INTRASPECIFIC LIFE HISTORY VARIATION IN THE INTRODUCED RANGE OF

CYNOGLOSSUM OFFICINALE

by

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B.A, Brown University, 2016

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Geography)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

July 2019

The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, a thesis entitled:

"Intraspecific life history variation in the introduced range of *Cynoglossum officinale*"

submitted by   Sophie Duncan   in partial fulfillment of the requirements for

the degree of   Master of Science

in   Geography

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Abstract

All organisms must allocate resources to reproduce and survive. The study of intraspecific life history variation can provide insight into how different selective pressures, such as herbivory or climate, can favor different life history strategies and constrain others depending on which life stages are most vulnerable to the selective pressures. I examined how variation in herbivory and climate influences variation in the flowering size of plants and the occurrence of semelparity versus iteroparity at sites across part of the introduced range of an invasive plant, houndstongue (*Cynoglossum officinale*, Boraginaceae). Houndstongue is a short-lived semelparous perennial in its native range. In its introduced range, a previous study documented increased rates of iteroparity and a higher threshold flowering size compared to the native range. I hypothesized that the recent introduction of a specialist biocontrol root-boring insect (*Mogulones crucifer*) would decrease threshold flowering size, and reduce the proportion of iteroparous plants in the introduced range at sites with the weevil present. I surveyed 24 sites across the northwestern United States to quantify the frequency of semelparity versus iteroparity and to estimate abundance of *M. crucifer*. I found that the proportion of iteroparous plants varied across sites and that winter precipitation and weevil presence best explained this variation. Sites with greater precipitation and no weevils had a higher frequency of iteroparity. I used demographic data collected from six sites to estimate threshold flowering size. Sites with a higher attack rate by weevils had a lower threshold flowering size than those with a lower attack rate. The variation in frequency of flowering and threshold flowering size that I documented in North American houndstongue populations and the relationships between this variation and herbivory and climate provide evidence for how selective pressures shape the life histories of invasive plants.

Lay Summary

In this study, I examined how the flowering strategies of an invasive plant, *Cynoglossum officinale* (houndstongue), changed in the northwestern United States in response to variation in climate and the introduction of a biological control insect. The biological control, in this case, a weevil, damages the root of the plant, which reduces fecundity. I conducted surveys in 2017 and 2018 and found that sites with more weevils had smaller flowering sizes and that sites with wetter winters and no weevils had more plants that flowered in consecutive years. I also found that plants that attempted to flower two years in a row, and did not survive to reproduce during the second year, produced on average fewer seeds than plants that only reproduced once. My findings show that houndstongue reproduction varies in North America, where it is invasive, which can influence invasive plant management.

Preface

This thesis is original, unpublished work by the MSc Candidate, Sophie Duncan. Dr. Jennifer L. Williams (University of British Columbia) provided the supervision for this project. I gained permission to access all of my research sites, which were in the northwestern United States. I collected and analyzed all of the data.

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Acknowledgements

Dedication

This thesis is dedicated to all of the glorious dogs who bring joy to me daily. In particular I want to name Miro, Tula, Darwin, Daisy, Brulee, Lucca, Gilly, Devereaux, Dela, Chloe, Zoe, Sadie, Marshall, Max, JJ, Cleaver Green, Pearl, Bear Bear, Charlie, Duke, Merlin, Skye, Humphrey, Babar, J.D., Truman, Tyler, T.J, Caine, Smudge, Barolo, Balto, Weenie, and last but certainly not least, Gromit.

Introduction

All organisms face tradeoffs that impact how they live, reproduce, and die. Organisms maximize their fitness in response to these tradeoffs by producing as many surviving and thriving offspring as possible (Roff 1992), and individuals within or across species may respond differently to the same tradeoffs (Stearns 1976, 1989, Roff 1992). The different outcomes that occur in response to different constraints and circumstances produce the variation in life history strategies observed within and across taxa (Young 1990, Roff 1992, Lesica and Young 2005, Wilbur and Rudolf 2006, Flatt and Heyland 2011). These different life history strategies can lead to optimal fitness given variation in selective pressures such as climate or herbivory across a geographic range. What allows an organism to survive in one circumstance might prove disadvantageous in another. Understanding why this variation exists, especially within one species, can provide a foundation for answering some of the fundamental questions driving ecological and evolutionary research: how do selective pressures drive variation in life histories and what are the consequences of these life history strategies for fitness?

Life history theory for reproductive strategies

All organisms must delay reproduction to a certain degree after they are born. How long individuals wait before and between reproductive episodes depends on resource allocation, physiology, and external factors (Roff 1992, Koons et al. 2008). Some organisms have a threshold reproductive size, below which it is unlikely that the organism will initiate reproduction. This threshold ensures that an organism will have sufficient resources allocated to successfully reproduce (Bonser and Aarssen 2009). For plant populations, threshold flowering size can be quantified as an estimate based on the median size at which more than half the plants flower (Williams 2009). Reproducing at a larger size increases fitness through higher seed

production, farther seed dispersal, and greater attractiveness to pollinators (Wesselingh and de Jong 1995, Sletvold 2002). However flowering at a larger size also has a potential cost: waiting to grow larger might mean that the plant dies before it ever has a chance to reproduce (Wesselingh et al. 1997). Thus, flowering size depends on the likelihood of a plant surviving to reproduction and the fitness gains associated with reproducing at a larger size (Metcalf et al. 2003, Koons et al. 2008).

Selection can increase or decrease threshold flowering size depending on the fitness gains versus the potential costs of shifting flowering size (Wesselingh and de Jong 1995). If a larger threshold flowering size leads to higher fitness, the organisms experiencing these fitness gains may forego present reproduction for future reproduction at a larger size (Sletvold 2002). However, selective pressures, such as herbivory for example, might decrease the threshold flowering size, particularly if herbivores favor larger plants (Prins et al. 1992, Wesselingh et al. 1997). The risk of waiting to flower at a larger size might no longer lead to greater fitness, because of reductions in stored resources due to herbivory, thus selecting for smaller flowering size (Prins et al. 1992).

Both natural selection and physiological constraints also influence when and how many times reproduction will occur. While semelparous organisms have one episode of reproduction, immediately followed by death, iteroparous organisms have multiple reproductive episodes throughout their life (Roff 1992). Investigating the costs and benefits associated with semelparity and iteroparity follows a vein of ecological exploration presented by Cole (1954) and later advanced by Charnov and Schaffer (1973). Cole's paradox asks why iteroparous organisms should exist given a constant environment. The paradox emerges from calculations that indicated semelparous organisms need only produce one more offspring to achieve the same fitness as

iteroparous organisms (Cole 1954). Later, Charnov and Schaffer (1973) resolved this paradox by integrating adult and juvenile survivorship into the framework. They established the association between iteroparity and relatively low juvenile survivorship, and conversely, that semelparity optimized fitness in conditions of low adult (and relatively higher juvenile) survival (Charnov and Schaffer 1973). Charnov and Schaffer's solution paved the way for a line of scientific inquiry, delving into how biotic and abiotic selective pressures can favor different life history strategies (Roff 1992). Since then, evolutionary ecologists have attempted to understand under what circumstances do these strategies occur and what drives these patterns.

