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Potential effects of short-term climate variation on shrubs, grasshoppers and lizards in the northern Great Basin desert scrub

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Potential effects of short-term climate variation on shrubs, grasshoppers and lizards

in the northern Great Basin desert scrub

By
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Accepted in Partial Completion
Of the Requirements for the Degree
Master of Science

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MASTER'S THESIS

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Phillip J. Dugger
May 24, 2012

Potential effects of short-term climate variation on shrubs, grasshoppers and lizards in the northern Great Basin desert scrub

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Phillip J. Dugger
May 2012

Abstract

Analyzing trophic interactions among organisms may refine our ability to predict the impacts of climate change on organismal communities in an ecosystem or biome. The Great Basin desert scrub biome comprises relatively simple biotic communities in which bottom-up trophic processes should be comparatively easy to document, analyze and understand. Observing 1) the direct effects of abiotic factors (precipitation and temperature) on desert primary producers, primary consumers, and secondary consumers and 2) the indirect effects of abiotic factors on desert community members—as mediated by biotic effects—should enhance our understanding of community trophic dynamics and may improve the accuracy of biotic predictions for desert communities facing climate changes.

Because the two ecologically dominant Great Basin shrub species, *Artemisia tridentata* and *Sarcobatus vermiculatus*, differ in root depth distributions and leaf morphology, I expected that differences in short-term responses to summer rainfall by these species may result in species-specific effects on higher trophic levels. To test the hypothesis that rain affects these perennial plants differently, I measured the short-term effects of simulated summer rain pulses (periodic watering over 18 d) on water content, nitrogen concentration, and carbon concentration in leaves of these two species. To study the climate-related consequences for representative and abundant primary consumers of these shrubs, I tested the hypothesis that year-to-year variation in grasshopper populations correlates with year-to-year variation in precipitation and temperatures. I analyzed the distribution and abundance of grasshoppers on and near these shrubs using data collected from a single Alvord Basin site over seven summers with respect to 1) seasonal and annual patterns of temperature and precipitation, and 2) predictions of among-summer variation

in water content of foliage of *A. tridentata* and *S. vermiculatus*. I also examined the consequences for body condition of secondary consumers—males of the long-nosed leopard lizard, *Gambelia wislizenii*—with respect to variation among years in weather and grasshopper abundance.

Using pre-treatment water content of leaves of *A. tridentata* as a covariate, I found a significant, direct effect of the watering treatment on water content of *A. tridentata* leaves; there was no apparent effect of watering on *S. vermiculatus* leaves. Analyses of leaf water content, nitrogen concentration, and carbon concentration revealed differences between *A. tridentata* and *S. vermiculatus* in rates of decline in leaf nutrient quality with the descent into the summer dry season. Insufficient data from single-factor analyses allowed weak inferences only about the effects of May weather on grasshopper abundance, but data were sufficient to infer that extremely low winter temperatures may directly reduce grasshopper abundance. Arthropod prey abundance, in turn, had a positive, direct effect on *Gambelia wislizenii* body condition; thus, bottom-up effects potentially extend to multiple higher trophic levels. Body condition of *G. wislizenii*, however, was inversely correlated with air temperatures in May, a result of either a direct effect on lizard physiology or indirect effect via plant quality and grasshopper numbers and sizes. Spearman rank correlation analysis revealed that grasshopper abundance was the best predictor of *G. wislizenii* body condition ($r_s = 0.901$), but abiotic variables (i.e., winter and spring weather) were also strong predictors ($r_s = 0.890$), thus illustrating the importance of considering multiple abiotic and biotic variables when predicting year-to-year differences in lizard fitness.

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Introduction

Empirical studies of the effects of climate change at the ecological community scale have documented changes in species distributions, ecological processes, and plant and animal phenology (Baker and Moseley 2007, Beaubien and Freeland 2000, Both et al. 2006, Westerling et al. 2006). Models of the impacts of global climate change at the community scale predict further changes in species composition and richness (e.g., Lawler et al. 2009, Wiens et al. 2009). Wiens and Bachelet (2010) suggest incorporating climate change models into conservation efforts while aligning the spatiotemporal scales of climate change predictions with the scales of conservation. Investigations of the direct impacts of local climate conditions on primary producers, concurrent with studies of interactions among primary producers, primary consumers and higher trophic levels, should increase the accuracy of predictions of climate change effects on community-scale structure and dynamics. Moreover, refining our understanding of biotic and abiotic influences on organismal fitness may improve our ability to understand and address local ecological community dynamics in the context of global and regional climate change (Martin 2001, Post et al. 2009).

The relative importance of biotic versus abiotic influences on community interactions depends in part on the interspecific dynamics of the system (Nowicki et al. 2009, Wolkovich et al. 2009). But the complexity of population dynamics, time lags in environmental impacts on populations, and variation among individuals of a species in the demographic responses to environmental influences can complicate ecological models (Benton et al. 2006). Thus, there is a need for empirical studies of specific communities to provide data that reinforce and refine predictive

models of climate change effects on biota (Benton et al. 2006). My thesis research was designed to contribute perspective on the effects of climate change on interactions among organisms and populations across trophic levels in a single community.

Top-down versus bottom-up trophic interactions

Biotic and abiotic factors may influence organismal population dynamics through top-down and bottom-up effects in the trophic chain, among predator (top), primary consumer (middle) and plant (bottom) levels (Boyer et al. 2003, Halaj and Wise 2001, Schmitz et al. 2000, Vucetich and Peterson 2004). Depending on the organismal components and habitat structure of an ecological community, biotic and abiotic influences may have differing impacts on a particular population. For example, the resource quality and quantity as represented by primary producers or primary consumers can affect organisms at two or more higher trophic levels through direct and indirect (effects on one trophic level, which in turn affect another) effects (e.g., Bukovinszky et al. 2008, Chen and Wise 1999). These effects of individuals of lower trophic levels on individuals of higher trophic levels are known as bottom-up effects (Figure 1), and may result in complex ecological consequences. For example, bottom-up effects of one trophic level upon the closest-linked higher trophic level may transduce into effects on yet higher trophic levels (Chen and Wise 1999) and may indirectly influence competition among species (Fromentin and Planque 1996). Conversely, individuals at higher trophic levels can directly or indirectly influence community structure at two or more lower trophic levels through consumption; this influence is known as a top-down effect (e.g., Ainley et al. 2006, Borer et al. 2006).

Because productivity in desert ecosystems is highly limited by the availability of water, deserts are excellent settings for investigations of bottom-up (primary producer) regulation. Top-down effects of predation may also play a role in desert ecosystems; however, predator-forcing has been more difficult to document in terrestrial systems, in part because top predators are sparse in many terrestrial systems, but also because in more xeric systems, bottom-up effects are more apparent (Gruner et al. 2008, Shurin et al. 2010). Consequently, this thesis focuses on bottom-up trophic interactions as the primary driver of community dynamics.

In a xeric community, precipitation (Figure 1a) and temperature (Figure 1b) are expected to have strong effects on all trophic levels. Precipitation, for example, is expected to have a direct positive resource effect on primary producers (Figure 1c, i.e., Evans and Black 1993). Greater precipitation also is expected to have a direct positive effect on primary, secondary, and tertiary consumers (Figure 1 d, e) as more consumable water (i.e., Ivans et al. 2003) or as snow insulation in winter (i.e., Riegert 1967). Greater precipitation, however, may also have a direct or indirect negative effect (via suffocation or fungal growth, i.e., Stauffer and Whitman 2007, Tracy 1980) on primary, secondary, and tertiary consumers (Figure 1 d, e). Higher temperature (Figure 1b) is expected either to have a direct positive (extended growing season and less cold stress) or direct negative effect (desiccation and photorespiration in summer) on primary producers (Figure 1c). Depending on when they occur, higher temperatures also may have either a direct positive effect (extended period of activity and increased rate of food processing) or a direct negative effect (via heat stress and desiccation, i.e., Stauffer and Whitman 2007, Tracy 1980) on consumers.

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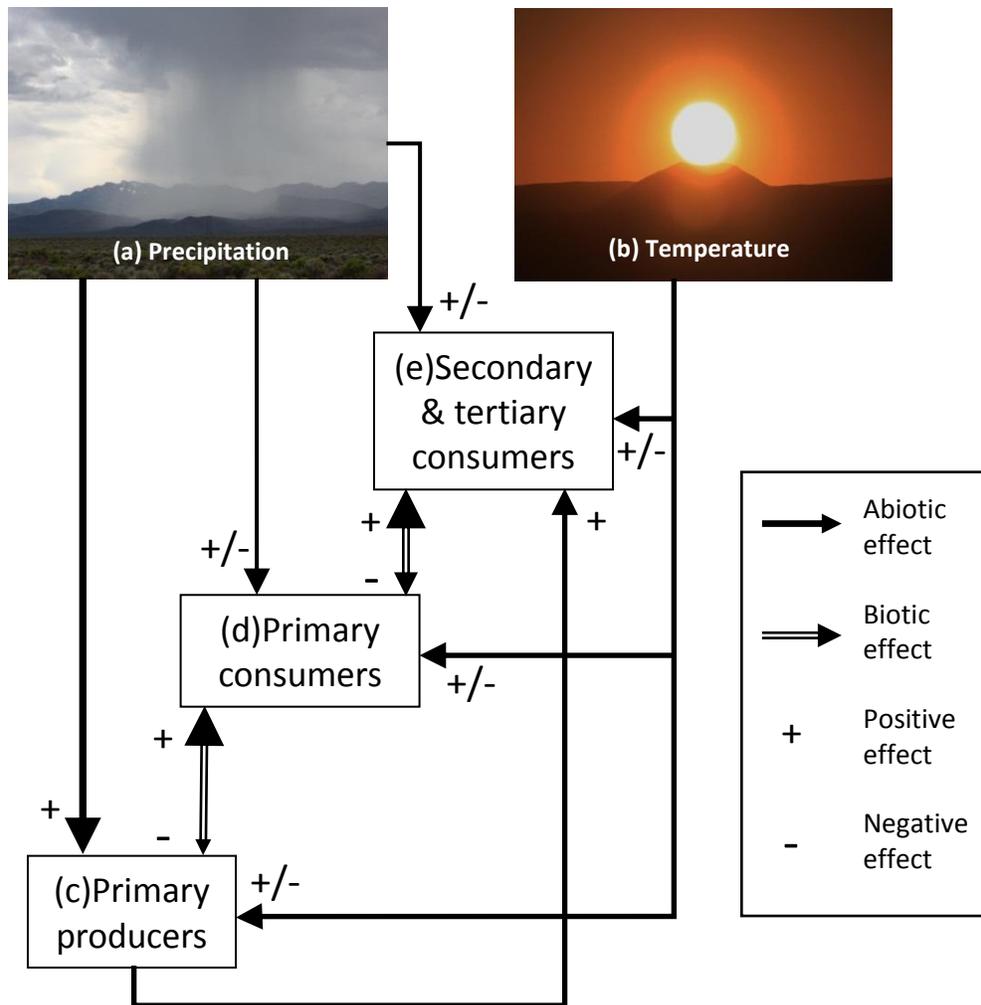
Figure 1. Flowchart of expected abiotic and biotic influences on each trophic level in xeric communities. Arrow sizes indicate the presumed strength of the effects. Note that increase in some abiotic factors may have both positive and negative (+/-) effects on organisms. See text for information on specific direct and indirect interactions.

The direct effects of precipitation and temperatures on primary producers transduce into bottom-up, direct effects of primary producers on primary consumers and the higher trophic levels. For example, increasing precipitation and temperatures are expected to have indirect positive effects on primary consumers by improving host plant leaf quality and quantity (Figure 1 c, d, i.e., Branson 2004, Gruner et al. 2008). Primary producers also may provide shade and shelter to consumers, an abiotic effect (Figure 1, c, d, e). The indirect effects of weather on primary consumers are expected to transduce into positive effects on higher level consumers (Figure 1 d, e, i.e., Steffen 2002). Hence, the biotically-mediated effects of precipitation and temperature on primary consumers are expected to be stronger than top-down biotic effects (i.e., Gruner et al. 2008, Shurin et al. 2010).

Climate change predictions have implications for bottom-up processes in desert scrub communities

Climate change models have predicted enhanced global precipitation extremes, such as elevated rainfall at warmer temperatures and diminished rainfall at cooler temperatures (Chou et al. 2007, Emory and Brown 2005, Meehl et al. 2005, Neelin et al. 2006, Seager et al. 2007). Regional climate change studies (e.g., Field et al. 1999, Gutowski et al. 2000) predicted warmer and wetter winters, warmer summers, and an enhanced El Niño Southern Oscillation (ENSO) in the western United States. Seager et al. (2007) predicted a more arid southwestern United States (an area including much of the Great Basin desert scrub biome) as a result of climate change. Greater precipitation and warmer temperatures in the winter may induce higher vegetation productivity in California shrublands. For example, in California deserts, wetter winters and warmer and

persistently drier summer months may lead to enhanced biomass of grasslands and consequential increases in fire, leading to a relative increase of grasses over trees (Lenihan et al. 2003).

Deserts are subjected to extremes of high temperature, low humidity, high winds, and saline soils (Sumner 1925). As a relatively cool desert scrub, the Great Basin has long, cold winters and cool spring and autumn seasons. Summers can be hot, however, and the Great Basin is highly moisture limited throughout the year (Comstock and Ehleringer 1992, Houghton 1979). The strong effects of climate on desert ecosystems and the simplicity of desert communities provide opportunities to study the direct and indirect effects of climate variation on multiple trophic levels, not just plants. Desert scrub ecosystems contain relatively simple communities (Noy-Meir 1974, Polis 1991) and thus may be more propitious for trophic studies than the more complex Sonoran and Chihuahuan desert scrub communities to the south. Thus, a biotic community in the northernmost Great Basin desert scrub biome can be used as a model for the study of climate variation on bottom-up community processes.

Studying species at their geographic extremes can lend useful information about their ecological constraints (i.e., Addo-Bediako et al. 2000, Gaston and Chown 1999). The Alvord Basin of southeastern Oregon is at the northern extreme of the Great Basin desert scrub biome—many species in the Alvord Basin are at or near their northern geographic limits. Thus, the Alvord Basin may be a valuable locale for studying the impacts of local climate change on the ecological communities. The effects of climate variation on the Alvord Basin desert scrub community may illuminate processes that affect the distribution of these species (i.e., Jacobsen 2008).

Organismal characteristics and trophic relationships of Alvord Basin denizens

Primary producers

Artemisia tridentata (basin big sage) and *Sarcobatus vermiculatus* (greasewood) are the two most prevalent perennial plants in both size and number not only across much of the Alvord Basin, but also in many communities in the northern Great Basin desert scrub (i.e., Romo and Haferkamp 1989). *Sarcobatus vermiculatus* is cold deciduous, with leaves lasting from early spring through early autumn, whereas *A. tridentata* is an evergreen that episodically sheds all leaves in response to summer drought (Evans et al. 1991, Kolb and Sperry 1999, Romo and Haferkamp 1989). Although leaves of both species are small, the leaves are distinctly different: *A. tridentata* leaves are tender, flat, slim triangles averaging 1.3 cm in length (Barker and McKell 1986), whereas *S. vermiculatus* leaves are succulent, tapered cylinders of 0.5 – 3.0 cm in length (Robertson 1983). Shrubs with succulent leaves are likely to use a storage and defense strategy to cope with water stress, rather than new growth (Díaz and Cabido 1997). These two species also differ markedly in root growth form. *Artemisia tridentata* has a widely spread, near-surface array of roots that can channel and absorb surface and near-surface water; thus, *A. tridentata* may be able to quickly use rain showers to relieve water stress (Ryel et al. 2004). In contrast, *S. vermiculatus* has fewer surface roots and a long tap root that extends deeper into the soil, and is able to use deep sub-surface moisture (perhaps even tapping the water table in some locales). Moreover, the deeper roots of *S. vermiculatus* avoid the high salinity of the near-surface soil (Donovan et al. 1996). Thus, whereas recent precipitation events are the primary source of the near-surface soil moisture used by *A. tridentata*, *S. vermiculatus* relies on the more predictable, longer-term source of soil moisture deeper in the ground (Romo and Haferkamp

1989). Not surprisingly, *S. vermiculatus* are much more abundant than *A. tridentata* on the saline, hardpan surfaces lower in the basin (Rose 2003).

Based on the differences in modes of coping with water limitation between *A. tridentata* and *S. vermiculatus*, I hypothesized that the comparative nutritional quality of the two species would be affected differently by summer precipitation. Field experiments by Fetcher and Trlica (1980) found that *A. tridentata* and other shallow-rooted desert shrubs were more likely to exhibit a short-term growth response to light spring rains than more deeply-rooted shrub species. Moreover, year-to-year differences in spring and summer precipitation may affect the timing of *A. tridentata* leaf water content decline in the summer (Evans and Black 1993). Greater moisture uptake may have positive effects on nutrient content of the plant leaves as well. Naturally-occurring and simulated summer rain pulses in Rush Valley in west-central Utah increased soil nitrogen uptake and diffusion in roots of *A. tridentata* with small amounts of rain in the driest part of the summer (Ivans et al. 2003). However, the study did not investigate subsequent changes in foliar nitrogen content; thus, my study investigates the nutritional consequences of short-term rainfall for leaves and for herbivores that feed on leaves of *A. tridentata*.

