advisor: (E.W.) Ted Evans
MEd	**University of Toledo**, Toledo OH, Science Curriculum and Instruction, 2007 Advisor: Carla C Johnson
BS	**State University of New York (SUNY) at Buffalo** & **Utah State University**, Logan UT, Biology, Biology Teaching Composite, 2005

Research Areas

Insect Population and Community Ecology, Ecological Basis of Conservation Biological Control

Landscape Moderation of Biodiversity Patterns and Processes

Science Education outside the Classroom, Cultural Relevancy, and Student & Teacher Self-Efficacy

Professional Experience & Service

2013-Current	**County Director, Elkus Ranch Director, and 4-HYD Advisor**, University of California Agriculture and Natural Resources, Cooperative Extension San Francisco & San Mateo Counties, Half Moon Bay, CA
2013	**Lecturer**, Utah State University, Department of Biology, Logan UT
2012	**Adjunct Professor**, University of Cincinnati, Online Blackboard Instructor
2012-2013	**No Child Left Inside Volunteer,** Cache Valley Chapter, Logan, UT
2009-2013	**Beekeeper and Small Business Owner of Honeylove Inc.,** Logan UT & Nashville MI

2008-2013	**Coordinator/Educator/Volunteer**, Biology Department Community Outreach-Insect Zoo and Museum Tours, Utah State University, Logan UT
2008-2013	**Research Assistant and Teaching Assistant** in Ted Evans' Lab in collaboration with the Utah Division of Wildlife & Natural Resources and U.S. Department of Agriculture, USDA-FS Forest Health Protection, Utah State University, Logan UT
2008-	**Consultant & Educational Specialist** for STEM Innovations LTD, Cincinnati OH in collaboration with Ogden City School District, Ogden UT
2008-2010	**Co-Chair**, Ecology Center Seminar Series Committee, Utah State University, Logan UT
2008-2010	**Group and Personal Tutor**, Student Athlete Services, Utah State University, Logan UT
2006-2007	**Interdisciplinary Team Member**, UT's STEMM Campus Community Initiative, University of Toledo, Toledo OH
2006-2007	**Tom Strain & Sons and Daughter Too Farm Market and Garden Center**, Manage 6 acres of greenhouses, marketing, and selling products, Toledo OH
2005-2007	**Research Assistant and Science Teacher** UTQ Program for Middle School Teachers, Toledo OH & Ogden UT
2004-2005	**Interim Coordinator**, Student Athletes' Life Skills Services, Utah State University, Logan UT
2004	**Legal Secretary**, Siegal, Hudson, Gee, & Longstreet Law Firm, Hastings MI
2002-2003	**Piston Ring Parts' Auditor**, Hastings Manufacturing Company, Hastings MI
2002-2005	**Substitute Teacher and Tutor**, Hastings MI & Logan UT
2000-2002	**Clinic Internship,** Roswell Park Cancer Institute Children's Ward, Buffalo NY
2000-2003	**Basketball Coach and Counselor**, Camp of Champions, Grand Rapids MI

Honors and Awards

♦ North American Congress for Conservation Biology Student Award for Excellent Abstract (2012)
♦ James and Patrice MacMahon, USU Biology Department Ecology Scholarship (2012)
♦ USU Research Assistantship (2008-2011, 2012), USU Teaching Assistantship (2008, 2012-13)
♦ U of Toledo Research Assistantship, Utah Quality Teacher Grant (2005-2007)

- ♦ SUNY at Buffalo & Utah State University, Student Athlete Award (basketball) (2000-2005), Coca-Cola Community All-American (2004), All-MAC Academic Team (2001 & 2002)
- ♦ Congressional Medal of Merit for the State of Michigan (2000), National Merit Scholar Recipient (2000), National Honor Society President (1999-2000)
- ♦ First-team All-State Girls' Basketball for the State of Michigan (1999-2000); Member of the U.S. Junior Olympic National AAU Girls' Basketball Team (2000)

Peer Reviewed Publications

When good intentions and reality meet: Large-scale reform of science teaching in schools with predominantly Hispanic ELL students (in review)
C.C. Johnson, **VLJ Bolshakova**, T. Waldron, & J.D. Fargo

''It depends on what science teacher you got'': urban science self-efficacy from teacher and student voices (2011)
VLJ Bolshakova, C.C. Johnson, & C.M. Czerniak, *Cultural Studies of Science Education* 6(4), 961-997, DOI: 10.1007/s11422-011-9346-2

Books/Book Chapters

STEM Stakeholder Response to Enacted Educational Policy (2011)
C.C. Johnson & **V.L.J. Bolshakova** in Johnson, C.C. (Ed.) *Secondary STEM Education Reform,* Palgrave MacMillan 159-192.

Other Manuscripts

Causes and Consequences of Local Variability in *Aroga Websteri* Clarke Abundance over Space and Time (2013) VLJ Bolshakova, PhD Dissertation, Utah State University

The Inner Scope: Exploring the Influence of Classroom Teachers' Sense of Efficacy on Hispanic Students' Science Efficacy at One Urban Middle School (2007)
VL Jennings, Master's Thesis, University of Toledo

Grant Support/Scholarships

$40,000-	P.I. Coca Cola National 4-H Council Healthy Living Grant, Youth Voice: Youth Choice (2013-2014)
$3,000-	Utah State University, School of Graduate Studies Dissertation Fellowship (2013)

$500- North American Congress for Conservation Biology Student Travel Award (2012)

$1,000- James A. and Patricia A. MacMahon Scholarship in Ecology (2012)

$60,000- Utah Division of Wildlife Resources (2008-2012)