Like threshold reproductive sizes, semelparity and iteroparity can vary within and across taxa depending on selective pressures (Young and Augspurger 1991, Williams 2009). For example, for plants of the same species that have flexible life histories, in circumstances that lead to low juvenile survivorship, selection might favor iteroparity if an iteroparous life history strategy leads to higher fitness (Klinkhamer et al. 1997). While in an individual reproductive cycle an iteroparous plant might produce fewer seeds than a semelparous plant, if it survives to flower the next year it might produce more seeds overall and also extend the longevity of the seed bank.

Intraspecific life history variation

Future advances in life history theory require a more developed understanding of intraspecific life history variation. Establishing the scope and extent of life history variation within one species will allow comparisons between species to more fully represent the variation or similarities in life history strategies among species. Comparisons between species' life histories require data that accurately reflects how selection maximizes fitness for each species. If species have a flexible life history but the available data does not reflect this intraspecific life

history variation, this limits the reliability of cross-taxa comparisons. Despite the utility of intraspecific variation for cross-taxa comparisons, the body of research documenting intraspecific variation in life history remains relatively scant (Frederiksen et al. 2005, Hesse et al. 2008, Bastianelli et al. 2017). Past and present comparative studies across taxa rely on species-level data, often collected only from one or limited populations, which does not account for the possibility that one population does not represent the full extent of variation in the life history of the taxa (Frederiksen et al. 2005, Blanck and Lamouroux 2007, Hesse et al. 2008). Populations of a species might vary within and across the range depending on how selective pressures, such as herbivory and climate, vary.

Additionally, introduction of species to a new range can interact with and influence life histories as individuals encounter different climates and competitors and leave behind selective pressures, such as specialist enemies, from their native range. Invasion provides an opportunity to assess how the introduction of a novel organism to an environment can facilitate changes in life history. For restoration applications, changes in life history fundamentally alter how noxious and invasive plants will respond to management strategies. Studying how high-priority weeds change in novel environments will contribute to management strategies of invasive plants (Chornesky and Randall 2003).

Climatic influences on reproductive life history strategies

Climatic variation within a species' range can create circumstances that favor different life history strategies in populations across the range. While delaying reproduction can expose an organism to heightened risk in some circumstances, in others, delay can increase fitness and spread the risk across years (Tuljapurkar and Wiener 2000). In certain circumstances, organisms might have lower mean fitness in a particular year but ultimately have more consistent, longer

term reproductive success across multiple years, and higher overall fitness, a phenomenon known as "bet-hedging" (Philippi and Seger 1989, Venable 2007, Childs et al. 2010). Bet-hedging can limit the risks of reproducing in unfavorable environments, such as drought, either through "risk avoidance" (conservative bet-hedging) or by "risk spreading" (diversified bet-hedging) (Childs et al. 2010).

Unexpected events, such as natural disasters, storms, freezes, or grazing, can influence the reproductive strategies of species with flexible life histories. While life history strategies such as iteroparity can spread the risks associated with uncertain or unfavorable environments, as a form of bet-hedging, for species with flexible life histories, the life history strategy can vary across populations with spatial variation in an unexpected event or climate, depending on which life stage has the greatest sensitivity (Young 1990, Young and Augspurger 1991, Kim and Donohue 2012). For example, for two closely related species of *Lobelia*, drought reduced adult survivorship and the likelihood of surviving to reproduce again, leading to higher rates of semelparity in populations with drier conditions (Young 1990, Young and Augspurger 1991). Drought conditions also led to increased semelparity in *Erysimum capitatum* populations, but due instead to its increased effect on juvenile mortality of branching rosettes that would allow future iteroparity in individuals (Kim and Donohue 2012). This increased semelparity in *Erysimum capitatum* highlights how environmental events can impact survivorship rates at different life stages, leading to life history shifts (Kim and Donohue 2012). Understanding how species with flexible life histories respond to variation in climate, and how this response influences fitness, can provide insight into how an organism's abiotic environment constrains or drives life history traits.

Impact of herbivory on reproductive life history strategies

While an organism's evolutionary history and intrinsic anatomical factors drive life histories, extrinsic factors like predation and herbivory also can influence life histories (Reznick 1982, Bastianelli et al. 2017). Predation and herbivory can shape how, when, and how successfully the prey organism can reproduce, because herbivores may favor some life stages or traits over others (Reznick 1982, Day et al. 2002, Metcalf et al. 2009). Which life stages or traits they favor can translate into population level shifts in the size and timing of reproduction (Day et al. 2002). For example, an herbivore or grazer might favor larger plants, and as a result possibly decrease the threshold flowering size of the plants in that population (Brys et al. 2011). In addition, when herbivory decreases adult survival, this can facilitate a shift toward semelparity (Klinkhamer et al. 1997, Metcalf et al. 2003).

Invasion dynamics provide a significant window into how herbivory can impact life histories (Maron and Vila 2001, Wolfe 2002), because introduced species are likely to leave behind specialist herbivores, pathogens, and predators in their native range. This escape from "enemies" can contribute to the unbounded success of an invasive species in the absence of selective pressures from the native range (Keane and Crawley 2002, Wolfe 2002, Metcalf et al. 2009). In the absence of selective pressures from specialist herbivores in its introduced range, a species' life history strategy can shift for species with flexible life histories. For example, plants might delay reproduction or spread reproduction out over multiple years without the threat of specialist herbivores (Williams 2009).

In particular, native specialist herbivores can have a particularly strong influence on the plants they target, decreasing abundance, contributing to defoliation, and reducing survival (Maron and Vila 2001). Biological control has emerged as a pest management strategy due to these tightly coupled relationships that exist between specialists and the organisms they eat,

which managers have identified as pests or noxious weeds (Müller-Schärer et al. 2004).

Biocontrol introduction creates an ideal scenario to test how life history strategies shift, as invasive organisms reencounter selective pressure from an enemy it has escaped (Müller-Schärer et al. 2004). In addition to the rapid evolution that can occur after the introduction of an invasive species (Sargent et al. 2017), species can rapidly evolve again with the introduction of a specialist biocontrol to the introduced range (Stastny and Sargent 2017). Capturing the life history traits of populations as they reassociate with their specialist herbivores from the native range can provide insight into processes of rapid evolution that might result from the introduction of a novel selective pressure.