Primary consumers

Grasshoppers are conspicuous herbivores of Great Basin desert scrub and shrub steppe communities, and may exert a strong influence on desert vegetation (Sheldon and Rogers 1978). As prey for higher trophic levels, grasshoppers may be an important trophic link within the Alvord Basin desert scrub community. Grasshoppers comprise an important food resource for the long-nosed leopard lizard *Gambelia wislizenii*, the abundant, dominant, ectothermic mesopredator in the northern Great Basin (Parker and Pianka 1976). In northern communities of

the intermountain west, grasshoppers are the most numerically and volumetrically important prey in *G. wislizenii* diets, with more than double the volume of the next most important prey eaten (Parker and Pianka 1976, Steffen 2002, Whitaker and Maser 1981). In a study of arthropod body parts found in fecal pellets of *G. wislizenii* from early June through early August of 2000 in the Alvord Basin, orthopterans (almost entirely grasshoppers) comprised 96% of total arthropod volume (Steffen 2002).

Trimerotropis pallidipennis (pallid-winged grasshopper) and *Cordillacris occipitalis* (spotted winged grasshopper) are two common species in the Great Basin (and in the Alvord Basin, R.A. Anderson, personal communication) with economic and ecologically important effects (USDA Agricultural Research Service website 2011). They are both polyphagous, feeding on a variety of plant species from different functional groups, such as forbs, grasses, shrubs (Otte and Joern 1976, USDA Agricultural Research Service 2011). In the northern latitudes, grasshopper oviposition occurs in mid-summer through fall; the eggs overwinter, and then hatch in late April to mid-June; nymphs develop through 5 instars in early-to-mid summer (Figure 2, USDA Agricultural Research Service 2011). Hence their peak availability to predators is in early-to-mid July, when the adult grasshoppers are typically out in the open seeking mates; during that time, males make short flights and conspicuous cracking sounds to attract females (USDA Agricultural Research Service 2011).
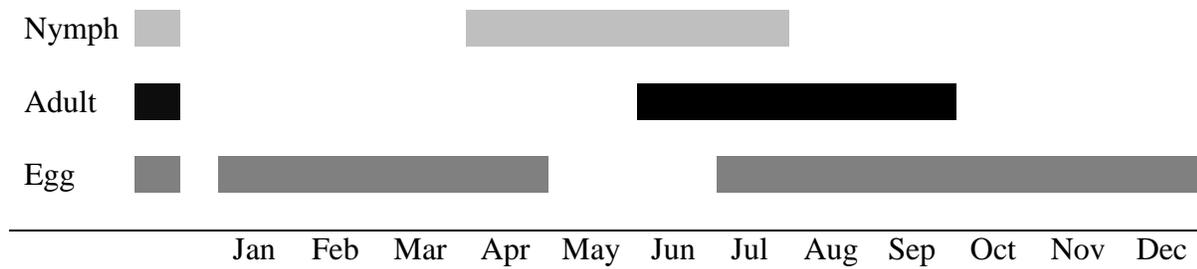
Figure 2. Typical expected life history of the common grasshoppers in the Alvord Basin. Timing of nymphal phases, adults, and eggs were estimated based on phenological descriptions of *Trimerotropis pallidipennis* and *Cordillacris occipitalis* in the USDA grasshopper identification guides (USDA Agricultural Research Service 2011).

Climate variation, via changes in precipitation and temperature patterns may affect leaf "quality" of desert shrubs; hence climate variation may have ecological implications for grasshoppers through bottom-up trophic effects. Desert grasshopper populations in Arizona increased after high early winter rainfall, which increased the abundance of spring vegetation (Nerny 1961). The effect on primary productivity presumably influences grasshopper abundance in the Great Basin, as in other ecological communities (e.g., Haddad et al. 2001, Pfisterer et al. 2003, de Wysiecki et al. 2000). The spring flush of annual forbs and grasses, for example, may be a strong influence on grasshopper populations, as grasshopper growth and survival depends on abundant, high quality nutrition at the nymphal stage (Branson 2004). However, reproductive output of common grasshoppers in the Great Basin is not affected by the nutrition availability for nymphs, but depends more on resource availability for adults (Branson 2004). Thus, summer food availability and quality may have a direct impact on grasshopper abundance in the following year. *Trimerotropis pallidipennis* feeds primarily on annual grasses when they are available but switches to perennial plants when annuals are absent (Otte and Joern 1976). By mid-June, annual grasses of the Alvord Basin have mostly browned or died back (unpublished field observations from Anderson 2003-2009). Similar late-spring die-offs are typical for *Bromus* (cheatgrass) and *Elymus* (native bunchgrass) species in northern Utah (Booth et al. 2003, Klemmedson and Smith 1964). Therefore, changes in climate that affect summer precipitation are most likely to impact grasshoppers via their effects on perennial shrubs.

Abiotic effects of precipitation on plants may transduce into biotic effects of host plant leaf quality on grasshoppers. Effects of nitrogen concentration (Johnson and Lincoln 1990, Redak and Capinera 1994, Ritchie 2000), digestibility (Redak and Capinera 1994), carbon

concentration, and allelochemical concentration (Johnson and Lincoln 1990) of food plant

foliage on growth and survival of grasshoppers have been observed in other communities

(Ritchie 2000), and have been corroborated through field experiments (Johnson and Lincoln

1990, Redak and Capinera 1994). Slight increases in leaf nitrogen concentration in *Artemisia*

tridentata can enhance the growth rate of grasshoppers (Johnson and Lincoln 1990), and

grasshopper growth efficiency (the conversion of digestible food to grasshopper biomass) can be

increased by nutrient enrichment of soil around roots of *A. tridentata* (Johnson and Lincoln

1991). Grasshopper growth efficiency also covaries directly with *A. tridentata* leaf water content

(Johnson and Lincoln 1991). Thus, it is likely that changes in precipitation regimes could

influence the growth rates of grasshoppers feeding on *Artemisia tridentata*.

Secondary consumers

Year-to-year variability in grasshopper abundance in the Alvord Basin may affect year-to-year

variability in body condition and population structure (i.e., proxies for fitness) of *Gambelia*

wislizenii. Population densities of Chihuahuan Desert lizards are directly correlated with the

relative abundance and productivity of arthropod species (Whitford and Creusere 1977). In the

Sonoran desert scrub, the foraging patterns of the western whiptail lizard, *Aspidoscelis tigris*

(also a denizen of the Alvord Basin) correlated with arthropod distribution and abundance, and

lizard population densities also correlated positively with year-to-year variation in rainfall and

plant productivity (Anderson 1994). Thus, it is expected that 1) the population density of

grasshoppers in the Alvord Basin is directly related to the amount of energy transferred from

primary producers (plants) to the grasshoppers, and 2) there are commensurate consequences for

G. wislizenii (Figure 1).

Primary questions

My thesis research aimed to clarify how changes in local weather patterns (i.e., short-term variation in climate) may affect the trophic-dynamic system (perennial plants to grasshoppers to lizards) in the northern desert scrub community. I hypothesize that environmental factors such as precipitation and temperature are likely to affect the availability and efficiency of energy and nutrients transferred from plants to grasshopper populations, and that grasshopper population fluctuations will similarly affect the body condition and population structure of *Gambelia wislizenii*.

To test for effects of summer rain pulses on desert shrub leaf quality, and to determine the potential weather influences on grasshopper populations and *G. wislizenii* body condition, I designed field experiments and statistical analyses to address the following primary questions:

Question 1*: What are the effects of simulated summer rain pulses on *Artemisia tridentata* and *Sarcobatus vermiculatus* leaf condition?

I designed a field experiment in the Alvord Basin study site to test the hypothesis that simulated summer rain showers would affect leaf quality of *Artemisia tridentata* and *Sarcobatus vermiculatus* as measured by water, nitrogen, and carbon content.

Question 2: Is grasshopper abundance correlated with short term climatic variation?

To test the hypothesis that year-to-year weather patterns correlate with year-to-year grasshopper populations, I analyzed data on grasshopper abundance collected by students in Roger

Anderson's summer field course (WWU, Biol 408 & 409) from 2003 to 2009 to determine what climatic factors potentially influence year-to-year differences in local grasshopper abundance and microhabitat preference.

Question 3: Are year-to-year changes in male *Gambelia wislizenii* body condition correlated with year-to-year changes in grasshopper abundance?

To test the hypothesis that *Gambelia wislizenii* body condition in mid-summer is directly related to year-to-year grasshopper abundance, I analyzed data on grasshopper abundance and the ratio of body mass to snout-vent length (SVL)—i.e., body condition—of male *G. wislizenii* collected by students in Dr. Roger Anderson's summer field course from 2003-2009.

Question 4: Can we use currently available information to form a predictive model of *Gambelia wislizenii* body condition?

I hypothesized that any one or a combination of abiotic or biotic factors—including precipitation, temperature, *Gambelia wislizenii* abundance, and grasshopper abundance—may be used to accurately predict male *G. wislizenii* body condition in the same year. To test this hypothesis, I analyzed the relationship between ranks of these predictive variables (individually ranked variables and different combinations of summed ranks) and ranks of *G. wislizenii* body condition from 2003-2009.

Methods

Study site

The study site is located near the southern end of the NNE trending Alvord Basin of southeastern Oregon in Harney County, approximately 5 km north-northeast of the unincorporated community of Fields, and south of Steens Mountain, at +42° 17' latitude and -118° 37' longitude. The Alvord Basin forms part of the northern boundary of the Great Basin. The Alvord Basin is geologically characterized as a graben, a depressed area of land bordered by parallel, uplifted faults (Whipple and Oldow 2004). The Alvord Basin is in a classic rain shadow east of the Steens Massif (the uplifted fault to the west and north) and NNE of the Pueblo Mountains. Mean annual precipitation from 2003-2009 in the basin was 14 cm (NOAA WRCC 2011). Most of the precipitation happens in late fall through spring, with proportionally very little rainfall in the summer (NOAA WRCC 2011). Winter precipitation consists mostly of snow, and winter snowmelt is likely to be a major source of annual input of moisture into the soil. Precipitation is typically lowest in July and August; occasional late summer and early autumn rains (September and October) may contribute significantly to water availability during the active season of perennial plants in the Alvord Basin.

The study site is restricted to light winter range use for cattle by the Bureau of Land Management because it is designated as "mixed fair and poor" range condition (BLM website), and is characterized by Great Basin desert scrub habitat dominated primarily by two perennial shrub species, *Artemisia tridentata* (big sage) and *Sarcobatus vermiculatus* (greasewood). Other

common perennial shrubs are *Atriplex confertifolia* (shadscale saltbrush), *Ericameria nauseosa* (grey rabbitbrush) and *Ericameria viscidiflora* (green rabbitbrush) (BLM website).

Question 1*:* What are the effects of simulated summer rain pulses on *Artemisia tridentata* and *Sarcobatus vermiculatus* leaf condition?

To test the effect of simulated summer rainfall on tissue quality of plant leaves, I designed an experiment to analyze the difference over time in water content, nitrogen concentration (percent by dry mass), and carbon concentration (percent by dry mass) between *Artemisia tridentata* and *Sarcobatus vermiculatus* plants in unwatered "control" plots and in artificially watered plots. I haphazardly chose 24 *A. tridentata* and 24 *S. vermiculatus* shrubs in an approximately 20 m x 100 m area located about 100 m south of the southernmost grasshopper survey plot at Dr. Roger Anderson's field course study site (WWU, Biol 408 & 409). Like the field course site, the plots were arrayed over a mix of hard pan, sandy flats, and shallow dunes, and contained a mixed stand of *A. tridentata* and *S. vermiculatus* of average size (approximately 0.5 to 1.5 m in canopy diameter).

Each shrub was to be the center of a plot of 1m radius that I randomly assigned to different watering treatments. I chose this radius after examining roots in the shallow subsoil and observing that most of the small, water-absorbing root mass at the surface was likely within a 1 m radius of the plant center for a shrub with 1 m canopy diameter. I chose shrubs that were of average size, about 1 m ($\pm$ 0.2 m) in diameter, and which were typically at least 1 m (perimeter-to-perimeter) to the nearest shrub of 0.25 m canopy diameter or larger. The chosen shrubs had to have enough young foliage to permit the collection of about 6 leaf samples, each of which would mostly fill 25 ml scintillation vials and would be about 20 mg of wet mass. I randomly assigned

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12 plots for each plant species to a watered treatment (the experimentals) and 12 plots per species to the unwatered treatment (the comparators). One of the *S. vermiculatus* plants in the watered treatment missed a watering episode, so I discontinued watering it, did not collect any more samples from it after the initial (pre-watering) sample, and excluded it from all analyses.

Watering calculations

The watered treatment was designed to mimic the effects of realistic, but greater-than-usual summer rain showers. Using weather data from the Fields, OR weather station from 1973-2009 and a probability of precipitation calculator on the Western Regional Climate Center website, I found that the probability of a total amount of 1.27 cm of precipitation over a period of 30 days in Fields, OR from late June through late July ranges from 5% to 20%, with the nadir of 5% occurring for the 30 day period centered on July 15 (Figure 3). Therefore, 1.27 cm in 30 days represents a relatively wet summer. As supporting evidence for this estimate, during the last 15 years of monthly rainfall totals in June and July for the Fields, OR weather station, 1.27 cm of rain in 30 days would rank second-highest among all 15 years for either June or July (Western Regional Climate Center historical data summaries). To account for additional evaporation that would likely occur in sunny weather (as opposed to cloudy weather that usually accompanies natural rainfall) and possible runoff, I increased the total simulated rain amount among the four watering periods from 1.27 cm to 1.8 cm. To achieve this amount of total simulated rainfall over the entire experimental period, each 1 m circular plot that was assigned the watered treatment was watered five times with 11.4 L (totaling 57 liters per plot), equivalent to five 0.36 cm rainfall events. Water for the experiment was taken from a well at Fields Station, Fields, OR.
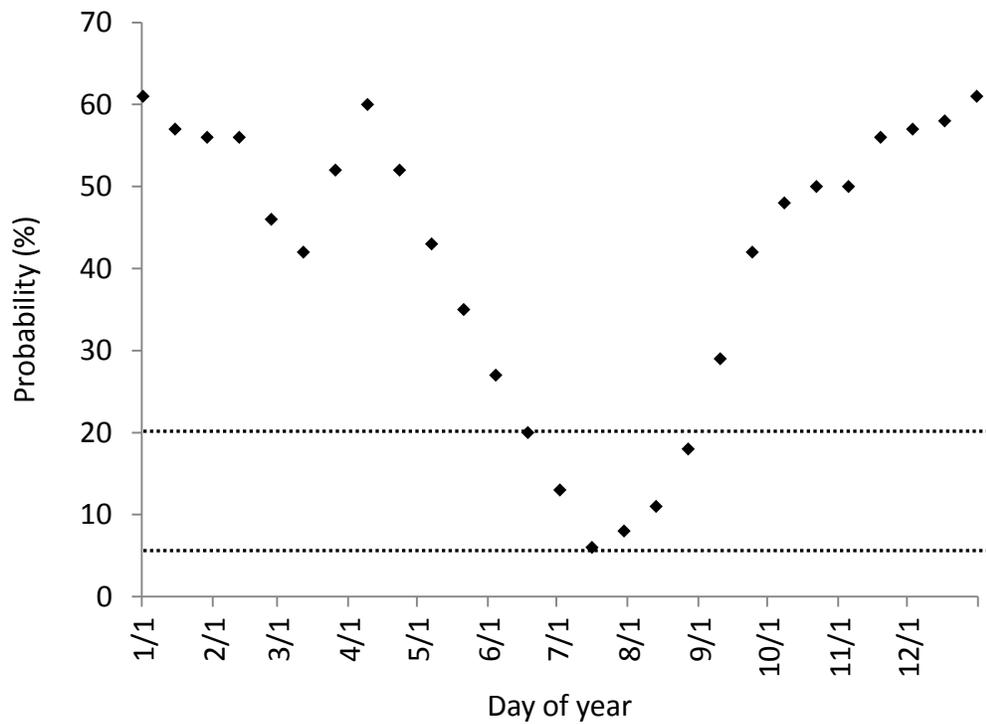
Figure 3. Probability of 1.27 cm (0.5") precipitation for a duration of 30 days (15 days on either side of the date), using historical precipitation data from the Fields, OR weather station (NOAA WRCC website). Dotted lines demarcate the range of probabilities during the annual field research season from late June through early July.

To coincide with the timing of Roger Anderson's field course, during which I had several undergraduate student volunteers to help with watering, I compressed my watering treatments to every four days in a 17-day time period: the first watering was administered on day 0 (June 28) and subsequent waterings were administered on days 4, 8, 12, and 16. Thus, the effective water level per day was raised by 76 percent, increasing the potential effect size while keeping the experiment representative of an ecologically plausible scenario.

Plants were given their assigned watering treatment every four days, beginning on the evening of June 28 and ending July 14. Watering began at about 1800 hrs on each day to allow enough daylight to apply the water correctly and to minimize evaporation of water from sunlit soil surface. To ensure consistency in watering treatments, student helpers were each individually trained to deliver water consistently within and among plots. 15 L watering canisters were used to apply an even spray, directly above the plot and the plants within the plot. Watering was done in 3.8 L increments to one-third of the plot at a time, to ensure even watering of 11.4 L over the whole (3.14 m^2) plot.