$15,000- USDA-FS, Forest Health Protection (2008-2012)

$1,000- Utah State University, Ecology Center Student Supplemental Travel Grant (2010)

$7,000- Utah State University, Ecology Center Student Research Support (2009-2010)

$5,000- Utah Department of Natural Resources-Forest Fire Division (2008)

Research Presentations

♦ *Invited Guest Speaker on Agriculture Technologies and Global Climate Change*, the League of Women Voters of San Mateo County National Study, San Mateo, CA, **VL Jennings** (Nov 2013)

♦ Utah Cooperative Research Unit Meeting, Logan, UT, **VLJ Bolshakova**, EW Evans (May 2013)

♦ National Association of Research in Science Teaching International Conference, San Juan, Puerto Rico, CC Johnson, **VLJ Bolshakova** (March 2013)

♦ *Invited* Presentation, Northern Great Basin Climate Forum, Oregon Institute of Technology, Klamath Falls OR, **VLJ Bolshakova,** EW Evans (Nov 2012)

♦ North American Society for Conservation Biology, Oakland CA, **VLJ Bolshakova**, EW Evans (July 2012)

♦ National Association of Research in Science Teaching International Conference, Indianapolis IN, CC Johnson, **VLJ Bolshakova** (March 2012)

♦ European Science Education Research Association (ESERA), Lyon, France, CC Johnson, **VLJ Bolshakova** (Sept 2011)

♦ Ecological Society of American (ESA), Austin TX **VLJ Bolshakova**, EW Evans (Aug 2011)

♦ American Educational Research Association International Conference, New Orleans LA, CC Johnson, **VLJ Bolshakova** (April 2011)

♦ National Association of Research in Science Teaching International Conference, Orlando FL, CC Johnson, **VLJ Bolshakova**, T Miller (April 2011)

♦ Intermountain Grad Research Symposium, Logan UT, **VLJ Bolshakova**, EW Evans (Mar 2011) –Second Place in Student Competition

♦ Intermountain Grad Research Symposium, Logan UT, **VLJ Bolshakova**, EW Evans (Mar 2010)

♦ Western North American Defoliator Working Group, Portland OR, **VLJ Bolshakova** (Dec 2009)

♦ Western North American Defoliator Working Group, Salt Lake City UT, **VL Jennings**, EW Evans (Dec 2007)

♦ National Science Teachers' Association (NSTA), St. Louis MO CC Johnson, **VL Jennings** (March 2007)
♦ Hawaii International Conference on Education, Honolulu HI, CC Johnson, **VL Jennings**, S Marx (January 2006)

Poster Presentations

♦ Utah Cooperative Research Unit Meeting, Logan, UT, **VLJ Bolshakova**, EW Evans (May 2012)
♦ Entomological Society of America, Reno NV, **VLJ Bolshakova,** EW Evans (Nov 2011)

Other Conferences, Meetings, and Professional Training

♦ The Hymenopteran Course, Rocky Mountain Biological Lab, Gothic CO (Aug 2010)
♦ Structural Equation Modeling Short Course, USU, Logan UT (Nov 2010)
♦ Species Distribution Modeling Short Course, USU, Logan UT (Mar 2010)
♦ Restoring the West Conference, Logan UT (Sept 2007, 2009)
♦ National Association for Research in Science Teaching Conference, San Francisco CA (March 2006)
♦ National Collegiate Athletic Association Student-Athlete Leadership Conference, Orlando FL (July 2003)

Courses Taught

BIO	4500	Applied Entomology
CI	799	Master's Research Seminar, Curriculum and Instruction (online course), Blackboard Environment

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Teaching Assistant

BIO	1620	Biology II
BIO	2420	Human Physiology
BIO	3220	Field Ecology
CI	7980	Culturally Responsive Science Teaching
BIO	4500	Applied Entomology
CI	701	Master's Research Seminar: Curriculum and Instruction

Guest Lectures

BIO	1350	Integrated Life Science for non-majors
BIO	5300	Insect Systematics & Evolution
CI	7980	Culturally Responsive Science Teaching

HONR 2100	Freshman Honors Inquiry Seminar for Science Majors
MHR 3400	Student Athlete Life Skills Management
RESM 6340	Qualitative Research and Design II

Curriculum Development

♦ **"Nutrition to Grow On (ENERGIZED!)"** modification and adaptation of garden-enhanced nutrition and physical education curriculum for upper elementary students delivered by teens in the afterschool program setting **2013-2014**

♦ **"Uinta Basin Ute Tribes' Garden Curriculum"** developing and implementing secondary science principles aligned to Utah State Standards emphasizing outdoor/environmental education **2012-2013**

♦ **"Applied Entomology"** developing and implementing lecture and laboratory-based materials for junior-level undergraduates at Utah State University in the Department of Biology **2013**

♦ **"Literacy through Ecology"** developed and implemented curriculum for an informal learning summer camp for at-risk youth in rural West Virginia funded by the West Virginia Department of Education Summer **2005**

Club / Professional Organizations & Services

2012-2013	No Child Left Inside Chapter of Logan, UT, Community Council Member
2010-	Society for Conservation Biology, member
2009-	Ecological Society of America, member
2009-2011	Aggies for 350, Founder and Event Organizer
2009-2013	Cache Valley Beekeepers' Association, member
2009-2012	Utah State University Student Organic Farm Club, manual laborer/volunteer
2008-2013	Utah State University Entomology Club, Community Outreach Coordinator, Insect Museum Educator and Caregiver
2008-	Entomological Society of America, member
2005-	National Association of Research in Science Teaching, member
2005-2007	National Science Teachers' Association, member