Cynoglossum officinale is an invasive plant that has lived in the absence of its specialist herbivore for almost 200 years, since its introduction to North America from Eurasia in the 19th century. Although *C. officinale* (houndstongue) is capable of iteroparity, in its native range it is primarily semelparous (Klinkhamer et al. 1997). In its introduced range, iteroparity levels were observed to be significantly higher compared to the native range, where most plants reproduce only once (Williams 2009). Additionally, in the introduced range, survival, growth, and flowering size increased (Williams 2009). Until recently, houndstongue has escaped its specialist herbivore, a root-boring weevil, *Mogulones crucifer*, which was introduced as a biocontrol in Canada in 1997. The current distribution of weevils in the introduced range provides a particularly unique opportunity to collect demographic data during the critical period when the weevil specialist has not yet arrived at all populations. Additionally, given how rapidly the weevils can decimate houndstongue populations, gathering sufficient data must occur quickly, before populations decline.

Research Questions

My research examines how life history traits of an invasive plant species, *Cynoglossum officinale* (houndstongue) vary across the introduced range in response to climate and herbivory by a specialist root-boring weevil, *M. crucifer*. In particular, I focused on threshold flowering size and the frequency of iteroparity. My study addressed three questions: (1) How does the frequency of iteroparity vary in the introduced range in response to variation in herbivory and climate? (2) How does threshold flowering size vary in response to herbivore pressure? (3) How does the frequency of flowering influence fitness?

Based on a previous study in North America (Williams 2009), I hypothesized that iteroparity and threshold flowering size would decrease in response to the introduction of the specialist herbivore because the herbivore targets larger plants, thus selecting for a smaller threshold flowering size (Wesselingh et al. 1997, Müller-Schärer et al. 2004, Williams 2009). I also expected to find increased semelparity in drier regions of the introduced range based on research demonstrating that drier conditions favors semelparity as a life history strategy (Young 1990, Kim and Donohue 2012). I hypothesized that if iteroparous plants successfully flowered two years in a row, they would have higher fecundity than semelparous plants. Life history theory predicts that semelparity confers an advantage when future reproduction through iteroparity is "unlikely, infrequent, or important" (Young 1990). Given previous findings from the introduced range that iteroparity frequently occurs and leads to higher fecundity, I anticipate that I will find that iteroparity confers greater fitness if plants survive to flower two years in a row (Williams 2009).

Methods

Cynoglossum officinale (houndstongue) is a monocarpic (semelparous) perennial with a flexible life history. In this context, I will use flexible to denote that we currently do not know whether houndstongue's capacity for both iteroparity and semelparity is genetic or plastic. In its introduced range, houndstongue has exhibited much higher rates of iteroparity (mean percent iteroparous plants ± SE: 18.9% ± 13.1%; range: 2%–45%) than in its native range where iteroparity rarely occurs (Williams 2009). Houndstongue grows as a vegetative rosette during its first year and requires vernalization to flower (Wesselingh et al. 1997). Plants can either flower in the second year or delay flowering to a subsequent year, with primordial inflorescences appearing in vegetative plants by late summer of the year prior to flowering (Wesselingh et al. 1997, de Jong et al. 1998). Houndstongue bolts in the spring and starts to flower in the early summer (Wesselingh and de Jong 1995). Houndstongue indicates the potential for iteroparity by retaining a vegetative rosette connected to the taproot simultaneous to flowering. This side rosette remains vegetative throughout the spring and summer flowering season and creates the capacity for a plant to flower the subsequent year.

In the native range of houndstongue, adults of a specialist root-boring weevil, *Mogulones crucifer* consume leaves, and larval development occurs in the root. Typically adult weevils feed on aboveground plant tissue and preferentially select larger plants to lay eggs in the roots during the fall and spring (Prins et al. 1992, Schwarzlaender 1997). Larvae feed on the roots during development and then emerge to pupate in the soil from mid-June through mid-October in the native range (Schwarzlaender 1997). Larvae can decimate root tissue, inhibiting houndstongue's ability to conduct water and nutrients (Catton et al. 2016). Given houndstongue's status as a noxious weed, due to is toxicity to cattle, controlling houndstongue has been an onerous task in

North America. However, in Canada, weed managers received permission in 1997 to release *M. crucifer* as biocontrol agent. Since its introduction, houndstongue populations in Canada have almost disappeared (Catton et al. 2016).

While *M. crucifer* is an approved biocontrol in Canada, concerns for other native members of the Boraginaceae family have prevented approval in the United States. Despite lack of official approval, weevils have started to move south over the U.S.-Canadian border toward populations of houndstongue in the northwestern United States. Additionally, *M. crucifer* has likely been illegally introduced without government approval, further expanding the range.

Site Selection and Locations

To find sites I contacted weed managers and ranchers in Washington, Idaho, and Montana. To meet the survey criteria, each site had to have at least 50 flowering plants within 50 meters, not received spray treatment in the past few years, and not be targeted for spray treatment the following year. In addition, I avoided sites on riverbanks or in wetlands so as not to introduce differences in site hydrology as a confounding factor. For my 2018 flowering surveys, I attempted to revisit 9 sites from a previous study (Williams 2009). At sites where populations still persisted, I resurveyed even if populations had fewer than 50 plants. I also noted where populations no longer existed.

Flowering plant surveys

At 24 sites, I surveyed all flowering plants within a 50 x 2 meter transect. For each plant surveyed I documented its height, stalk number, and the presence or absence of a side rosette. The presence of the side rosette indicated the potential for iteroparity. At every site I counted cymes for the first ten semelparous plants in the transect.

Weevil assessment

At each of the 24 sites, I also conducted root dissections in 2018 on the first 15 flowering plants on the right-hand side of the transect to confirm weevil presence, and assess the weevil attack rate if weevils were present. I assessed the attack rate by determining how many roots had weevils present of the roots surveyed. If weevil larvae were present I stopped dissections after 15 plants. If no weevil larvae were present I conducted 20 root dissections. I conducted all larval assessments prior to mid-July to ensure that larvae had not matured and exited the roots.

Demographic surveys

In July and August 2017, I established six field sites in Washington (western portion of all sites sampled) to quantify the influence of weevil presence on iteroparity and the size-dependent probability of flowering. At each site I recorded data for each flowering plant in one 2 x 50 m transect that I haphazardly placed in the middle of the population. For each flowering plant I measured height of the tallest stalk, number of stalks, number of inflorescences, position on the transect, and whether it had a side rosette (an indicator of the potential for iteroparity). For each potentially iteroparous plant, I also recorded the number of leaves and the length of the longest leaf. I then tagged and recorded distance from the transect to follow the fates of individuals. I also tagged the first 50 vegetative rosettes with at least 3 leaves on the right-hand side of the transect, and again measured the length of the longest leaf and counted the number of leaves. These size measures were shown to correlate highly with biomass and predict survival and probability of flowering by Williams (2009).