I collected leaf tissue samples from each plant in the experiment (watered and control) on the morning of June 27, the day before the first watering. I then collected samples again from each plant on the morning immediately following each watering. I began sampling at sunrise; sampling required from two to four hours. Due to the possibility that water and nutrient content of the leaves could be affected by the precise time of collection, I recorded the collection time of each sample to test if the specific time of collection had an effect on water or nutrient content. I also alternated the order in which I collected samples among days; for example, I first started

from the west side of the study area and worked my way east, then reversed the order of collection for the subsequent collection day.

I chose to collect leaf samples predominantly from what appeared to be younger leaves in the upper crown of the shrubs because 1) grasshoppers are known to feed selectively on more tender leaves on plants of better foliage condition (Gangwere 1961, Parker 1984), and 2) I observed grasshoppers feeding primarily on the upper crowns of plants. After clipping, samples were immediately packed into 25mL airtight scintillation vials. Typical samples contained approximately 100 leaves. No inflorescences were observed; therefore, assessing the nutritional value of inflorescences for grasshoppers was deemed unnecessary for this project.

Upon returning to camp, I performed an initial weighing of each vial with its contents using an Ohaus portable balance, accurate to the nearest 0.01g. The samples were placed on ice (to minimize leaf metabolism) until the vial and its contents were weighed. Samples were weighed as soon as possible after collection (field conditions, such as strong winds in the middle of the day, occasionally prevented immediate weighing of the samples). Immediately after weighing each sample, I poured a 90% denatured ethanol solution into the vial to completely immerse the leaves. Note that the original intention of the sample collection was to also allow for total nonstructural carbohydrates analysis, though time and resource constraints did not allow for that analysis. The denatured ethanol served to stop any enzyme activity that may diminish the amount of nonstructural carbohydrates in the leaf tissue (Donart 1969).

Upon return to Western Washington University, I opened the sample vials under a drying hood

to allow the alcohol to evaporate. Once the alcohol was mostly evaporated, I placed the vials

without lids in a 65°F drying oven for 72 hours. I then removed the vials from the drying oven,

placed the lids back on the vials, and weighed the vials and their contents. I then removed and set

aside the contents of the vials and weighed the empty vials. Most of the vials contained a yellow-

green residue after the alcohol that used to preserve the leaf samples had evaporated. Using a test

sample that I had collected in May 2008 using the same alcohol-preservation methods, I weighed

the vial containing residue, then cleaned the vial by dissolving and removing the residue, and re-

weighed the vial. I determined that the mass of the residue was well under 0.1 % of the mass of

the sample, which was well below the variability between samples of leaf tissue water content. I

then used the vial weights and total weights at the time of the sample collection to determine the

net wet mass and dry mass of each sample, which I used to calculate the percent water per total

wet mass of leaf tissue.

To test the effect of the watering treatments on tissue quality, I ground the leaf samples into a

fine powder in a Cyclotec grinder (Tecator Instruments, Saskatoon, SK, Canada). I analyzed

samples for nitrogen concentration and carbon concentration using an Elantech EA Elemental

Analyzer (CE Elantech Inc., Lakewood, NJ). I ran samples in the predetermined sequence of 48

samples at a time, 12 samples for each treatment-by-species combination. Because preliminary

assessment of the data indicated that the plants selected for watering were higher in mean initial

water content than the control plants, I used SPSS to run two-factor repeated-measures ANOVAs

for each factor with plant species and watering treatment as independent factors, using pre-

treatment water content as a covariate. Because the water content for treatment and control plants

converged throughout the study period (see Results), a treatment effect may have been masked by the initial difference in mean water content.

Testing the effects of alcohol preservation methods

Because the leaf tissue samples were preserved in 90% denatured ethanol prior to analysis, I tested whether the use of alcohol could cause variation in the carbon or nitrogen concentration of the samples. I placed commingled *Artemisia tridentata* leaf tissue that had been collected a day earlier from live plants in eastern Washington State in 24 scintillation vials (25mL capacity) and added 90% denatured ethanol to 12 of the samples, thus duplicating my preservation methods in the field. The other 12 samples were immediately placed in a 65°C drying oven for 72 hours. After 5 days, I placed the 12 ethanol-preserved samples in a fume hood without the caps to evaporate the alcohol, and then placed the samples in a 65°C drying oven for 72 hours. I then ran all 24 samples in the EA Elemental Analyzer using the same methods as the experimental samples. I tested for the effect of alcohol preservation on nitrogen and carbon concentration using single-factor (ethanol presence or absence) Analysis of Variance.

Ethanol-preserved samples had significantly higher percent carbon concentration (p = 0.0007) than non-ethanol preserved samples. However, the difference between the two means, 49.9% and 49.5%, was only 0.4%, which I considered biologically meaningless, because it was within the range of the standard deviation for samples in a given treatment on a given day of the watering experiment. Specifically, the standard deviation for carbon concentration in the watering experiment ranged from 0.34% to 0.66% (average 0.51% for all watering days) for *A. tridentata* and from 0.55% to 0.98% (average 0.79% for all watering days) for *S. vermiculatus* (Figure 10).

There was no significant difference in nitrogen concentration between ethanol-preserved and control samples ($p = 0.101$).

Question 2: Is grasshopper abundance correlated with short term climatic variation?

During summer field courses in the Alvord Basin from 2003 through 2009, Dr. Roger Anderson's undergraduate student research teams performed visual surveys of grasshopper abundance on standard field plots. Nine 10 m x 40 m plots were set up on three mesohabitat types: dunes, sandy flats, and hardpan (three plots for each mesohabitat). Each plot was separated into sixteen 5 m x 5 m quadrats, situated in two rows of eight squares. The same eight squares, all diagonally touching (no common sides), were surveyed each time.

During 2003, plots were surveyed during six time periods per day, twice in the morning, afternoon, and evening, using an alternating schedule of specific plots that were surveyed at any given time period, so every plot was observed twice during each time period. During subsequent summers, each plot was surveyed thrice each at three time periods per day: early and late morning, and early evening (9 times per day total). A student surveying one of the 16 quadrats within the plot would identify the sex, species, and life stage (nymph or adult) of any grasshoppers present. Students would visually inspect the plant, and then manually-and-visually search each plant in the quadrat by gently running their fingers up from the base to the top of the plant through the outer 10-20 cm of foliage. In 2003, students also recorded the location and species of all perennial plants within the standard grasshopper plots. Height, long diameter, and short diameter were recorded for each plant.

I sorted the data for each standard plot for each field season to determine the mean number of grasshoppers observed per plot visit for each plot (all species pooled), to obtain means for each of three mesohabitats per year. Because grasshopper abundance in hardpan mesohabitats were low and sporadic in all years (relatively few plants reside in hardpan), I excluded those data from my analyses. Moreover, frequent high winds in the afternoon were a potential source of variability in grasshopper counts (almost no grasshoppers were found when it was windy), so only morning data from dune and sandy flat mesohabitats were analyzed.

Data analyses

I used Pearson's simple correlation to test whether grasshopper abundance varied with precipitation and temperature across years. I used the known phenology of the two most common grasshopper species expected at the study site, *Trimerotropis pallidipennis* (pallid-winged grasshopper) and *Cordillacris occipitalis* (spotted winged grasshopper) (Personal communication, Roger Anderson; USDA Research Service website), as a basis for selecting the time frames for the correlations. For example, *T. pallidipennis* in Colorado, Wyoming, and Utah, and *C. occipitalis* in northern ranges develop as nymphs through five instars beginning no sooner than late March or early April, and become adults in early June through late July (USDA Agricultural Research Service website). April through July would therefore be the most likely time frame for weather conditions to affect nymphal development (although some time lags may factor in, since weather conditions may take time to affect grasshopper habitat or food resources, which may in time affect nymphal development). In the data analyses, I used monthly total precipitation and monthly average temperature data from the NOAA weather station in Fields, OR (42° 16' latitude and -118° 41' longitude, Figure 4), which I obtained from the Western Regional Climate Center's historical data summaries online (http://www.wrcc.dri.edu/Climsum.

html). For some months in some years, temperature and precipitation data were either completely missing (March through September 2005) or more than three days of the month were missing from the data used to produce the monthly averages for the Fields weather station (October 2004 through February 2005 and five additional sporadically distributed months from 2003 through 2009, in which anywhere from five to thirteen days were missing). For those months, I obtained data temporally corresponding to those missing months or days from the Rome 2NW weather station (42° 52' latitude and -117° 39' longitude, Figure 4), approximately 100 km to the northeast of the study site. I made corrections to all data from the Rome 2NW weather station according to the mean recorded difference in temperature and precipitation between Rome 2NW and Fields. To verify the consistency of the Fields and Rome 2NW weather stations with nearby weather stations (locations depicted in Figure 4), I compared the monthly mean precipitation (Figure 5) and temperature (Figure 6) from the corrected Fields data with the data from weather stations at Rome 2NW, Bly 4 SE (42° 23' latitude and -120° 58' longitude), Hart Mountain Refuge, OR (42° 33' latitude and -119° 39' longitude), McDermitt, NV (42° 00' latitude and -117° 43' longitude), and Paradise Valley, NV (41° 30' latitude and -117° 32' longitude). All weather data used in the correlation analyses are listed in Appendix.
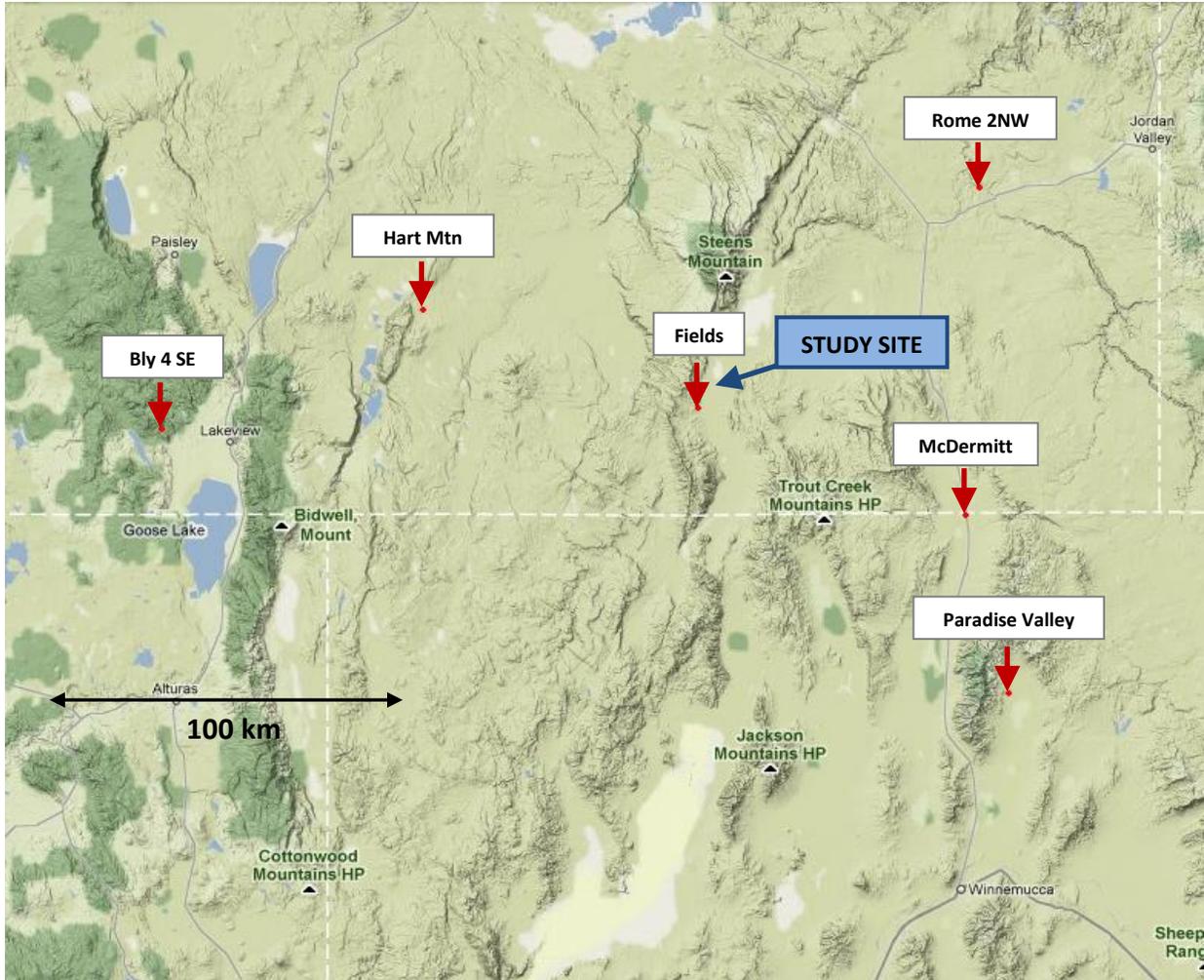
Figure 4. Weather station locations at Fields, OR (42° 16' latitude and -118° 41' longitude),
Rome 2NW (42° 52' latitude and -117° 39' longitude), Bly 4 SE (42° 23' latitude and -120° 58'
longitude), Hart Mountain Refuge (42° 33' latitude and -119° 39' longitude), McDermitt, NV
(42° 00' latitude and -117° 43' longitude), and Paradise Valley, NV (41° 30' latitude and -117°
32' longitude). (Map source: http://maps.google.com)
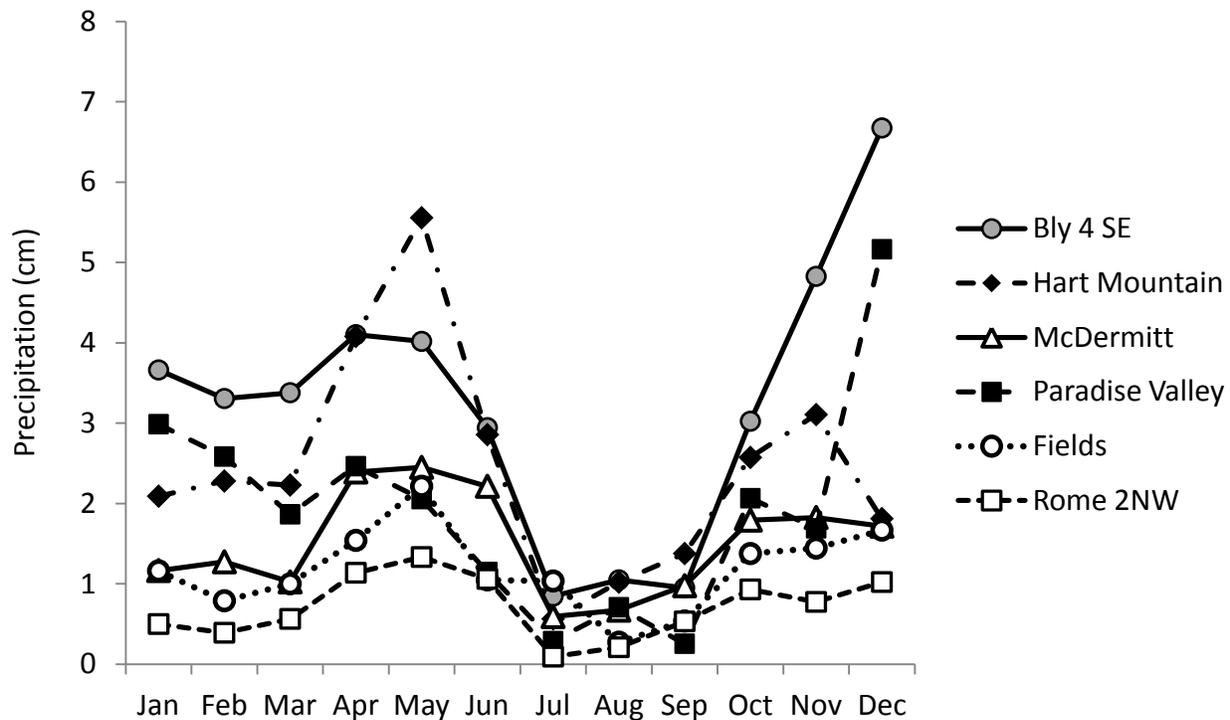
Figure 5. Mean monthly precipitation from 2003-2009 monitored by weather stations at Fields, OR, and 5 nearby field stations (see legend and Figure 4). Note that adjusted data from Rome 2NW were used to substitute missing data from Fields (i.e., missing data for some months in some years at Fields were substituted with correction factor based on data from Rome 2NW for those months). Source: Western Regional Climate Center historical climate summaries.
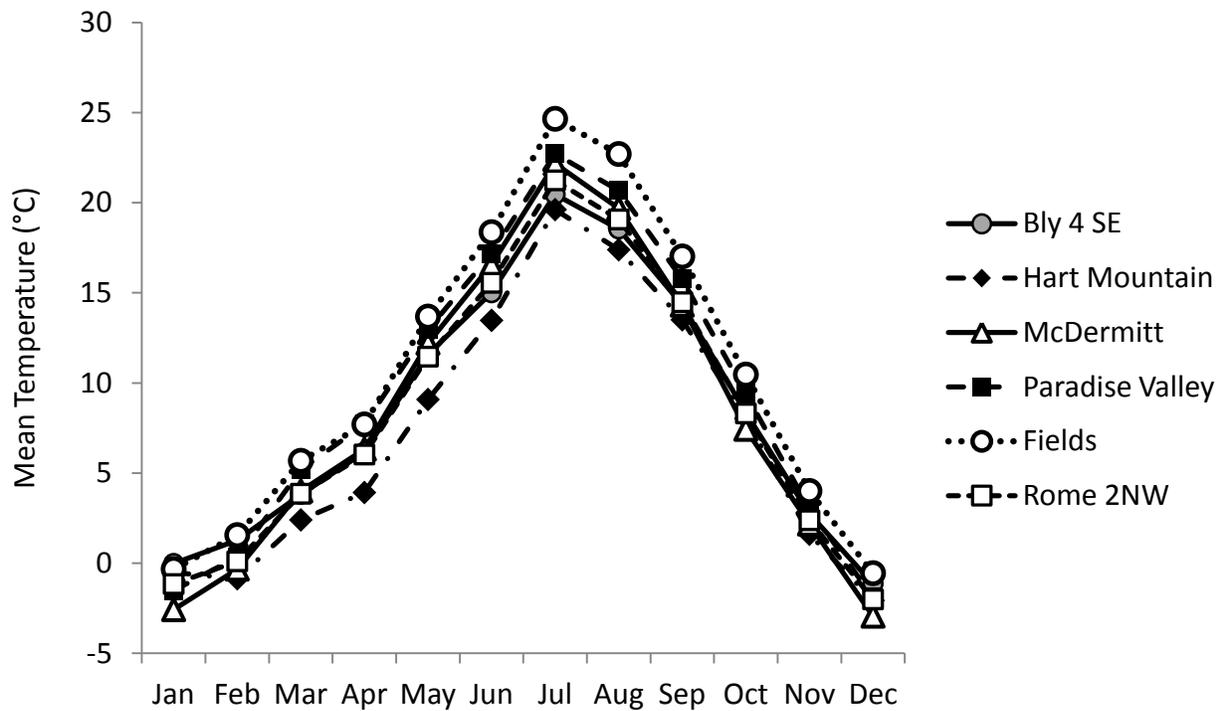
Figure 6. Mean monthly temperature from 2003-2009 monitored by weather stations at Fields, OR (see comment, Figure 5), and five nearby weather stations. Source: Western Regional Climate Center historical climate summaries.