I assessed *M. crucifer* abundance at each site by digging up and dissecting the first ten semelparous flowering plants on the left hand side of the transect. However, for three sites (two in Yakima County, and one in Stevens County), I was unable to confirm weevil presence or absence in 2017 given the late date of the surveying (August) and high temperatures. In 2018, I

returned to these sites in June and July to confirm weevil presence, follow the fates of previously

tagged plants, and survey flowering plants. For plants tagged as vegetative in 2017, I marked

whether they flowered and recorded size measurements. For plants tagged as potentially

iteroparous in 2017, I recorded whether they survived to flower a second year and if they did,

how many cymes (inflorescences) they produced. Cymes are the inflorescences on each stalk,

each containing 10 to 35 flowers, which ultimately produce 4 seeds per flower, making the

number of cymes a useful estimate of fecundity (de Jong et al. 1990).

Analyses of frequency of iteroparity

To determine what biotic and abiotic factors best explained the variation in frequency of

potentially iteroparous plants (referred to as iteroparous plants) across the introduced range in

2018, I built generalized linear models (GLMs) with a binomial error distribution. I calculated

the proportion of potentially iteroparous plants at each site as the response variable and weighted

each observation by the number of plants sampled. Specifically, I examined climate and weather

variables including precipitation and temperature and weevil presence to determine the impacts

of moisture availability and herbivory on life history strategies. I identified climate, weather, and

environmental variables relevant to the lifecycle of houndstongue (spring precipitation, summer

precipitation, autumn precipitation, winter precipitation, annual precipitation, winter

temperature, summer temperature, and annual temperature) *a priori* from which to build the

candidate models due to the role of vernalization in the winter and the importance of water for

seedling success and survival (de Jong and Klinkhamer 1988, 1989, Wesselingh 1995,

Wesselingh et al. 1997). Since plants can only flower starting in the second year, climate data

from the year prior to flowering provides insight into the growing conditions that influenced the

initiation of flowering. I sourced climate data from 2017 (year prior to surveys) and the 1981-

2010 normals from ClimateWNA.com (Wang et al. 2016). I used a nested approach to first

determine which of the climate variables best explained variation in frequency of iteroparity. I

also compared those models to one that tested weevil presence without any climate variables. I

compared and ranked models based on Akaike's information criterion (AIC) (Burnham and

Anderson 2004). I then built a model that included weevil presence and the five best-supported

climate variables to test for a contribution of both climate and herbivory.

Threshold flowering size analyses

To calculate how probability of flowering depends on size and weevil attack rate, and

thus estimate the threshold flowering size, I used the demographic data collected from six sites in

2017 and 2018. I first calculated rosette size as:

Rosette size = log(number of leaves*maximum leaf length).

Then, using a generalized linear model with a binomial error distribution, I modeled the

probability of flowering as a function of rosette size (as in Williams 2009) and weevil attack rate.

I included an interaction between rosette size and weevil attack rate, thus allowing weevil attack

rate to influence both the slope and intercept of the model. I classified the six demography sites

into two groups: high weevil attack rate (weevils present in more than ten stems) and low weevil

attack rate (weevils present in fewer than two stems). Three sites qualified as having a high

attack rate and three sites qualified as having a low attack rate. Finally, I calculated threshold

flowering size for each population, the median size at which over half of the plants flowered

using the coefficients from the probability of flowering model:

Threshold flowering size = (-)intercept/slope

Fecundity Analyses

I assessed how fecundity differs for iteroparous plants and semelparous plants at the six demography sites by quantifying how the total number of cymes a plant produced was influenced by life history strategy. I calculated the total number of cymes per plant from both years of flowering for iteroparous plants that survived and flowered a second year. I then compared the number of cymes produced in the first year of flowering for iteroparous plants (2017) to the total number of cymes for both years of flowering for iteroparous plants, and the number of cymes semelparous plants produced each year (2017 or 2018). Using linear mixed-effects models (with the package lme4), I conducted a likelihood ratio test to determine whether the number of cymes (log-transformed to meet model assumptions) differed significantly among iteroparous and semelparous plants by comparing an intercept only model to one with life history as a fixed effect (Bates et al. 2014). I included site as a random effect to account for variation among sites in both models. I then conducted pairwise comparisons using the emmeans package to calculate the estimated marginal means to determine which groups differed significantly (Lenth 2019). I used R version 3.4.1 for all analyses.

Results

Iteroparity

Iteroparity varied substantially across the 24 sites surveyed in the introduced range (mean percentage of iteroparous plants ± SE: 12.9 % ± 13.1%, range: 0%-42.3%) (Figure 1). Only one site had 0% iteroparity and at five sites, more than 30% of the plants were iteroparous. Of the climate variables tested, average winter precipitation from the prior growing season (December 2016, January 2017, Feburary 2017) best explained variation in the proportion of iteroparous plants across sites (Figure 2, Table 1, Appendix B). Sites with higher winter precipitation had a greater proportion of iteroparous plants (Figure 2) and precipitation varied by region. Sites in or East of the Rocky Mountains had significantly lower winter precipitation (t_{19}= -2.0871, P = 0.05). Sites with weevils present had a significantly lower proportion of iteroparous plants and including weevil presence improved the model from the null (Table 1, Appendix B). Including weevil presence in a model with average winter precipitation from 2017, the best climate variable, significantly improved the overall model fit (Appendix B). Together, weevil presence and average winter precipitation from 2017 best explained the variation in iteroparity across the introduced range.
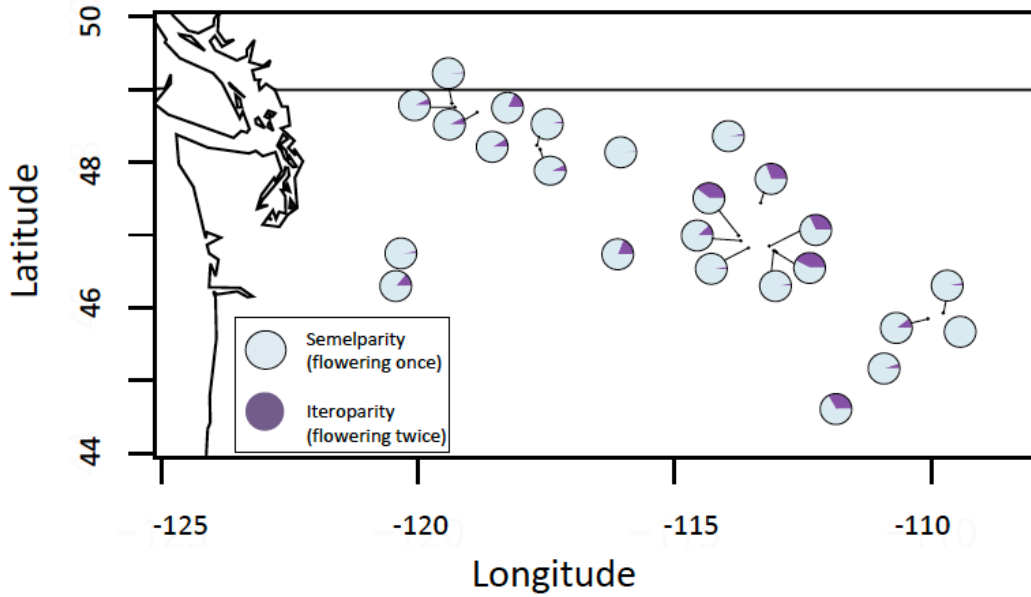
Figure 1. Map of 24 sites in introduced range of *Cynoglossum officinale* surveyed with proportion of semelparity (grey) and iteroparity (purple) indicated at each site.
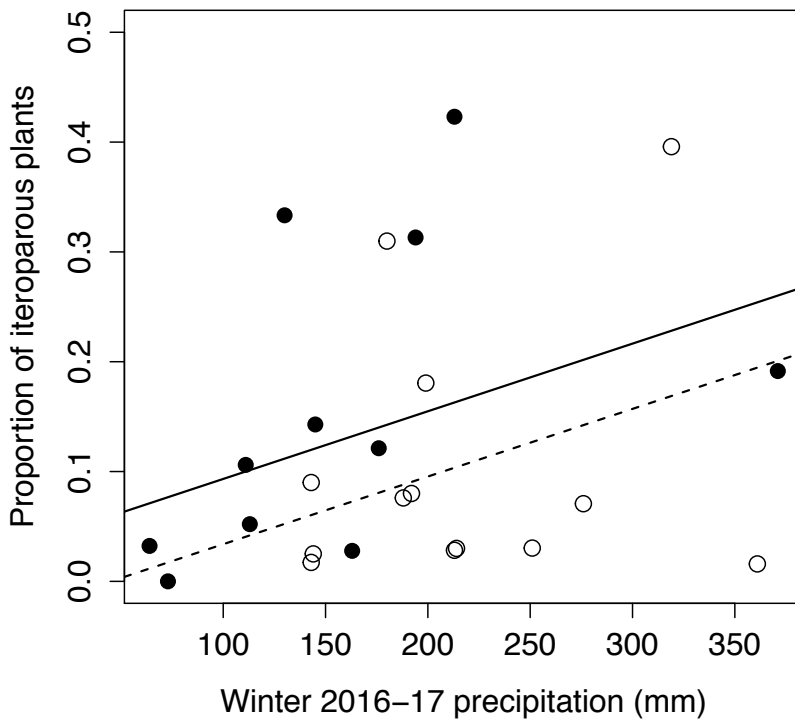
Figure 2. Relationship between spring precipitation in the previous year, weevil presence, and the frequency of iteroparity at sites across the introduced range of *C. officinale*. The dashed line and open circles correspond to sites with weevils present and the solid black circles and black line correspond to sites with weevils absent.

Table 1. Coefficents for a generalized linear model for the effect of weevil presence and 2017 winter precipitation (mm of rainfall from December 2016 – February 2017) on the proportion of iteroparity.

Proportion of iteroparity ~ 2017 winter precipitation + Weevil presence	Estimate	Std. Error	Z Value	P Value
Intercept	-0.0278	0.0241	-1.154	0.247
Weevil presence	0.0594	0.0156	3.810	<0.001
2017 winter precipitation	0.0006	0.0001	5.547	<0.001

Threshold flowering size

As predicted, I found that the probability of flowering increased with increasing rosette size (Figure 3, Table 2). Weevil attack significantly reduced the probability of flowering and shifted the threshold flowering size to a smaller size; the model with an interaction between weevil attack rate and rosette size best predicted the probability of flowering (Table 2). Threshold flowering size increased by 40% at sites with a low weevil attack rate compared to those with a high weevil attack rate.

Table 2. Coefficients from a generalized linear model for the effect of rosette size and weevil attack rate on probability of flowering.

Probability of flowering ~ Rosette size * weevil attack rate	Estimate	Std. Error	Z value	P value
Intercept	-10.086	1.846	-5.465	<0.001
Rosette size	2.040	0.393	5.190	<0.001
Weevil attack rate	5.310	2.382	2.229	0.026
Rosette size * weevil attack rate	-1.000	0.506	-1.977	0.048
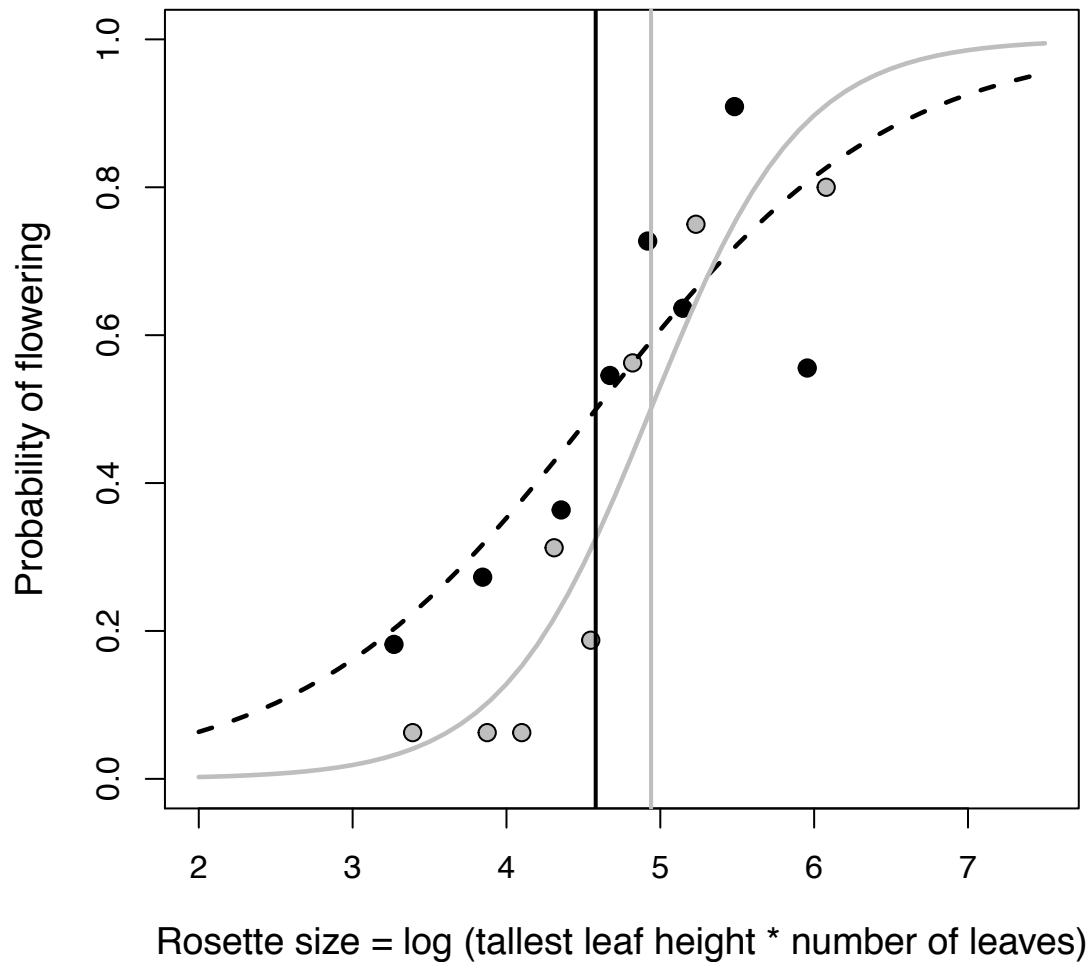
Figure 3. Threshold flowering size for sites with a high weevil attack rate (black) and sites with a low weevil attack rate (grey). Vertical lines indicate median threshold flowering size.