To test if summer grasshopper abundance during mid-summer were correlated with precipitation in the spring of the same year (spring is when the largest portion of the time is spent in nymphal development), I used precipitation data from the preceding May. I also tested the correlation using data for April-May, May-June, and April-June to verify that the precipitation characteristics for those timeframes were about the same as May. The correlation values were similar; thus, values from May adequately represented spring precipitation and paralleled the use of May temperatures in the analyses. To test if climate would have a one-year time lag, I used precipitation data from May of the previous year. To test if grasshopper abundance during summer was correlated with precipitation in the dry, hot part of the summer—during the period of grasshopper reproduction and egg-laying—I tested the effect of the amount of precipitation from the previous year's July-August on summer grasshopper abundance. To test if summer grasshopper abundance was correlated with temperatures in the preceding winter, during which grasshopper clutches could be adversely affected by abiotic low temperatures, I used monthly mean minimum daily temperature data from the preceding December through March. To test if summer grasshopper abundance was correlated with high late spring and early summer temperatures, I used mean maximum daily temperature data from the preceding May and June.

To test whether the relative abundance of grasshoppers on *Artemisia tridentata* versus *Sarcobatus vermiculatus* was correlated with precipitation in the preceding spring, I performed the following four calculations to produce the data used in Pearson's correlation:

(1) I used the short width, long width, and heights of plants recorded by students in 2003 to calculate the volume (assuming plants were elliptical cylinders) of *A. tridentata* and *Sarcobatus vermiculatus* shrubs available on the plot.

(2) I divided the total volume of *A. tridentata* (ARTR) on the plots by the cumulative

total volume of both *A. tridentata* and *S. vermiculatus* (SAVE) on the plots to determine the

proportional volume of *A. tridentata.*

(Total V of ARTR / Total V of ARTR+SAVE) = (Proportional V of ARTR)

(3) Similarly I divided the number of grasshoppers observed on *A. tridentata* by the total

number of grasshoppers observed on either of the two shrub species to determine the actual

proportional abundance of grasshoppers on *A. tridentata*.

(Total GH on ARTR) / (Total GH on ARTR and SAVE) = (Proportional abundance of GH on

ARTR)

(4) As an index of electivity, which should reflect the relative preference of grasshoppers

for the two shrub species, I divided the actual proportional abundance of grasshoppers on *A.*

tridentata by the proportional volume of *A. tridentata* on the plots.

(Proportional abundance of GH on ARTR / (Proportional V of ARTR) = (Electivity Index)

This index is analogous to the Forage Ratio of Strauss (1979). Values less than 1 indicate a

preference for *S. vermiculatus*, values greater than 1 indicate preference for *A. tridentata*, while

values equal to 1 indicate no preference. Using this electivity index, I could test the hypothesis

that there is a direct relationship of microhabitat preference in the summer with precipitation during the preceding spring (for years 2003-09).

Question 3: Are year-to-year changes in male *Gambelia wislizenii* body condition correlated with year-to-year changes in grasshopper abundance?

Using data on grasshopper (and grasshopper mass-equivalence of cicada abundance in 2005) and male *Gambelia wislizenii* body mass to snout-vent length ratio collected by Dr. Roger Anderson's summer field course students from 2003-2009, I used linear regression analysis to determine whether grasshopper (and cicada availability in 2005) affected *G. wislizenii* body condition. Data on female *G. wislizenii* body mass to snout-vent length ratio were not used because females' body mass measurements included individuals just before and just after oviposition and thus generated extreme variability. Because of the direct correlation of mass with body length in animals (Brown and West 2000), I truncated the size distributions of adult males used for my analyses. The minimum and maximum used in all analyses was thus the same for all years, ranging from 90-103mm. I determined that cicadas in 2005 would be necessary to include in the analysis, because it was apparent from a preliminary review of the data that adult grasshoppers did not become prevalent in 2005 (a year of cicada emergence) until the adult cicada population had diminished. Cicadas were plentiful early in the counting period, and Dr. Roger Anderson (personal communication) noted that lizards captured during that time period consistently had full bellies, an observation that was consistent with other observations of occurrences of predator satiation (e.g., Karban 1982, Williams et al. 1993). Therefore, in 2005, the presence of cicadas was presumed to add to the effect of grasshopper abundance on *G. wislizenii* body condition. However, cicadas had much larger body mass than the common grasshopper species on the plot and were presumed to have higher nutritional value than

grasshoppers. Consequently, each cicada observed in 2005 was estimated (by wet body mass comparisons of four cicadas to four each of the dominant two species of grasshoppers) to have the equivalent nutritional value of about six adult grasshoppers.

Question 4: Can we use currently available information to form a predictive model of *Gambelia wislizenii* body condition?

To assess the potential for using a combination of abiotic and biotic variables to predict *Gambelia wislizenii* body condition, I used weather, grasshopper, and lizard data from years in which data for grasshopper abundance and *G. wislizenii* body condition and abundance had been collected by Dr. Roger Anderson's summer field course students (2003 to 2009). Because the presence of cicadas in 2005 made the data for that year anomalous, I excluded the 2005 data from the analyses. For the other six years I ranked four primary factors according to their predicted effects on *G. wislizenii* body condition: male *G. wislizenii* abundance, grasshopper abundance, May precipitation, and May mean maximum daily temperature. High grasshopper abundance was regarded as a beneficial factor, so the top-ranked, most beneficial value was ranked 1 of 6 and the bottom-ranked, least beneficial value was ranked 6 of 6. High lizard abundance was regarded as a detrimental factor because of intraspecific competitive effects, so the top-ranked, least detrimental value was ranked 1 of 6 and the bottom-ranked, most detrimental value was ranked 6 of 6. High May precipitation was regarded as beneficial because it is presumed to increase primary productivity, and was ranked as above. Low May mean daily maximum temperature was also regarded as beneficial across the range of values observed because of lower energy requirements for lizards, and was also ranked as above. There was a potential concern that in addition to high May maximum temperature having a detrimental effect, very low May maximum temperatures could have a detrimental effect on lizard body condition,

thus necessitating bimodal ranking. However, no May maximum temperature was so low that it would likely have a detrimental impact on lizard body condition, given that most species of lizards at the latitude and altitude of the Alvord Basin should be seasonally inactive during much of May (Angilleta, 2009), so bimodal ranking was deemed unnecessary. I hypothesized that the top-ranked variables and combinations of variables would predict the top-ranked male *G. wislizenii* body condition.

I tested the correlation of the ranks of *G. wislizenii* ratios of body mass to snout-vent length with the individual ranks of the aforementioned abiotic and biotic variables using Spearman rank correlation analyses. To compare these individual correlations with correlations based on composite variables, I also summed the ranks of grasshopper, lizard abundance, and weather conditions for 2003-2009, excluding 2005, and calculated the Spearman correlation coefficient, r_s, according to the methods in Siegel (1954). Similarly, to correlate lizard body condition with composite rankings for specific subsets of the variables, I ran the same analyses using: a) summed ranks for all variables, excluding lizard abundance (to assess whether intraspecific competition played a role), b) the summed ranks of biotic variables (lizard and grasshopper abundance), and c) the summed ranks of abiotic variables (precipitation and temperature). This suite of analyses allowed me to determine the degree to which specific groups of variables (with or without intraspecific competition and abiotic versus biotic factors) were correlated with lizard body condition, and whether those groups were more strongly correlated with body condition than was any single variable.

Results

Question 1: What are the effects of simulated summer rain pulses on *Artemisia tridentata* and *Sarcobatus vermiculatus* leaf condition?

Water content decreased as summer progressed ($p < 0.001$) for unwatered and watered *Artemisia tridentata*, whereas water content remained roughly the same for unwatered and watered *Sarcobatus vermiculatus* (Figure 7). For both watered and unwatered treatments, the water content in *S. vermiculatus* was significantly higher than in *A. tridentata* (two-factor ANOVAR $p < 0.001$, Table 1).

Unwatered *A. tridentata* had higher average water content than watered *A. tridentata* before the experimental treatments were applied, and the mean values for control and watering plants converged over time (species x treatment x time interaction $p = 0.029$; Figure 7). Accounting for the initial difference in water content may therefore expose a significant effect of the watering treatment. Consequently, using water content as a covariate I performed a two-factor ANOVAR, which revealed a significant effect of the watering treatment on *A. tridentata* water content. Unwatered plants declined in water content faster than watered plants. There were no changes in significance for the other tested effects and interactions (Figure 8, Table 2).

[a]
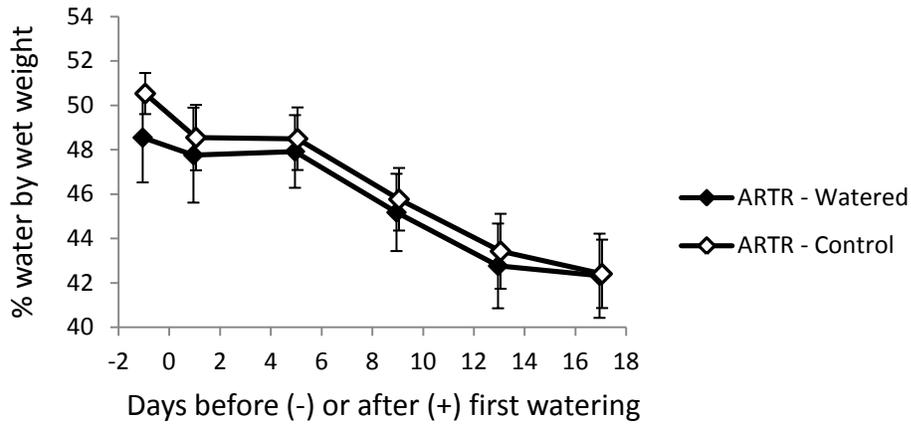
[b]

Figure 7. Water content of leaves collected from [a] *Artemisia tridentata* (ARTR) and [b] *Sarcobatus vermiculatus* (SAVE) (note different Y-axis scales in the two panels). Leaves were first sampled on the morning of 6/27/08, the day before simulated summer rain (with watering cans) was applied to 1 m diameter plots. Subsequent samples were collected on mornings immediately following watering: 6/29/08, 7/3/08, 7/7/08, 7/11/08, and 7/15/08. Twelve shrubs of each species were unwatered and served as controls; 12 *A. tridentata* and 11 *S. vermiculatus* received the simulated rainfall. Error bars denote 95% confidence interval (total N = 47 shrubs).
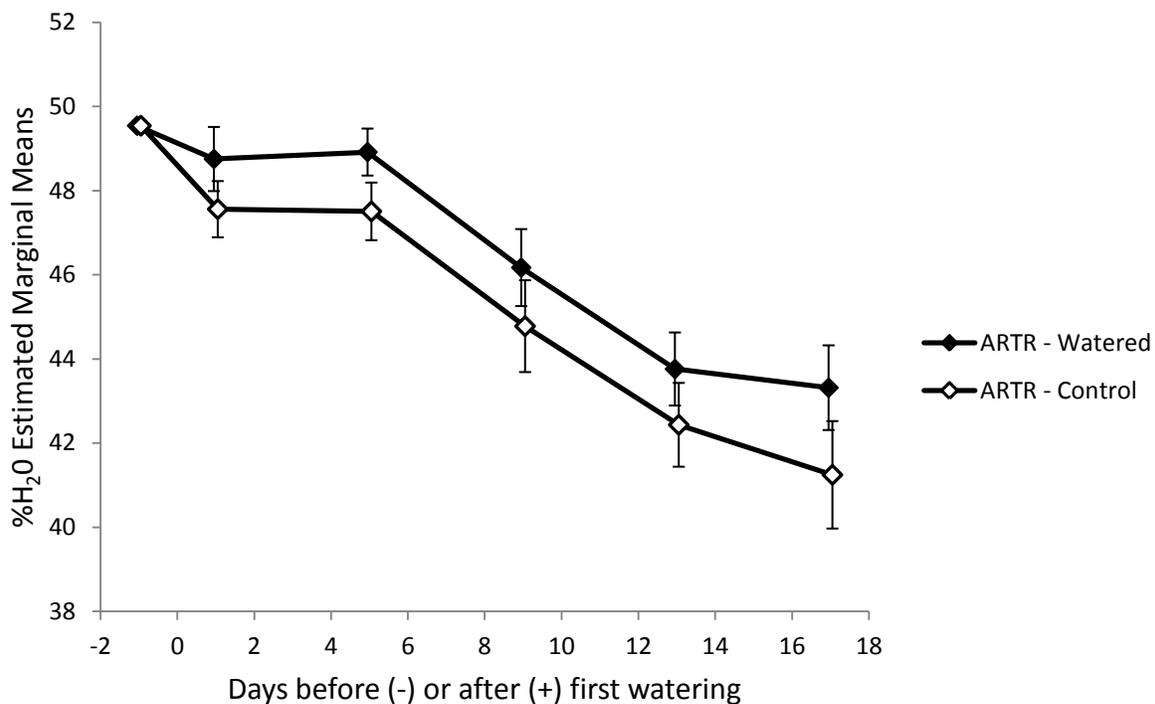
Figure 8. Estimated marginal means of water content of leaves collected from *Artemisia tridentata* (ARTR) adjusted with pre-treatment water content as a covariate. See Figure 7 for a summary of the watering experiment. Twelve *A. tridentata* were unwatered and served as comparators, and 12 received the simulated rainfall. Error bars denote 95% confidence interval (total N = 47 shrubs). Note that the pre-treatment mean (one day before the first watering) has no error bars, as all data points were normalized for the mean pre-treatment water content.

Table 1. Summary of ANOVAR results for *Artemisia tridentata* and *Sarcobatus vermiculatus* water content, percent nitrogen by dry mass and percent carbon by dry mass. Within subjects effects indicate changes in individual plants over time; between subjects effects indicate differences between groups of plants due to one or more factors. Bold font indicates significant effects ($p < 0.05$). Total N=47 shrubs.

Statistical Test/ Subject / Parameter(s)	Within or between subjects?	Factor(s)	SS	F	df	p value
Water Content	Within	date	512	91.0	5	**< 0.001**
		treatment x date	5.42	0.965	5	0.434
		species x date	528	94.0	5	**< 0.001**
		treatment x species x date	15.0	2.66	5	**0.029**
	Between	treatments	5.46	0.111	1	0.741
		species	48,100	974	1	**< 0.001**
		treatment x species	24.9	0.504	1	0.481
% N by dry mass	Within	date	5.48	104	5	**< 0.001**
		treatment x date	0.054	1.03	5	0.399
		species x date	0.152	2.89	5	**0.015**
		treatment x species x date	0.020	0.381	5	0.862
	Between	treatments	0.055	0.235	1	0.631
		species	3.56	15.1	1	**< 0.001**
		treatment x species	0.046	1.94	1	0.171
% C by dry mass	Within	date	5.45	10.8	5	**< 0.001**
		treatment x date	0.620	1.24	5	0.294
		species x date	20.5	40.9	5	**< 0.001**
		treatment x species x date	0.279	0.554	5	0.735
	Between	treatments	0.293	0.139	1	0.711
		species	7520	3570	1	**< 0.001**
		treatment x species	1.40	0.664	1	0.420

Table 2. ANOVAR results for *Artemisia tridentata* water content with initial water content used as a covariate. Within subjects effects indicate changes in individual plants over time; between subjects effects indicate differences between groups of plants due to one or more factors. Bold font indicates significant effects ($p < 0.05$). Total N=24 shrubs.