Fecundity and iteroparity

Fecundity varied significantly across semelparous and iteroparous plants ($P < 0.001$), with differences among sites taken into account. Iteroparous plants in their first year of reproduction (2017) had significantly lower fecundity compared to semelparous plants from 2017 or 2018 (Figure 4, Table 3). If iteroparous plants survived to a second year they produced on average, over 45% more inflorescences (cymes) over the course of two years than semelparous individuals produced in one year. However, this difference was not significant

(Figure 4, Table 3). In addition, across all sites, only 30.6% of iteroparous plants survived to reproduce in 2018.

Table 3. Pairwise comparisons of the estimated marginal means for average cyme production (log-transformed) for iteroparous and semelparous plants in 2017 and 2018. Bolded comparisons are significant.

Pairwise comparison	*P* value
2017 Iteroparous Plants- 2017 + 2018 Iteroparous Plants	**0.001**
2017 Iteroparous Plants –2017 Semelparous Plants	**<0.001**
2017 Iteroparous Plants –2018 Semelparous Plants	**<0.001**
2017 + 2018 Iteroparous Plants –2017 Semelparous Plants	0.172
2017 + 2018 Iteroparous Plants –2018 Semelparous Plants	0.404
2017 Semelparous Plants –2018 Semelparous Plants	0.805

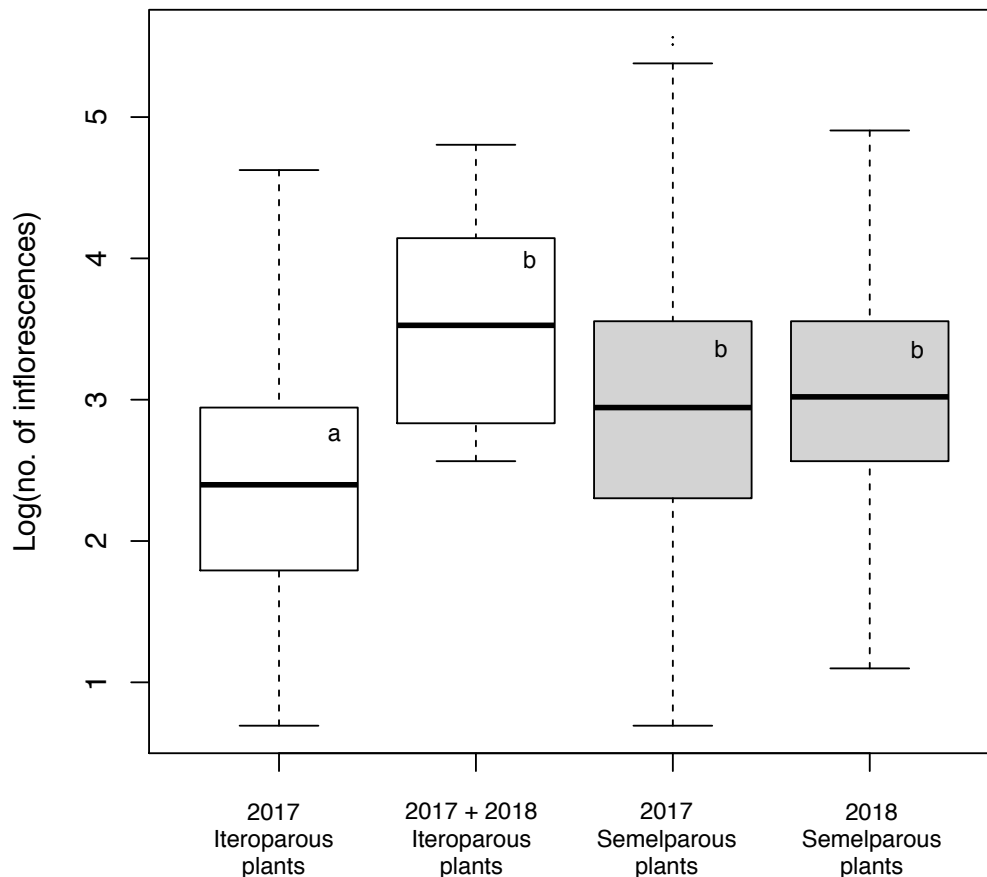**Figure 4. Fecundity (measured as number of inflorescences, or cymes) of iteroparous and semelparous plants in 2017 and 2018. Grey boxes indicate semelparous plants. Different letters indicate groups significantly different from pairwise comparisons; see Table 3)**

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Discussion

In response to selective pressures, organisms maximize fitness while also prioritizing survival. Both flowering size and frequency of flowering are life history traits that can vary in response to selective pressures such as herbivory and the environment. In surveys of *Cynoglossum officinale* (houndstongue), I found that threshold flowering size and the frequency of iteroparity varies across the introduced range. Both variation in the presence of a recently introduced specialist root-boring weevil biocontrol herbivore *Mogulones crucifer*, and climate, in particular winter precipitation, provide insight into the life history patterns I observed.

Variation in iteroparity

The frequency of iteroparity I observed in the introduced range (mean percentage of iteroparous plants ± SE: 12.9% ± 13.1%, range: 0-42.3%) indicates that iteroparity has continued to persist in the introduced range and at similar rates as a previous study that surveyed a subset of the same sites in 2004-2005 (mean percentage of iteroparous plants ± SE: 18.9% ± 13.1%; range: 2%–45%) (Williams 2009). However, not all populations persisted – of the seven sites I was able to revisit, three no longer had any houndstongue individuals. Either local invasive plant management such as spraying or hand-pulling, or metapopulation dynamics, similar to those observed in the native range (Van Der Meijden et al. 1992), could explain the disappearance of these populations. Of the four I resurveyed, three populations had fewer than 50 plants. Three populations maintained similar levels of iteroparity, while one population had a dramatic decrease in the frequency of iteroparity from 35.3% to 3% in 2018. Since long-term demographic studies have not tracked the frequency of iteroparity at the same houndstongue populations in the introduced range over several years, there is limited evidence for how often and to what extent the frequency of iteroparity changes at particular sites. Future long-term demographic studies

could explore whether houndstongue populations that currently or historically have had a high frequency of iteroparity continue to maintain this life history strategy.

Across the 24 sites I surveyed in 2018, sites with increased precipitation and weevil absence had a higher frequency of iteroparity indicating that wetter conditions and absence of the specialist herbivore favored iteroparity. My findings confirmed my hypothesis that drier conditions and weevil presence would lead to increased semelparity as a form of conservative bet-hedging and based on established links between drought, herbivory, and shifts to semelparity in other systems. The only documented instances of increased iteroparity in the native range occurred under "good growing conditions in a common garden experiment" in England, where 10% of flowering plants reproduced a second year (Klinkhamer et al. 1997), suggesting that adult survival was higher where growing conditions were favorable (Charnov and Schaffer 1973). Similarly, in the introduced range, higher amounts of winter precipitation might create favorable spring growing conditions for vegetative rosettes by increasing moisture availability through snowmelt, and thus lead to higher adult survival. While previous studies have documented the importance of precipitation for houndstongue's fitness, distribution, and seedling survival in both the native and introduced ranges (de Jong and Klinkhamer 1988, 1989, de Jong et al. 1990, Moyer et al. 2007, Momayyezi and Upadhyaya 2017), my findings establish a relationship between increased winter precipitation and a higher frequency of iteroparity in the introduced range. Future studies could investigate the link between adult survival and life history strategies in response to winter precipitation in the introduced range.

In the native range, where the specialist weevil coexists with houndstongue populations, iteroparity is rare and plants are for the most part semelparous (Klinkhamer et al. 1997). The root damage caused by the specialist herbivore increases the risk of infection by micro-organisms,

possibly leading to selection against an iteroparous life history (Klinkhamer et al. 1997). The root-boring nature of the weevil also might make houndstongue plants more susceptible to drought. Particularly in drier areas, where a healthy taproot facilitates access to water, weevil damage could limit adult survival. Given the recent arrival of the weevil to many of these sites, the full extent of measurable life history shifts might not have occurred yet. As the weevil herbivore spreads across the introduced range, it is possible that the proportion of iteroparity at sites in the introduced range will continue to decrease further. Continued monitoring could determine whether and to what extent the presence of the weevil facilitates a reduction of the proportion of iteroparity across the introduced range.

My demographic data indicate that plants with the capacity for iteroparity have on average reduced fitness, measured by total fecundity, compared to semelparous plants, if plants with the capacity for iteroparity do not survive to flower a second year. My data also suggest that although there is no significant advantage conferred if iteroparous plants survive to flower a second year, due at least in part by the small sample size of plants surviving to flower twice, these iteroparous plants still achieve higher reproductive success than semelparous plants did in one year. While I could not detect an advantage conferred by iteroparity, the higher fecundity of iteroparous plants confirms both my hypothesis and previous evidence that found iteroparity led to greater fitness if the individual survived to the second year in the introduced range (Williams 2009). However, my data indicate that while iteroparity is possibly beneficial, it is a risky strategy since so few plants survived to flower the subsequent year. Iteroparity, in this case, is possibly a form of bet-hedging that attempts to reduce the risk associated with limiting reproduction to one year (Wilbur and Rudolf 2006, Childs et al. 2010).

Threshold flowering size

Although I could not detect an influence of the weevil's presence on frequency of iteroparity, I did find that weevil attack rate impacted threshold flowering size. The reduction of threshold flowering size at sites with a high weevil attack rate confirms my hypothesis that weevils can reduce threshold flowering size. The size-dependent nature of the herbivory selects for a smaller flowering size since the weevils prefer larger plants (Prins et al. 1992). In the case of houndstongue populations at sites with a high weevil attack rate, the cost of waiting to reproduce outweighs the reduced fitness of producing fewer seeds sooner at a smaller flowering size. The reduction in flowering size associated with higher weevil attack rates, provides evidence for conservative bet-hedging, in which reduced reproductive delay prevents organisms from facing future risks (Childs et al. 2010). The illegal nature of the weevil biocontrol in the United States creates an unmonitored and non-uniform pattern of weevil dispersal. The difference in threshold flowering size between sites with low and high weevil attack rates suggest that not only weevil presence or absence, but also the level of weevil attack can impact the life histories of houndstongue.

Limitations

Due to the unmonitored movement of the biocontrol in the United States, I do not know how long weevils have occurred at the sites I surveyed. Additionally, for the six sites where I conducted two-year demographic surveys, I could not confirm weevil presence during the first year of surveying due to the timing of the survey, since weevils might already have exited the roots. Although I surveyed for weevils during the second year, sites that I categorized as having the weevil present might have not had weevils present the previous year. Knowing the length of time weevils have infested a site provides vital insight into how quickly life history can shift in response to weevil attack.

Additionally, the movement of the weevil has drastically reduced available study sites in the range of interest. Since houndstongue populations are challenging to locate without prior knowledge, I found most of the populations I surveyed through weed managers with local knowledge of potential survey sites. Many of the sites that had recently had robust populations had very few or no individuals remaining by the time I arrived. Both metapopulation dynamics and the introduction of the weevil in Canada could explain the disappearance of populations that I planned to survey. Given the difficulty of finding sites, my site selection was haphazard, potentially introducing selection bias to my sites. Also, access to sites posed unexpected challenges. I could not gain access to two of the sites I planned to resurvey from a previous study, which limited my ability to follow the fates of all of the sites in the introduced range surveyed previously.

While my evidence builds on previous studies about life history changes observed in the introduced range in response to enemy escape, climate, and biocontrol reintroduction, whether these changes are phenotypically plastic, and what the underlying genetic contributions or adaptive functions are, are unknown. To date, a study established a genetic basis to the plasticity of threshold flowering size, indicating both genetic and environmental contributions to observed threshold size (Wesselingh and de Jong 1995, Williams and Fishman 2014). A study comparing neutral genetic markers across the invasive and native ranges of houndstongue established a loss of genetic diversity in the introduced range, and at least two different source populations for North America (Williams and Fishman 2014). In addition to the spatial structure documented for the region where I conducted surveys, common garden experiments comparing the native and introduce range have also provided evidence for founder effects in the introduced range (Williams et al. 2008). For my study, founder effects and the loss of genetic diversity that

occurred with the introduction of houndstongue to North America might shape some of the patterns I observed depending on the genetic variation of the source populations. Additionally, since a genetic basis for iteroparity has not yet been established, non-adaptive phenotypic plasticity might explain some of the patterns I observed.