Statistical Test/ Subject / Parameter(s)	Within or between subjects?	Factor(s)	SS	F	df	p value
Water Content	Within	date	23.9	3.97	5	**0.003**
		treatment x date	11.5	2.32	5	0.099
	Between	treatments	37.7	6.08	1	**0.023**

Watering did not influence nitrogen concentration (percent by dry leaf mass) of leaves for either

A. tridentata or *S. vermiculatus* (Figure 9, Table 1). Leaves of *S. vermiculatus*, however, had

significantly lower nitrogen concentration than leaves of *A. tridentata*. Leaf nitrogen

concentration for both species declined significantly ($p < 0.001$) with advancing date, and the

rate of decline differed between species (significant species-by-date interaction: $p = 0.015$).

There was no significant interaction between treatment and species.

Leaves of *A. tridentata* had significantly higher carbon concentration (percent of dry leaf mass)

than leaves of *S. vermiculatus* ($p < 0.001$, Figure 10). Within either species, however, there was

no statistically significant watering treatment effect on carbon concentration. Carbon

concentration in leaves of *A. tridentata* was higher in samples from later dates ($p < 0.001$, Figure

10). In contrast, the carbon concentration in leaves of *S. vermiculatus* was lower in samples from

later dates ($p < 0.001$, Figure 10). Table 1 summarizes the ANOVAR results of the watering

experiment.

[a]
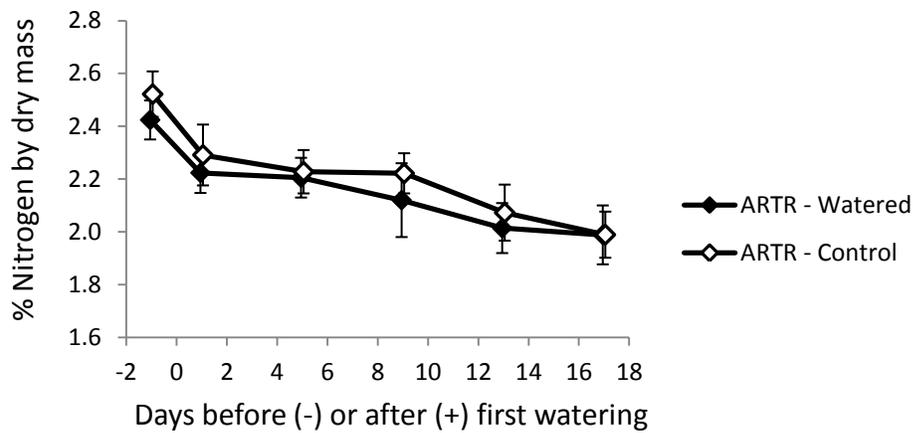
[b]
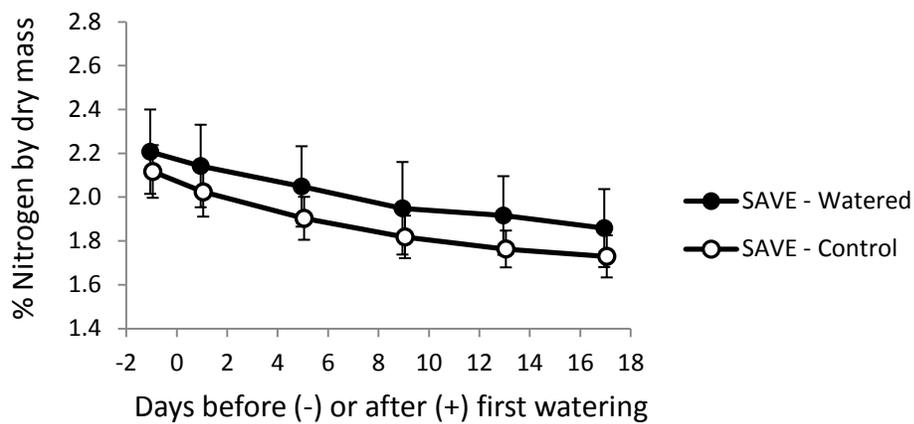
Figure 9. Nitrogen concentration (percent nitrogen by dry mass) of leaves collected from [a]
Artemisia tridentata (ARTR) and [b] *Sarcobatus vermiculatus* (SAVE). See Figure 7 for a
summary of the watering experiment.
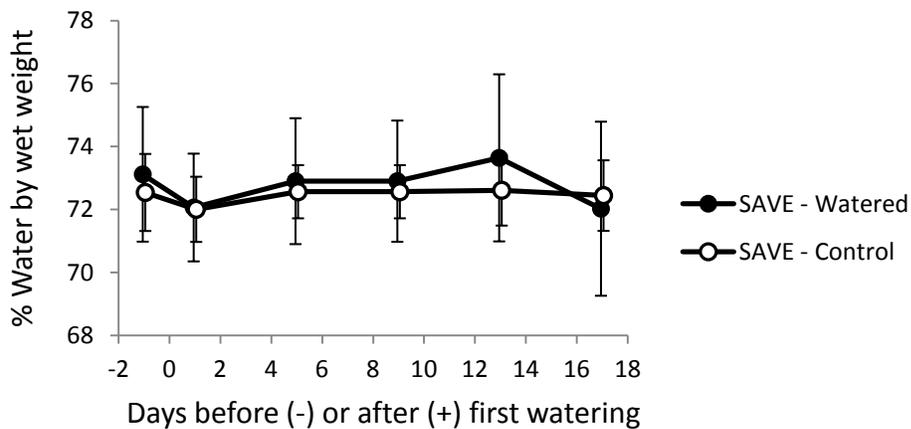
[a]
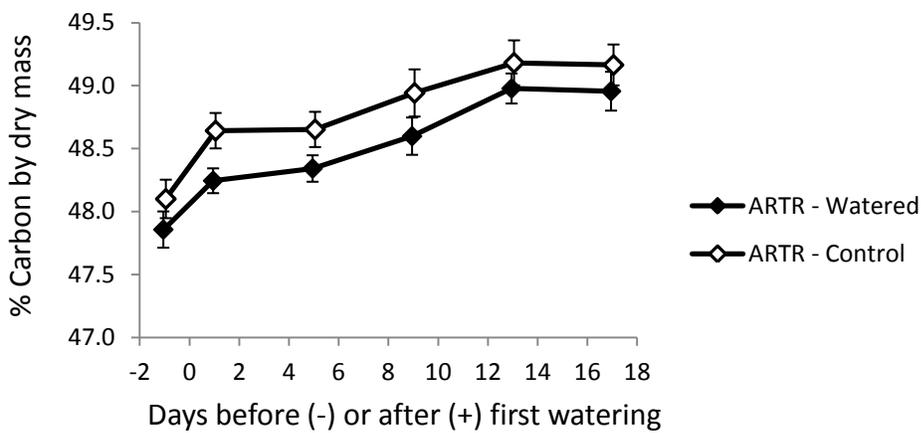
[b]
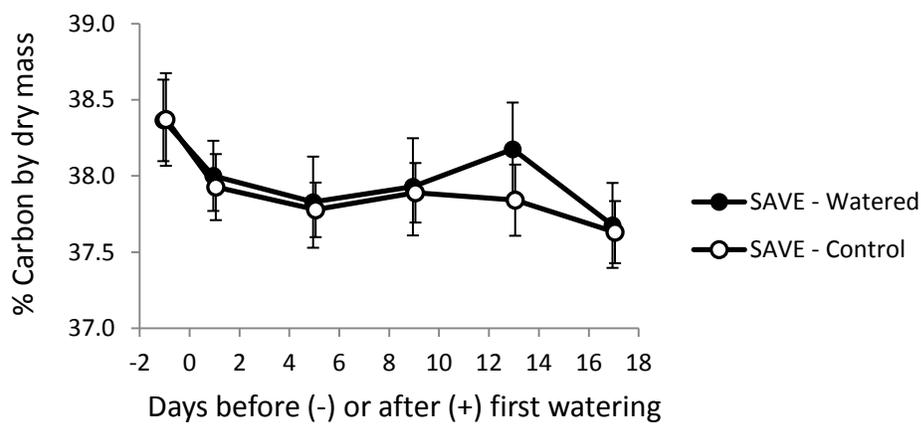
Figure 10. Carbon concentration (percent carbon by dry mass) of leaves collected from [a] *Artemisia tridentata* (ARTR) and [b] *Sarcobatus vermiculatus* (SAVE) (note different Y-axis scales in the two panels). See Figure 7 for a summary of the watering experiment.

Question 2: Is grasshopper abundance correlated with short term climatic variation?

The four grasshopper species that comprise 97% of the adult grasshoppers observed in the Alvord Basin from 2003-2009 are listed in Table 3. There was no apparent effect of rainfall on total grasshopper abundance. Grasshopper abundance did not correlate with precipitation for any of the time frames tested, whether abundance was compared with precipitation within the same year (May of the same year, Figure 11a) or in the year before (May and July through August, Figure 11 b-c). Grasshopper abundance was directly correlated with monthly mean daily minimum temperature in December through March of the preceding winter ($p = 0.012$, Figure 12). There were no other significant correlations among grasshopper abundance and the tested temperature time frames during the seasonal activity of grasshopper (Figure 12). Several countervailing factors, including 1) an anomalously warm winter, 2) a comparatively cool May, or 3) a relatively dry May, may have caused the lack of significance in some of these single-factor analyses. As such, the effects of these countervailing factors on the results of the single-factor correlation analyses will be considered in the Discussion.

For all years, grasshoppers were proportionally more abundant on *Sarcobatus vermiculatus* than on *Artemisia tridentata*, as evidenced by the fact that the electivity index was consistently below 1 (Figure 13). However, there was no significant correlation between the electivity index and April-May precipitation ($p = 0.086$, Figure 13).

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Table 3. Relative abundances of the four most common grasshopper species (percent of total grasshopper adults) that comprised 96.4% of the grasshoppers observed in the Alvord Basin from 2003-2009 (data were similar among years, hence pooled). Total N = 1074 grasshoppers.

Species	Percent of total adults
Trimerotropis pallidipennis	51.6%
Cordillacris occipitalis	28.7%
Melanoplus rugglesi	9.5%
Paropomala pallida	6.6%
	96.4%
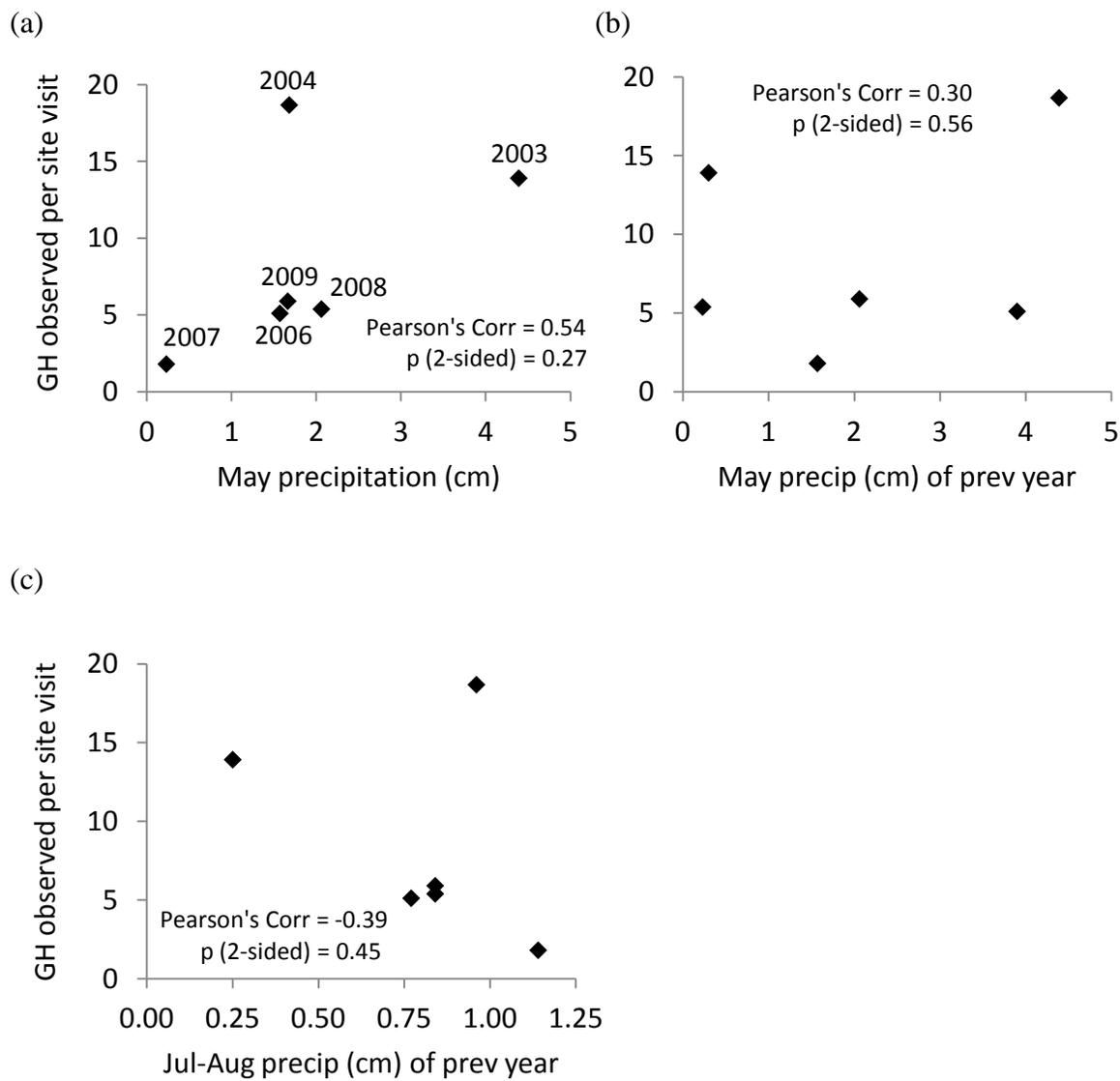
Figure 11. The mean number of grasshoppers observed per plot on dunes and sandy flats in the summer relative to the amount of precipitation during (a) May of the same year, (b) May of the previous year, and (c) July through August of the previous year, for the years 2003-2009, with 2005 excluded.

(a) (b) (c) (d)
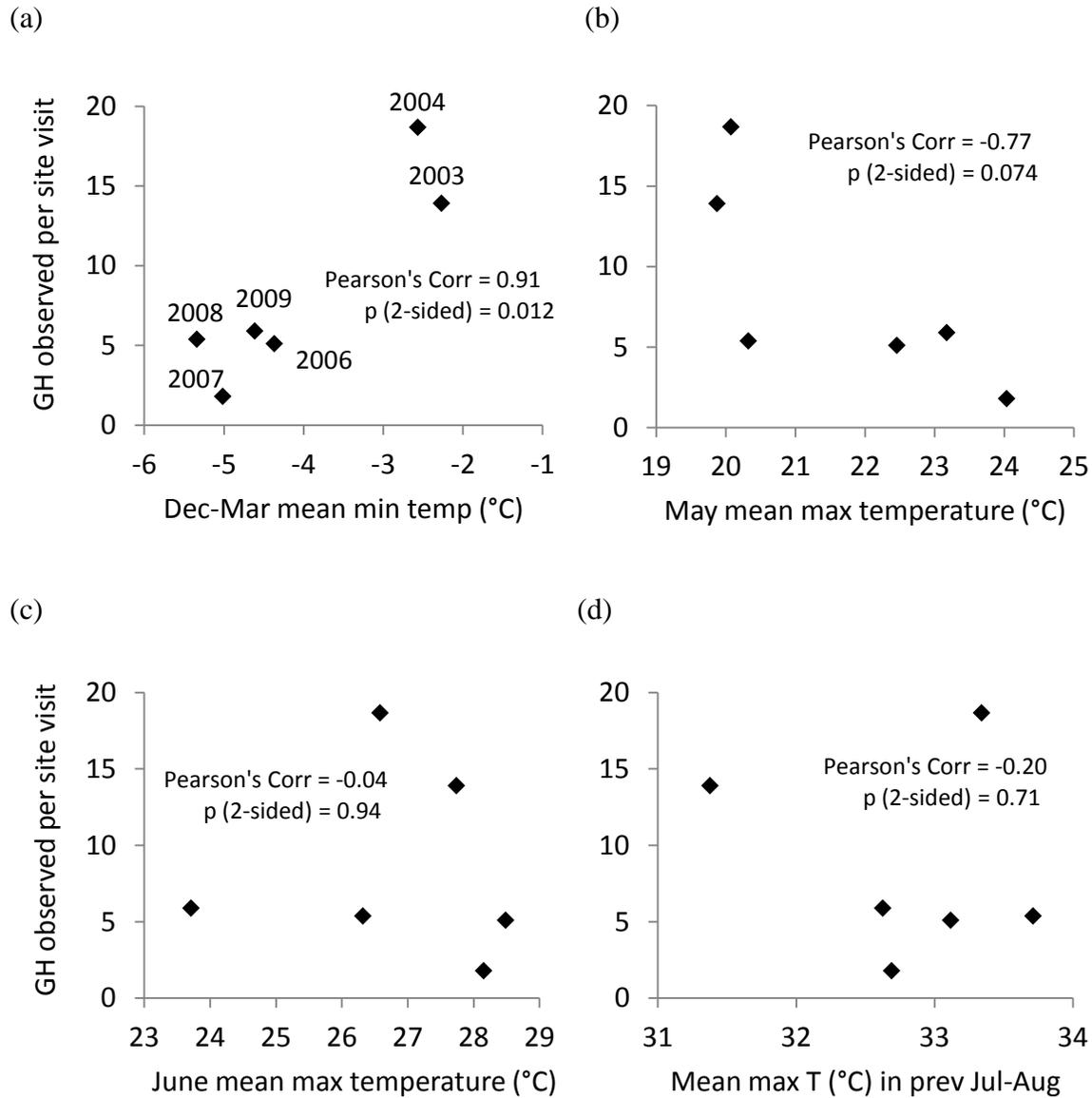
Figure 12. The mean number of grasshoppers observed per plot on dunes and sandy flats in the summer relative to mean daily minimum air temperature during December-March (a), mean daily maximum air temperature in May (b), and June (c) of the same year; and (d) mean daily maximum air temperature in July-August of the previous year, for the years 2003-2009, with values relevant to 2005 excluded.
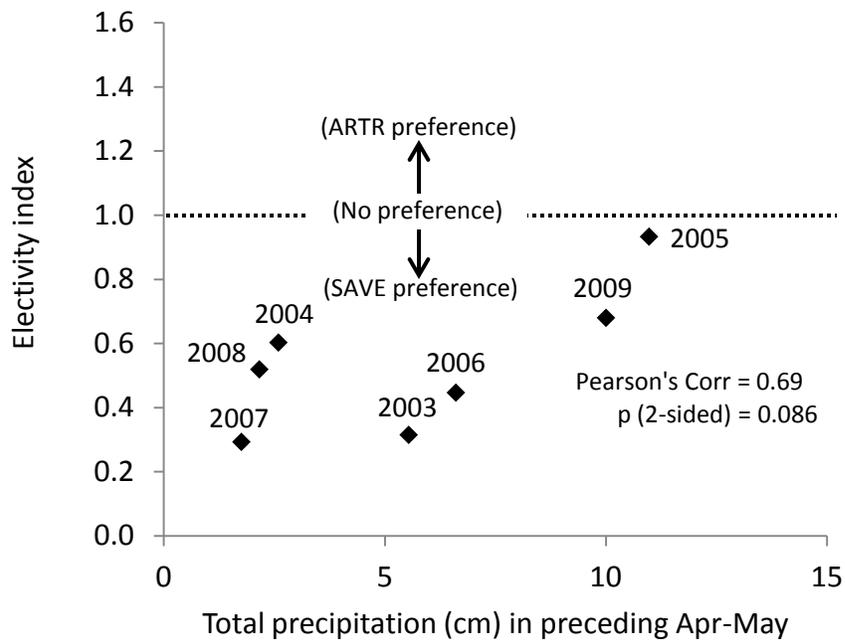
Figure 13. Electivity index of shrub species preference by grasshoppers in the 2003-2009

summer field seasons, as a function of precipitation during the spring (April through May)

immediately before each field season. Values below 1 indicate preferential microhabitat use of *S.*

vermiculatus over *A. tridentata*.

Question 3: Are year-to-year changes in male *Gambelia wislizenii* body condition correlated with year-to-year changes in grasshopper abundance?

I verified the assumption that annual variation in adult male *Gambelia wislizenii* body size was low by examining ranges and standard errors of the mean SVL. The mean minimum SVL ($\pm$ SE) and body mass ($\pm$ SE) of adult males among years were 90.5mm ($\pm$ 0.42mm) and 18.96g ($\pm$ 0.47g). The mean maximum SVL ($\pm$ SE) and body mass ($\pm$ SE) among years were 102mm ($\pm$ 0mm, reflecting the 90-103 mm range in body sizes chosen) and 29.60g ($\pm$ 0.99g). The mean annual sample size ($\pm$ SE) was 35 males ($\pm$ 3.63; range was 23 in 2007 to 49 in 2006). The mean of annual means of SVL ($\pm$ SE) was 97.03mm ($\pm$ 0.30mm) and the range of means among years was 95.67mm (in 2006) to 97.73mm (in 2009, Figure 14). The only year that was statistically different from other years in SVL distribution was 2006 ($p = 0.028$), a year in which there was high young male recruitment. The annual means of body mass ranged among years from 20.4 (in 2007) to 26.7 (in 2004) (in contrast to their very similar SVLs), with a grand mean ($\pm$ SE) of 24.63g ($\pm$ 0.79g) (Figure 14). The annual means of body mass to SVL ratio ranged among years from 0.212 (in 2007) to 0.275 (in 2004), with a grand mean ($\pm$ SE) of 0.254 ($\pm$ 0.008) (Figure 14).

There was a significant positive linear relationship ($p = 0.018$) between log-transformed grasshopper and cicada availability and *G. wislizenii* body mass to snout-vent length ratio (Figure 14). There was a significant negative linear relationship ($p = 0.013$) between mean maximum daily temperature in May and log-transformed *G. wislizenii* body mass to snout-vent length ratio (Figure 15).

Question 4: Can we use currently available information to form a predictive model of
***Gambelia wislizenii* body condition?**

Spearman rank correlation between lizard body condition and individual factors revealed that
ranks of male *Gambelia wislizenii* body mass to snout-vent length ratio were significantly
correlated with grasshopper abundance, May precipitation, and mean daily maximum
temperature for May (Table 4). The following summed ranks of variables also revealed
significant correlations with male *G. wislizenii* body mass to snout-vent length ratio: (1) all
predictive variables combined, (2) grasshopper abundance combined with abiotic variables, (3)
only biotic variables, and (4) only abiotic variables. Of all individual variables and combinations
of variables, grasshopper abundance had the highest correlation, mean daily maximum
temperature in May had the next highest, followed by the combined ranks of *all* abiotic variables
(Table 4). Ranks of winter minimum temperature did not correlate significantly with ranks of *G.*
wislizenii body condition, but when combined with other abiotic variables, winter minimum
temperatures tightened the correlation. Combining grasshopper abundance with abiotic variables
did not tighten the correlation with ranks of *G. wislizenii* body condition.
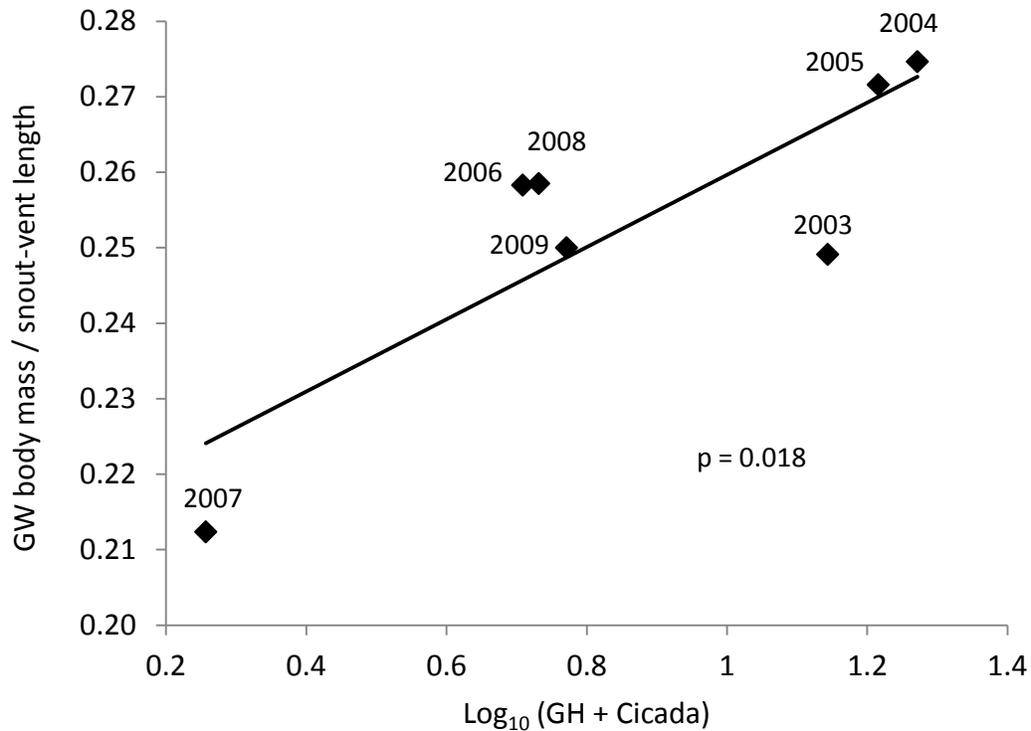
Figure 14. Linear regression of male *Gambelia wislizenii* (GW) body condition (g body mass per mm snout-vent length) as a function of log-transformed grasshopper plus cicada availability ($\log_{10}$ of the sum of the mean number of grasshoppers per site visit plus 6 times the mean number of cicadas per site visit, assuming 6 grasshoppers per cicada by body mass) per site visit, for each year during the 2003-2009 summer field seasons [$\log_{10}$(GH+Cicada) = 0.0479 (GW body mass/SVL) + 0.212]. Mean SVL by year (2003-09, respectively) was: 97.44, 97.42, 97.7, 95.67, 96.17, 97.09, and 97.73 mm. Mean mass by year (2003-09, respectively) was: 24.3, 26.8, 26.5, 24.7, 20.4, 25.1, and 24.5 g.
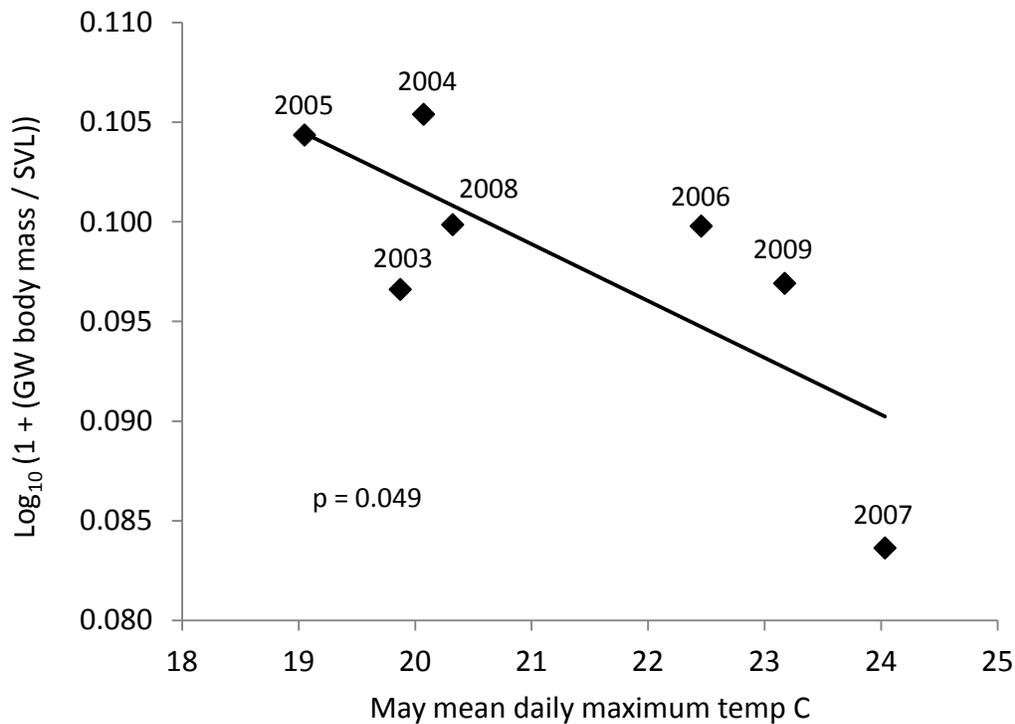
Figure 15. Linear regression of log-transformed body mass to snout-vent length ratio of *Gambelia wislizenii* for each year during the 2003-2009 summer field seasons relative to the mean daily maximum temperature during the preceding May. Numbers for *G. wislizenii* body mass/snout-vent length ratio were transformed by adding 1 (to avoid negative numbers that would result from taking the log of decimal), then taking the log of each data point $[\log_{10}(1+(GW \text{ body mass/SVL})) = 0.159 - 0.0029(\text{Temperature})]$.

Table 4. Spearman rank correlation of male *Gambelia wislizenii* (GW) body mass to snout-vent length ratio with (a) ranks of individual predictive variables and (b) ranks of summed ranks of predictive variables. Numbers in parentheses denote the ranking of variables or summed ranks of variable combinations. Due to a major cicada emergence in 2005 the data for 2005 were excluded from the analysis. Asterisks denote significant correlations (significance level was $r_s >$ 0.829 at N = 6 and α = 0.05).

(a)

	GW Mass/ SVL	Male GW Count	GH per site visit	May Precip (cm)	May Max Temp C	Dec-Mar Min Temp C
2003	0.249(5)	39 (4)	13.9(2)	4.39(1)	19.9(1)	-2.27(1)
2004	0.275(1)	36 (3)	18.7(1)	1.68(3)	20.1(2)	-2.57(2)
2006	0.258(3)	59 (6)	5.1(5)	1.57(5)	22.5(4)	-4.37(3)
2007	0.212(6)	30 (1)	1.8(6)	0.23(6)	24.0(6)	-5.02(5)
2008	0.259(2)	47 (5)	5.4(4)	2.06(2)	20.3(3)	-5.34(6)
2009	0.250(4)	33 (2)	5.9(3)	1.66(4)	23.2(5)	-4.61(4)
r_s		0.714	0.901*	0.868*	0.890*	0.813

(b)

	GW Mass/ SVL	Summed Ranks (All)	Summed Biotic Ranks	Summed Abiotic Ranks	GH + MinT + MaxT + P
2003	0.249(5)	8 (1)	6 (3)	3 (1)	5 (1)
2004	0.275(1)	9 (2)	4 (1)	7 (2)	8 (2)
2006	0.258(3)	20 (6)	11 (6)	12 (4)	17 (4.5)
2007	0.212(6)	19 (5)	7 (4)	17 (6)	23 (6)
2008	0.259(2)	14 (3.5)	9 (5)	11 (3)	13 (3)
2009	0.250(4)	14 (3.5)	5 (2)	13 (5)	17 (4.5)
r_s		0.879*	0.835*	0.890*	0.887*

Summary of results: context of trophic interactions

Simulated summer rain showers affected the water content of *Artemisia tridentata* leaves differently from *Sarcobatus vermiculatus* leaves. Both watered and unwatered *A. tridentata* declined in water content through the duration of the study, though the decline was slower for watered *A. tridentata* (Figure 8, Table 3), a direct resource effect of precipitation on plant quality (Figure 1 a, c). Simulated summer rain showers did not affect nitrogen concentration or carbon concentration in the leaves of either species (Figures 9, 10, Table 1). The foliage of the two shrub species differed in 1) water content, 2) water content change over time, 3) nitrogen concentration, 4) nitrogen concentration over time, 5) carbon concentration, and 6) carbon concentration over time (Figures 7, 9, 10, Table 1). Grasshopper abundance was not correlated with precipitation during any of the time frames tested (Figure 11) and grasshopper preference of shrub species was not correlated with April-May precipitation (Figure 13), so there was no statistically observable indirect effect of spring precipitation on primary consumers (Figure 1 a, d). Monthly mean daily minimum temperature in December through March was correlated with grasshopper abundance during the following summer field season (Figure 12a), revealing what is likely to have been a direct abiotic effect of temperature on primary consumers (Figure 1 b, d). The anomalously warm winter of 2004 may have caused the high abundance of grasshoppers despite the average precipitation for 2004.

The direct biotic effect of grasshopper and cicada availability (Figure 1 d, e) on *Gambelia wislizenii* body condition seems readily apparent (Figure 14). In contrast, body condition of male *G. wislizenii* was inversely related to higher mean daily maximum temperature in May (Figure 15). This abiotic effect could be either 1) a direct (Figure 1 b, e), or 2) an indirect effect

mediated by biotic effects (Figure 1 b, d, e), or 3) a combination of direct abiotic and biotic effects. In the Spearman rank correlation analysis, grasshopper abundance was the individual variable that was most tightly correlated with male *G. wislizenii* body condition, reflecting a direct (potentially cause-effect) biotic relationship (Figure 1 d, e). Ranks of May precipitation and May mean daily maximum temperature were also correlated with ranks of *G. wislizenii* body condition, revealing direct or indirect abiotic weather influences on secondary consumers (Figure 1 a, e and b, e). The tightest correlation of a combination of predictive variables with *G. wislizenii* body condition resulted from the summed ranks of grasshopper abundance, winter mean daily minimum temperature, May precipitation, and May mean daily maximum temperature. No correlation of a combination of variables, however, was any more predictive than the direct biotic effect of grasshopper abundance (ranked individually, Table 4). It is difficult to disentangle the effect of grasshopper abundance on *G. wislizenii* body condition from the direct effects of the abiotic variables used in these combinations, as grasshopper abundance was significantly correlated with winter minimum temperatures and (though not significantly correlated) trended towards higher abundance with a wet May and lower abundance with a dry May.