Implications and Conclusions

Understanding how *C. officinale's* reproductive life history shifts in response to its environment, and its reunion with its weevil specialist, has implications for future management strategies and contributes to knowledge about intraspecific life history shifts. The higher frequency of iteroparity that I found across the introduced range can contribute to the invasiveness of houndstongue by extending the life of the seed bank through multiple years of flowering. Weed management programs could target plants with the capacity to flower multiple years in a row by hand-pulling any plants with side rosettes to eliminate the possibility of survival and seed dispersal in future years of iteroparous reproduction. The relationship between precipitation and iteroparity also can inform weed management programs. For populations in regions with wetter winters, weed managers should pay extra attention to detecting and eliminating plants with side rosettes that indicate the capacity for iteroparity. The specialist weevil's impact on threshold flowering size has positive implications for houndstongue management. Plants that flower at a smaller size have reduced fecundity and seed production. The natural dispersal of the biocontrol agent will likely continue to reduce flowering size in the introduced range when the weevil reaches higher densities in a houndstongue population.

Additionally, more invasive organisms, which formerly "escaped" their predators, are facing predator "reunification" with the increasing use of biocontrols. Just as invasive species can rapidly evolve in the absence of specialists, rapid evolution can also happen in response to

the introduction of a specialist as a biocontrol (Stastny and Sargent 2017). So far, houndstongue has not exhibited the development of any resistance to the specialist biocontrols introduced in Canada. However in the native range, houndstongue populations persist despite weevil presence, indicating that it is possible for houndstongue and its specialist to coexist. This does not necessarily mean that the biocontrol will become ineffective. However, in the United States where weevils randomly disperse at low-levels, weed management programs should monitor how quickly small weevil populations can reach outbreak levels and how long houndstongue populations can tolerate lower weevil attack rates. If the biocontrol agent receives approval in the United States, targeting priority populations with at least 100 weevils released, the smallest release size so far documented to be effective, can reduce the risk associated with houndstongue developing tolerance to low-level weevil presence (De Clerck-Floate and Wikeem 2009).

My findings also contribute to the growing body of knowledge about intraspecific life history variation, highlighting that life histories can vary substantially within species, making cross-taxa comparisons challenging. The variation I observed within the introduced range of houndstongue thus underscores the importance of surveying extensively throughout a species range or ranges, especially for species with flexible life histories. Investigating how life histories shift in response to a "reunification" between specialists from the native range of invasive plants and invasive plants in their introduced range provides further insight into the ways herbivory and evolution interact. As invasive species expand their ranges and encounter changes within their existing ranges, such as the introduction of biocontrols or changing climate conditions, how species respond to these changes provide vital information about the potential for adaptive evolution to shift life history strategies.

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Appendices

Appendix A

Sites included in 2018 flowering surveys. Demographic monitoring in 2017 and 2018 took place at bolded sites. Italicized sites were sites surveyed in a previous study of houndstongue in 2004-2005. Plant No. indicates how many plants were sampled. Average precipitation (avg. ppt), average winter precipitation (avg. wt. ppt), and average annual temperature (avg. temp.) data are the 1981-2010 normals (Climate WNA). The winter precipitation data (wt. ppt. 2017) includes December 2016, January 2017, and February 2017.

Site	County, State	Plant No.	Weevil	Wt. Ppt. 2017 (mm)	Avg Wt. Ppt .(mm).	Avg. Temp. (C°)	Avg. Ppt. (mm)
1	**Okanogan County, WA**	**79**	**Yes**	**188**	**178**	**4.8**	**568**
2	**Okanogan County, WA**	**58**	**Yes**	**143**	**132**	**6.7**	**427**
3	Okanogan County, WA	72	Yes	199	157	5	503
4	**Okanogan County, WA**	**25**	**Yes**	**192**	**167**	**4.8**	**537**
5	Flathead County, MT	100	Yes	214	150	5.7	622
6	**Stevens County, WA**	**99**	**Yes**	**251**	**157**	**8.1**	**498**
7	Okanogan County, WA	100	Yes	143	98	8	335
8	Stevens County, WA	99	Yes	276	171	7.4	531
9	Bonner County, ID	63	Yes	361	270	7.7	816
10	Missoula County, MT	98	No	194	131	6.2	512
11	Missoula County, MT	96	Yes	319	221	5.6	759
12	Missoula County, MT	99	No	176	122	6.5	502
13	*Missoula County, MT*	108	No	163	106	5.7	422
14	Missoula County, MT	80	Yes	144	97	6.6	447
15	Missoula County, MT	69	Yes	180	115	5.8	461
16	*Missoula County, MT*	26	No	213	132	5.1	578
17	**Yakima County, WA**	**104**	**Yes**	**213**	**165**	**8**	**417**
18	Latah County, ID	94	No	371	303	7.2	833
19	**Yakima County, WA**	**112**	**No**	**145**	**114**	**10.2**	**256**
20	*Sweet Grass County, MT*	62	No	64	36	4.9	445
21	Park County, MT	66	No	111	67	4.7	507
22	*Sweet Grass County, MT*	37	No	73	37	8.2	389
23	Gallatin County, MT	96	No	113	81	3.1	501
24	Beaverhead County, MT	33	No	130	94	2.4	468

Appendix B

Explanatory variables for a generalized linear model of how the proportion of iteroparity at each site responded to weather, climate, and herbivory, ranked by AIC. I only added weevil presence to the top 5 climate and weather models. The data for the normals are the 1981-2010 normals (Climate WNA).

Proportion of iteroparity ~	AIC	Δ AIC	Rank
Weevil + 2017 winter precipitation	275.8	0	1
Weevil + 2017 mean annual precipitation	279.8	4	2
Weevil + mean annual precipitation normals	284.1	8.3	3
Weevil + winter precipitation normals	284.2	8.4	4
Weevil + spring precipitation normals	284.5	8.7	5
2017 winter precipitation	288.7	12.9	6
2017 mean annual precipitation	289.4	13.6	7
Mean annual precipitation normals	291.4	15.6	8
Spring precipitation normals	291.43	15.63	9
Winter precipitation normals	294	18.2	10
2017 summer precipitation	294.9	19.1	11
Summer temperature normals	297.9	22.1	12
Mean annual temperature normals	299.3	23.5	13
2017 spring precipitation	299.9	24.1	14
Longitude	299.9	24.1	15
Latitude	300	24.2	16
2017 summer temperature	300.5	24.7	17
Elevation	300.79	24.99	18
Summer precipitation normals	300.8	25	19
Weevil	302.6	26.8	20
2017 autumn precipitation	302.9	27.1	21
2017 winter temperature	304.2	28.4	22
Null	305.7	29.9	23