Discussion

Key findings and inferences

The results of this study suggest that summer rain pulses in the Alvord Basin desert scrub are unlikely to affect grasshopper abundance either directly or indirectly via biotic effects on food plants (i.e., direct effect on the water, nitrogen, and carbon content of food plants). Instead, warmer winters, which are directly correlated with grasshopper abundance in the subsequent summers, presumably benefit grasshoppers, because grasshopper eggs are subject to mortality under cold stress (Mukerji and Braun 1988). Given the strong association between lizard condition and grasshopper abundance, it is likely that *Gambelia wislizenii* also benefits indirectly from warmer winters. However, warm temperatures in May appear to be detrimental to *Gambelia wislizenii*, perhaps because increased feeding cannot compensate for the higher daily metabolism, as seen for similar situations in other northern desert lizards (Zani 2008, Zani and Rollyson 2011). Overall, it appears that *Gambelia wislizenii* body condition is influenced by multiple direct and indirect effects: 1) indirect abiotic effect of winter minimum temperature via its effects on grasshopper abundance, 2) indirect abiotic effects of mean daily air temperature and precipitation in May via a) direct abiotic effects on plant productivity, and b) direct biotic effects of plants on grasshopper growth and survival, and 3) direct effects of grasshopper abundance as a food source. Figure 16 summarizes the hypothesized and observed abiotic and biotic interactions in this study.

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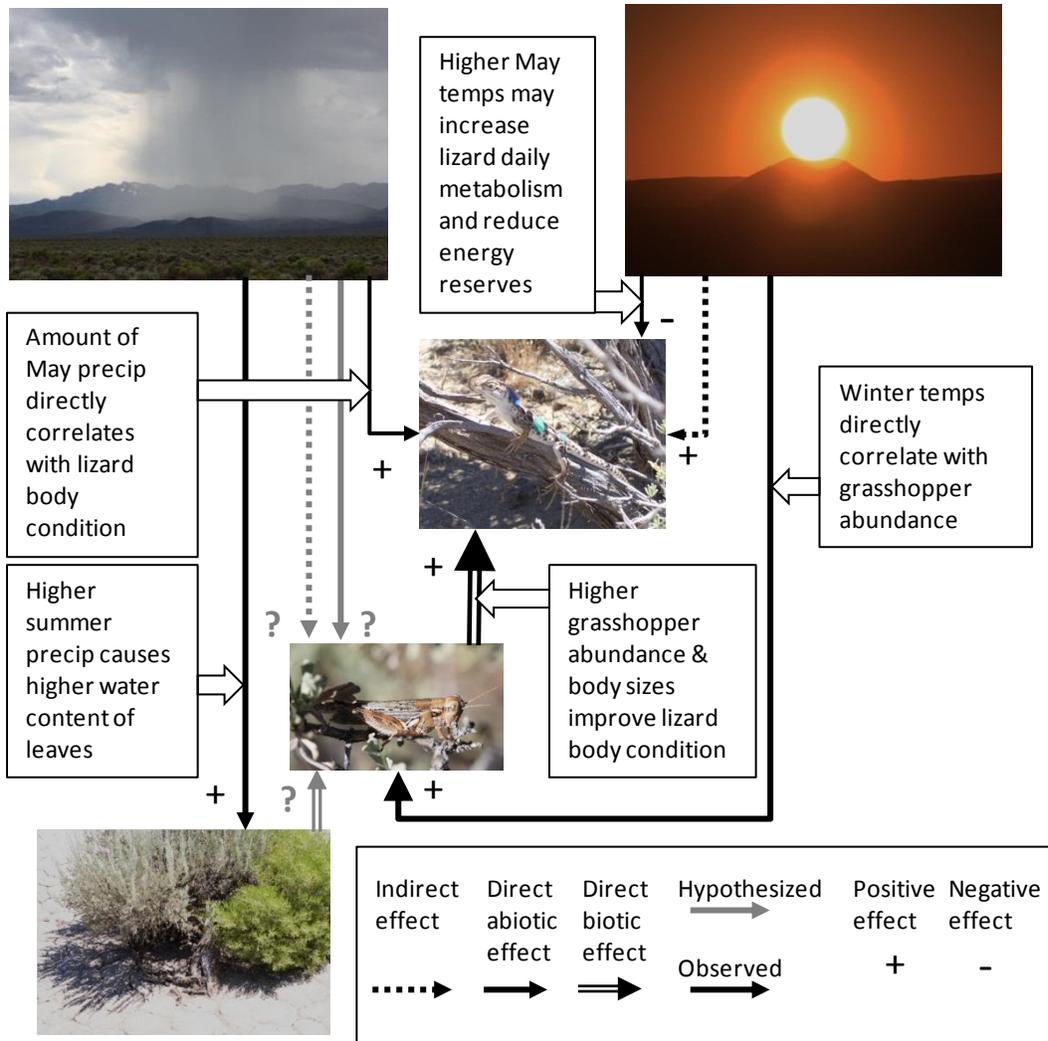
Figure 16. Flowchart of hypothesized (gray) and observed (black) abiotic and biotic interactions

in the Alvord Basin desert scrub. Arrow size denotes the relative strength of observed effects.

Bottom-up influences on primary producers and primary consumers

<u>Direct and indirect effects on grasshopper abundance</u>

If precipitation has a direct effect on host-plant leaf quality that transduces into an indirect effect of precipitation on grasshopper abundance, that indirect effect is not likely due to differences in summer rain shower frequency or amplitude. Summer rain showers may mitigate the seasonal decline of water content in leaves of *Artemisia tridentata* (Figure 7). However, based on the lack of a significant effect of simulated summer rain showers on foliar nitrogen and carbon concentration of *A. tridentata* and *Sarcobatus vermiculatus*, I infer that summer rain showers have little or no impact on nitrogen availability for grasshoppers. Ivans et al. (2003) used similar watering levels in a simulated summer rainfall experiment, and found that watering treatments increased nitrogen uptake in the roots of *A. tridentata*. However, it is possible that nitrogen uptake in the roots does not translate to increased foliar nitrogen concentration if plants store nutrients or allocate them to other structures or more growth. Evans and Black (1993) found that leaf growth in *A. tridentata* occurs mostly in the spring, when water is not limiting, whereas inflorescence growth occurs in the summer. *Artemisia tridentata* may thus allocate soil nutrients taken up during summer rain showers to inflorescence growth instead of leaf growth. However, no inflorescences were observed on the experimental plants in my study in July 2008.

The effects of two naturally occurring summer rain showers on June 22 and July 1 (six days before the first watering treatment and one day before the second watering treatment, respectively) may also have masked any potential treatment effects on nitrogen and carbon concentration. After the rain showers, there was about the same amount of soil penetration by water as was typical for an experimental watering treatment. The total precipitation recorded for June 2008 was close to the 2003-2009 mean for June, whereas precipitation in July 2008 was lower than the 2003-2009 mean for July (Figure 17). Note, however, that the second shower occurred at the beginning of July; thus, the monthly total may not reflect the overall soil wetness during the study period. Although April 2008 had abnormally low precipitation compared to the 2003-2009 mean, May 2008 had higher than normal rainfall and likely would have compensated for the effect of a dry April in that year. In contrast to the significant correlation of May precipitation with *Gambelia wislizenii* body mass to snout-vent length ratio using Spearman rank correlation, there was no significant correlation of spring precipitation with grasshopper abundance (Using Pearson's correlation, Figure 11a). However, it appears that the lack of correlation was driven by the anomalous, extreme warm winter temperatures directly preceding summer 2004 (Figure 12a), presumably improving grasshopper survival.
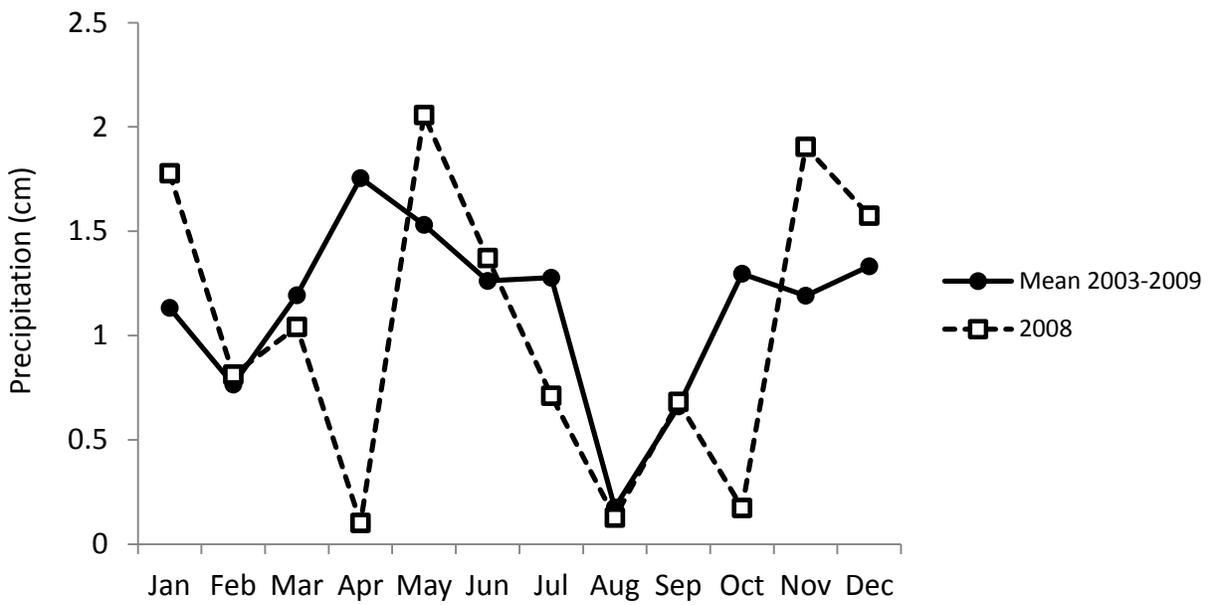
Figure 17. Monthly total precipitation in Fields, OR in 2008 compared to mean precipitation in Fields, OR from 2003 to 2009 (including 2008). Source: Western Regional Climate Center historical climate summaries.

The decline of nitrogen concentration in leaves through the course of the watering study in both species (Figure 9) may result from dilution of nitrogen due to rapid leaf growth (i.e., Kitajima et al. 1997). High variability in water and nutrient content among individuals of *A. tridentata* may have masked treatment effects, but the strong seasonal (date) effect for both species emphasizes the importance of phenology in leaf condition and potential consequences for consumers. Plant leaf phenology is important for insect herbivores in other systems. For example, Lepidoptera larval abundance is negatively correlated with leaf tannin concentrations, which vary according to season (Forkner et al. 2004). Moreover, early spring feeding by Lepidoptera larvae coincides with maximum leaf protein content, and leaf tannins may inhibit growth by limiting the availability of nitrogen (Feeny 1970). Similarly, variation in host plant leaf production phenology explained 61% of the statistical variation in leaf miner densities (Mopper and Simberloff 1995). The seasonal decline of nitrogen and water content in desert shrubs may have a similar phenological effect on grasshopper growth and abundance.

The higher nitrogen concentration in leaves of *A. tridentata* could have important nutritional implications for grasshopper host plant choice. *A. tridentata* leaves had 12% higher nitrogen concentration than *S. vermiculatus* leaves (2.19% vs. 1.96% by dry mass). Grasshoppers had higher growth rates when fed on *A. tridentata* leaves at 3.70% N by dry mass than on *A. tridentata* leaves at 3.16 % N dry mass (Johnson and Lincoln 1990). Grasshoppers experience higher survival, growth, and reproductive allocation at the "optimal" nitrogen concentrations of 4-5 % N by dry mass (when tested in a range of 1-7%, Joern and Behmer 1997). Moreover, grasshopper density is positively correlated with higher soil nitrogen, likely mediated by the

effect of soil nitrogen on host-plant leaf nitrogen content (Ritchie 2000). However, in this study, I infer from the electivity index data that grasshoppers prefer to forage on *S. vermiculatus*, which has relatively low nitrogen concentration. The higher preference of grasshoppers for *S. vermiculatus* over *A. tridentata* (Figure 13) may have been due to the higher water content of *S. vermiculatus* (Figure 7). Secondary chemical defenses may also play a role in grasshopper microhabitat preference for *S. vermiculatus* over *A. tridentata*: allelochemicals in *A. tridentata* may limit feeding by generalist grasshoppers (Ritchie 2000). A grasshopper feeding study comparing the consumption of *A. tridentata* versus *S. vermiculatus* may provide further perspective on the feeding preferences of grasshoppers (i.e., Figure 13).

As leaves mature, carbon concentration typically increases while nitrogen concentration decreases (Field and Mooney 1983); thus, the seasonal increase in carbon concentration of *Artemisia tridentata* leaves was expected. Moreover, *A. tridentata* leaves contain many secondary defense compounds, including carbon-rich terpenoids (Striby et al. 1987), and these defenses may be induced by herbivore-feeding (Karban et al. 2004, 2006). Late spring or early summer feeding by grasshoppers, or my own clipping of leaf samples, may have induced chemical defenses in *A. tridentata*, and that may have also contributed to the increase in *A. tridentata* leaf carbon concentration. A decrease in carbon concentration was not observed for *S. vermiculatus* leaves. The ecological importance of treatment effects and seasonal carbon decline for *S. vermiculatus* may be masked by the high variability among individual plants in carbon concentration. The standard error in carbon concentration of *S. vermiculatus* leaves was 0.24 and the standard deviation was 0.79 for individual sampling days. These values were higher than mean difference between watered and unwatered treatments (0.089% C by dry mass), and

comparable to the differences between consecutive sampling days (range of 0.05% - 0.50% C by dry mass). The range of carbon concentration for individual samples was 36.2% - 40.0% C by dry mass (Figure 10b). Even if mean carbon concentration increased throughout the season, grasshoppers would encounter plant-to-plant differences in carbon concentration almost as high as the seasonal increase. Regardless of carbon concentration, however, nitrogen is the more important macronutrient responsible for grasshopper diet selection (Jonas and Joern 2008) and demographic responses (Joern and Behmer 1997). Thus, further studies of the seasonal shifts of nitrogen concentration in relation to leaf phenology (discussed above) and the demographic responses of grasshoppers may clarify bottom-up, biotic influences on grasshopper populations.

The direct, abiotic effects of temperature in winter (Figure 12a) may have more impact on grasshopper population densities than the indirect resource effects of precipitation on grasshopper population densities (Ritchie 2000). The direct relationship between mean daily minimum temperature in winter (December-March) and grasshopper abundance (Figure 14a) is consistent with the hypothesis that year-to-year weather patterns correlate with year-to-year grasshopper populations. Timing of hatching in most grasshopper species is influenced by accumulated temperature (more warm winter days results in earlier spring hatching), and low minimum winter temperatures may cause freezing-induced egg mortality (Joern and Gaines 1990). Grasshopper eggs from Saskatchewan, Canada experienced increasing mortality at lower temperatures—egg mortality increased at each interval when tested at 0, -7, -11, -15, and -18°C (Mukerji and Braun 1988). Winter temperatures in the Alvord Basin can fall in this range; the lowest 2003-2009 winter minimum temperature (monthly mean daily minimum temperature) in

Fields, OR was -9.9°C in January 2007 (see Appendix, Table S4). Thus, extremely low winter temperatures may directly impact grasshopper populations in the following summer.

Density dependence may play an important role in dryland grasshopper populations. Montana grassland grasshopper populations exhibited significant density dependence in a forty-year study from 1951-1991 (Kemp and Dennis 1993). However, the mean carrying capacities for grasshopper populations in Kemp and Dennis' study ranged between 6.3 and 8.9 adult grasshoppers per m^2 (Kemp and Dennis 1993), whereas grasshoppers in my study were at maximum density in 2004 at only 0.09 per m^2 (18.7 grasshoppers per site visit of 200 m^2). It is possible that a desert scrub habitat such as the Alvord Basin could have a much smaller carrying capacity than Montana grasslands; however, there was little evidence of chewing on the leaves of shrubs in my study, so competition for food resources seems unlikely. Regardless, as a post-hoc precautionary check, I plotted annual July grasshopper abundance on the standard plots as a time series to visually assess whether density dependence could be a key factor affecting adult grasshopper abundance (Figure 18a). I also plotted the key potential response variable to adult grasshopper abundance, annual body condition of male *Gambelia wislizenii*, as a time series (Figure 18b). It is apparent from the time-series graph of adult grasshopper abundance that a drop in population density may have occurred following the peak in 2004 (Figure 18a). However, due to the short time-frame used in this study, it is not possible to determine if the lower adult grasshopper abundance in July 2005 was due to later maturation of grasshoppers or fewer grasshoppers. The lower population densities of grasshoppers in 2005-2009, however, may be more representative of the Alvord basin, and 2003-2004 may be somewhat anomalous. In contrast, the low numbers of grasshoppers in 2007 were expected given the dry spring of 2007.

With the exception of the cicada outbreak of 2005, which may have masked the effect of low grasshopper abundance in 2005, the annual sequence of *G. wislizenii* body condition was similar to the annual sequence of grasshopper abundances (Figure 18b).

Direct and indirect effects of abiotic factors on the body condition of *Gambelia wislizenii*

Direct abiotic effects on *G. wislizenii* body condition may either mask or interact with bottom-up, biotic effects. I found a strong relationship between abiotic variables and *G. wislizenii* body condition (Table 4). Paralleling the results of this study, others have found that extremes in abiotic factors may mask the effects of bottom-up, biotic influences (Dunson and Travis 1991, Hunter and Price 1998, Hunter et al. 1997, Kingsolver 1989, Ritchie 2000). Weather may also affect the importance of various biotic determinants by mediating interactions between primary and secondary consumers (Kingsolver 1989). Desert spider populations are influenced by interactive abiotic effects and bottom-up effects of precipitation on invertebrate prey (Polis et al. 1998). *Aspidoscelis tigris* populations in the Chihuahuan Desert also may be influenced by the direct and indirect effects of weather patterns and invertebrate prey abundance (Whitford and Creusere 1977). Through direct effects on grasshopper populations, weather patterns may ultimately influence male *G. wislizenii* body condition. Higher insect prey availability apparently had a positive effect on *G. wislizenii* body condition (Figure 14). Steffen (2002) indicated that *G. wislizenii* body condition should be highest in locales where food abundance is high. Moreover, because arthropod abundance affects the size and abundance of the lizard *Aspidoscelis tigris* (Anderson 1994), which is also eaten by *G. wislizenii*, then lizard prey abundance may correlate with grasshopper abundance.

(a)

(b)
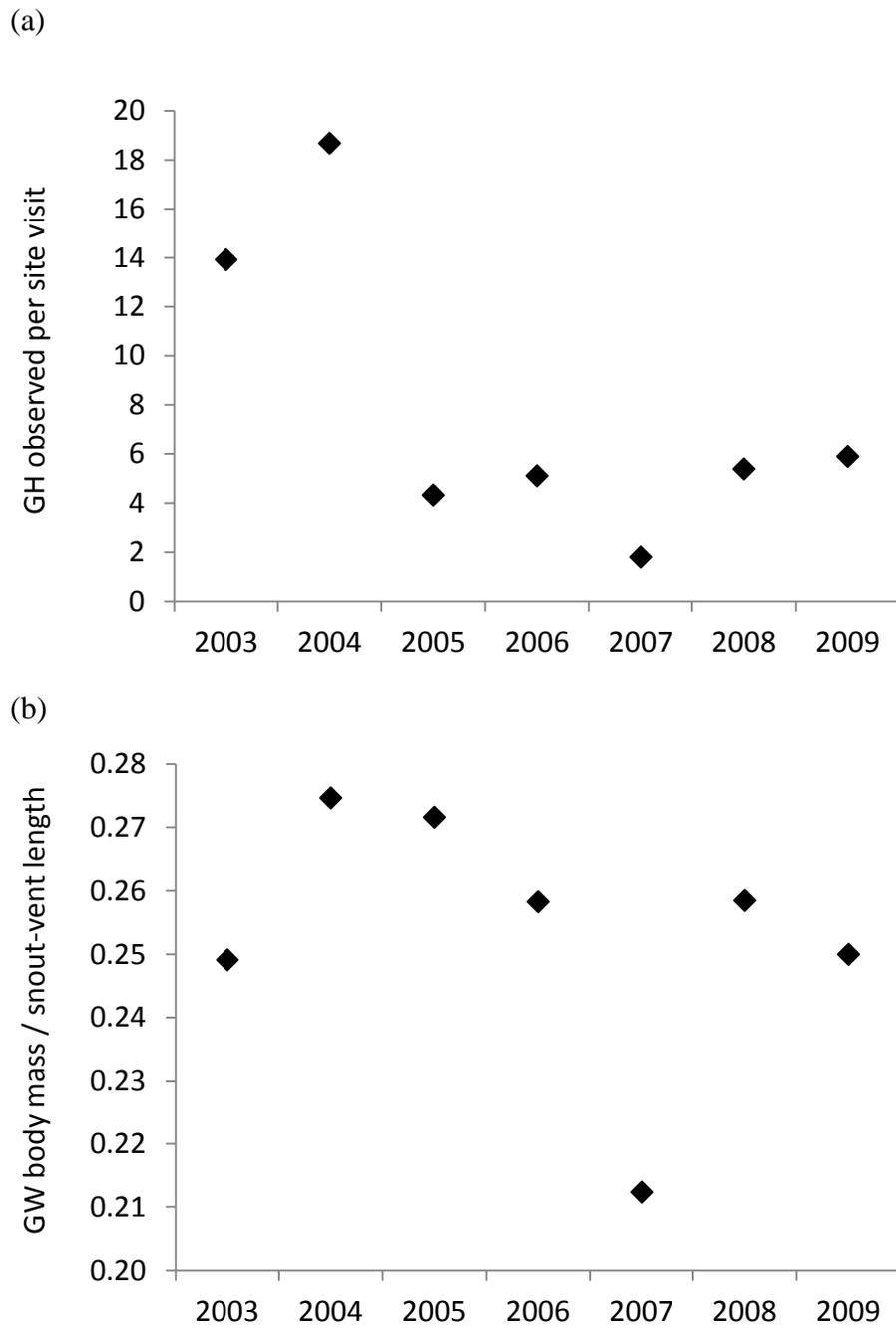
Figure 18. Grasshopper abundance (a) and *Gambelia wislizenii* body mass to snout-vent length ratio (b) for 2003-2009.

Direct temperature effects likely influence lizard body condition as well. Weather may affect physiological rates of animals, thereby mediating interactions between trophic levels (Angilletta 2009, Kingsolver 1989). For example, higher body temperatures resulted in a higher resting metabolic rate of the zebra-tailed lizard, *Callisaurus draconoides* (Karasov and Anderson 1998). Because deserts have low productivity, I expected that the body condition of *G. wislizenii* would be inversely related to mean daily maximum temperature in May if feeding rates of *G. wislizenii* were not commensurately high. Because higher mean daily maximum temperatures in May were inversely related to *G. wislizenii* body condition (Figure 15), lizard feeding rates may not compensate for higher metabolism during warmer springs. Because May temperatures are typically too low for daily activity by *G. wislizenii*, as is expected for most lizards at the altitude and elevation of the Alvord Basin (Angilletta 2009), I hypothesize that higher temperatures in May cause the lizards to continue to use lipid and protein reserves, thus contributing to lower body mass to snout-vent length ratio.

Several ecological factors can influence *G. wislizenii* body condition: I found significant correlations of *G. wislizenii* body condition with grasshopper abundance, spring precipitation, and spring temperatures over the study period (Table 4). Grasshopper abundance appears to be the most consistent and strongest predictor of lizard body condition (Figure 14, Table 4), emphasizing the importance of bottom-up regulation to *G. wislizenii* in the Alvord Basin. Although mean daily maximum temperature in May was the next best predictive variable (Figure 15, Table 4), I cannot differentiate between these two potential causes: 1) a direct effect of body temperature on metabolism and energy use in lizards or 2) an indirect (albeit presumed strong) effect of the high temperatures, concomitant with low rainfall, that may reduce plant production

in the spring and consequentially reduce grasshopper production. That is, it appears that ranks of May precipitation in some years were the inverse of the ranks of May temperatures in the same year. Thus, salubrious temperatures along with increased rain presumably increased plant productivity (both spring annuals and the young leaves of *S. vermiculatus*, in particular) which, in turn, is expected to increase individual grasshopper growth rate and possibly grasshopper survival and abundance. As expected, along with warmer minimum daily temperatures in winter, higher May precipitation in combination with lower mean daily maximum temperature in May all appear to improve *G. wislizenii* body condition (despite a lack of significant effect when winter temperature was examined as a lone effect, Table 4). The significant correlation of summed ranks of biotic variables (*G. wislizenii* abundance and grasshopper abundance) with ranks of *G. wislizenii* body condition is probably mostly attributable to grasshopper abundance; ranks of *G. wislizenii* abundance alone did not significantly correlate with lizard body condition (Table 4). Given the low number of annual samples, more years of data are necessary to resolve the relationships of winter temperature and *G.wislizenii* abundance with *G. wislizenii* body condition. The rank analysis used in the present study could be modified and tested with data on other prey (i.e., lizards and other arthropods) from past and future field seasons. Such analyses may further clarify the importance of abiotic environmental factors and bottom-up biotic processes that influence lizard fitness and the overall trophic interactions of lizards, grasshoppers, and desert shrubs in the Alvord Basin.

Conclusions

This study's findings demonstrated the complexity of interactive biotic and abiotic influences, even in relatively simple trophic systems. For example, there is a decline with the advance of summer in nutritional content of leaf tissues in *Artemisia tridentata* and *Sarcobatus vermiculatus,* and summer rain may alter the timing of the seasonal decline in water and nutrient content. However, it may be that spring rain has a much greater effect than summer rain on the timing and amplitude of seasonal decline in *A. tridentata* leaf nutrient content (Evans and Black 1991).

Multiple correlations and regression analyses revealed a suite of potentially interacting biotic and abiotic effects. At the primary consumer level, effects of short-term weather variation on grasshopper abundance were likely through direct (abiotic), rather than indirect (biotic) effects. Grasshopper abundance varied directly with winter minimum temperatures (Figure 12a), which is a finding similar to previous studies showing that grasshopper egg mortality increases when winter season temperatures are lower (Mukerji and Braun 1988, Riegert 1967). Grasshopper abundance in turn influenced *Gambelia wislizenii* body condition (Figure 14). The inverse relationship of maximum daily temperatures in May with *G. wislizenii* body condition in the following summer (Figure 15) may have resulted from the direct, abiotic effects of temperature on *G. wizlizenii*. The direct, abiotic effect of temperature on grasshoppers may have also transduced into an indirect effect on *G. wislizenii* body condition. Therefore, these variables likely all interact to form a complex set of weather factors and time lags to consider when trying to predict future grasshopper abundance and the consequential impacts on lizard fitness.

No one weather variable or time frame emerged as the single most important factor influencing grasshopper abundance. Similarly, Joern (2000) indicated that correlations with single weather variables accounted for less than 30 percent of the variance of grasshopper populations. Whereas species distributions may be determined by ecological extremes, Skinner and Child (2000) indicate that grasshopper populations may depend on the combined effects of multiple seasons. Joern (2000) suggests the replacement of climate-driven, niche based models used to predict grasshopper population fluctuations with nonlinear models that predict the combined effects of abiotic environmental variables and biotic interactions. A model to predict grasshopper abundance should consider single-season, single-year, multi-season, and multi-year effects of multiple weather variables. Multivariate analyses that track effects of weather over time will be necessary to account for complex time lag effects. Such a model could be used in conjunction with multivariate analyses on ecological factors that predict lizard abundance and fitness. However, this will require a substantially longer time-series than the one used in the present study.

Future studies in the Alvord Basin could clarify the influence of time and weather variables on bottom-up trophic interactions. The comparative simplicity of desert ecosystems offsets the immense complexity that is typical of most natural ecosystems. Moreover, the effects of climate variation, such as severe recent droughts (McKinney et al. 2006, Miriti et al. 2007), can be relatively easily and effectively studied in desert scrubs in the American west. The recent strong swings in the ENSO (El Niño and La Niña) conditions may have strong effects on the plants and the native mammalian herbivores (e.g., ground squirrels, jackrabbits, and pronghorn) and granivores (e.g., heteromyid rodents; Waltz 2005) as well as on the lizards and birds that feed on

grasshoppers and other arthropods during the summer, and on the coyotes that depend on

mammalian prey. The Alvord Basin desert scrub would be a valuable model system for a

community study of the effects of climate variation on bottom-up trophic processes in desert

scrub. Future studies in the Alvord Basin and other arid temperate communities in the Great

Basin and around the world can build on the findings of this study by providing more in-depth

specifics on the interactive effects of multiple weather variables on grasshopper populations and

the consequences for higher trophic levels. Such studies would strengthen our understanding of

the biotic and abiotic, bottom-up and top-down influences of weather patterns in desert

ecosystems, and could be used to formulate, improve, and expand upon models that could

reliably predict the impacts of climate change at the local ecological community level.

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Appendix

Table S1. Monthly total (mm) of precipitation in Fields OR. *Data from the Rome 2NW weather station that were modified with a correction factor equal to the mean difference in precipitation between Fields and Denio for the same month for the years between 2002-2009.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2002	1.50	0.89	0.97	0.51	0.30	0.61	0.00	0.25	0.74	0.05	0.33	0.36
2003	0.99	0.33	0.74	1.14	4.39	0.38	0.30	0.66	0.51	0.03	1.24	2.18
2004	2.08	1.55	0.74	0.91	1.68	0.41*	0.51	0.79	0.13	1.88*	0.97	0.71
2005	0.17*	0.39*	0.48*	1.34*	3.90*	0.65*	0.77*	0.00*	0.33*	2.34	2.95	3.38
2006	1.50	1.04	3.45	5.03	1.57	1.17	1.14	0.00	0.23	1.52	0.79	1.22
2007	0.18	1.32	0.15	1.52	0.23	1.24	0.66	0.18	1.88	2.64	1.07	1.80
2008	1.78	0.81	1.04	0.10	2.06	1.37	0.71	0.13	0.68*	0.17*	1.91	1.57
2009	1.43*	0.08*	0.39*	0.73*	1.66*	2.12*	3.15*	0.16*	0.00*	1.05*	1.19*	0.81*

Table S2. Monthly mean maximum daily temperature (degrees C) in Fields, OR from 2002-2008. *Data from the Rome 2NW weather station that were modified with a correction factor equal to the mean difference in temperature between Fields and Denio for the same month for the years between 2002-2008. **Missing data.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2002	4.5	7.3	10.1	16.8	19.4	27.0	33.6	29.1*	25.5	16.1	11.0	7.7
2003	8.8	7.4	13.0	12.7	19.9	27.7*	34.8*	31.9*	26.3	21.6*	6.9	5.9
2004	2.0*	5.4	15.6	16.5	20.1	26.6*	32.6*	30.7*	24.1	17.4*	8.0*	7.0*
2005	4.3*	7.9*	12.4*	14.5*	19.1*	23.7*	33.7*	32.5*	24.8*	19.3	10.2	3.9
2006	6.7	7.7	8.2	14.1	22.5	28.5	34.8	30.6	26.5	19.0	10.4	5.1
2007	4.6	9.4	15.7	16.2	24.0	28.2	35.0	32.4	25.1	16.8	12.0	2.7
2008	1.6	7.8	11.1	14.5	20.3	26.3	33.0	32.2	26.3*	19.0*	13.3	5.1
2009	6.4	7.3	10.5*	15.3	23.2	23.7*	31.7*	**	28.1*	14.5*	11.0*	3.3*

Table S3. Monthly mean daily temperature (degrees C) in Fields, OR from 2002-2008. *Data from the Rome 2NW weather station that were modified with a correction factor equal to the mean difference in temperature between Fields and Denio for the same month for the years between 2002-2008.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2002	-0.1	1.0	3.7	9.6	11.9	18.9	25.2	20.1*	17.2	8.6	4.0	2.2
2003	3.6	1.4	6.8	6.3	12.9	18.9*	25.5*	23.3*	17.7	13.1*	1.3	1.7
2004	-1.9*	0.9	8.6	9.3	13.1	18.8*	23.8*	22.6*	16.5	11.0*	3.5*	1.6*
2005	-0.2*	1.4*	5.5*	7.7*	12.5*	15.7*	24.0*	23.0*	16.0*	10.7	3.6	-0.7
2006	1.8	0.8	2.7	8.0	14.1	19.8	26.0	21.4	16.7	10.1	4.4	-1.0
2007	-2.6	3.0	8.0	8.5	15.4	19.7	25.9	22.9	15.8	9.4	4.8	-1.8
2008	-3.2	2.1	3.9	6.4	12.7	17.9	23.9	22.9	16.9*	10.3*	6.5	-0.3
2009	0.3	1.3	4.2*	7.7	15.2	17.8*	23.5*	22.8*	19.5*	8.6*	4.0*	-3.2*

Table S4. Monthly mean minimum daily temperature (degrees C) in Fields, OR from 2002-2008. *Data from the Rome 2NW weather station that were modified with a correction factor equal to the mean difference in temperature between Fields and Denio for the same month for the years between 2002-2008. **Missing data.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2002	-4.8	-5.3	-2.6	2.4	4.4	10.9	16.8	-17.8	8.9	1.2	-2.9	-3.2
2003	-1.7	-4.7	0.6	0.4	5.9	10.0*	16.3*	10.0*	9.2	4.8*	-4.4	-2.5
2004	-5.8*	-3.6	1.6	2.0	6.1	10.9*	15.0*	10.0*	8.9	4.8*	-0.9*	-3.4*
2005	-4.7*	-6.5*	-1.4*	1.1*	6.1*	7.7*	14.2*	8.9*	7.1*	3.2*	-3.0	-5.4
2006	-3.1	-6.2	-2.8	1.8	5.7	11.2	17.2	12.2	6.9	1.2	-1.6	-7.2
2007	-9.9	-3.4	0.4	0.9	6.7	11.2	16.9	13.3	6.5	2.0	-2.5	-6.4
2008	-8.0	-3.6	-3.3	-1.7	5.1	9.4	14.7	13.6	7.6*	1.7*	-0.3	-5.7
2009	-5.9	-4.6	-2.3*	0.1	7.3	11.9*	15.3*	**	11.0*	2.9*	-3.0*	-9.3*