

SEED PREDATION ON SLICKSPOT PEPPERGRASS
BY THE OWYHEE HARVESTER ANT

By

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The thesis presented by Joshua P. White entitled “Seed Predation on Slickspot
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CHAPTER 1: INTENSE SEED PREDATION
BY OWYHEE HARVESTER ANTS (*POGONOMYRMEX SALINUS*)
ON A RARE MUSTARD (*LEPIDIUM PAPILLIFERUM*)
ENDEMIC TO IDAHO

Abstract

- (1) Seed predation can significantly restrict the reproductive output and individual fitness of plants, particular those plants that are rare or endangered. In some cases the total seed loss can reach 100%. Owyhee harvester ants, *Pogonomyrmex salinus*, actively remove the fruits and seeds of slickspot peppergrass, *Lepidium papilliferum*, a rare mustard endemic to southwest Idaho.
- (2) Several experiments were conducted to quantify seed predation on *L. papilliferum* located within the foraging distance of *P. salinus*. Individuals exposed to harvester ants experienced a direct loss of fruits and seeds (> 40%), whereas plants shielded from ants suffered almost no seed loss. Harvester ants were also effective scavengers of seeds on the ground (removing > 90% of seeds from the ground).
- (3) All fruits and seeds collected by ants were returned to their nests and taken below ground. Of 100 successful foragers monitored all returned the fruit or seeds to the nest. A search of 30 middens revealed many empty *L. papilliferum* fruit husks but no intact seeds. Thus, it does not appear that the ants benefit *L. papilliferum* by dispersing their seeds.

(4) *Pogonomyrmex salinus* is the main seed predator of *L. papilliferum* and in some cases can remove and destroy complete seed sets of individuals. Seed removal of this magnitude suggests that *P. salinus* may significantly limit recruitment of new individuals of *L. papilliferum* and lead to further decline of this rare plant species.

Introduction

Individual plants are often faced with the consequences of herbivory, including reductions in growth, survival, and reproductive performance, all of which may impact their fitness (Harper, 1977; Maron, 1998; Mueller *et al.*, 2005). Loss of leaf and flower tissue can lead to reductions in the resources plants require for growth and chemical defenses, and it can create alterations to floral and vegetative structures, which adversely affect pollinator visitations (Herms & Mattson, 1992; Agrawal *et al.*, 1999; Leavitt & Robertson, 2006). An individual plant's fitness is affected directly when herbivory is focused on seeds or fruits because such actions cause an immediate reduction in the plant's reproductive success (Janzen, 1971; Castro *et al.*, 1999; Louda & Potvin, 1995; Weppeler & Stocklin, 2006). Over time, the selective pressure of seed loss may result in changes to the timing of reproduction as well as alteration of floral morphology and abundance (Brody, 1997; Parachnowitsch & Caruso, 2008). Seed predation can also affect biotic communities by altering a species' demographics, recruitment, and composition (Harmon & Stamp, 1992; Louda & Potvin, 1995; Weppeler & Stocklin, 2006).

The population-level consequences of seed predation are likely to be most evident in rare plants (i.e., species with small population sizes, high habitat specificity, and restricted geographic distributions [Rabinowitz, 1981]) because these plants are often reside in small, isolated populations with low reproductive potential and high risks of extinction (Fischer & Matthies, 1998). However, despite the heightened vulnerability of rare plants to seed predation, relatively few studies have examined the effects of seed removal on rare or threatened plants (but see Albert *et al.*, 2005). Nevertheless, because seed predation may accelerate a rare plant's decline, from a conservation perspective it is critical to assess whether seed predation is occurring, and if so, measure the magnitude of seed loss in order to gain a better understanding of how seed predation affects the species' population processes. The present study examined the occurrence and magnitude of seed predation by Owyhee harvester ants, *Pogonomyrmex salinus* Olsen (Hymenoptera: Formicidae), on slickspot peppergrass, *Lepidium papilliferum* [(L. Henderson) A. Nels. & J.F. Macbr.] (Capparales: Brassicaceae), a rare mustard endemic to sagebrush-steppe habitat in southwestern Idaho.

Within sagebrush-steppe habitat, *L. papilliferum* is restricted to micro-sites known as slick spots – shallow depressions of soil devoid of most other plants and characterized by high levels of clay and salt, as well as subsurface water retention that is higher than that of surrounding areas (Fisher *et al.*, 1996). Two main life history patterns have been described for the species - annual and biennial (Meyer *et al.*, 2005). Annuals germinate, grow, reproduce and die in one season, whereas biennials germinate and grow in the first summer, over-winter as vegetative rosettes, and then reproduce and die the following season. White and Robertson (unpublished data) identify a third, albeit uncommon, life

history pattern in which individuals flower to a limited extent late in their first year, and then again in their second year if they survive the winter. The life history trajectory an individual takes is influenced by environmental cues and an individual's physical state (Meyer *et al.*, 2005); however, no specific mechanisms controlling this pattern have been identified.

Lepidium papilliferum populations have experienced declines in number per population as well as the number of individual populations over the past century (Moseley, 1994). These declines have been attributed in large part to the degradation and fragmentation of suitable sagebrush-steppe habitat caused by wildfire, livestock grazing, rural development, and exotic species invasion (Moseley, 1994). However, to date researchers have not considered the possible role of seed predation on offspring recruitment and the long-term viability of the plant, even though throughout much of its range *L. papilliferum* shares habitat with the Owyhee harvester ant, *P. salinus*, a member of a genus known to be voracious consumers of plant seeds (MacMahon *et al.*, 2000). Until recently it was thought that *P. salinus* had little ecological relevance to *L. papilliferum* apart from being a minor contributor to pollination of its flowers (Leavitt, 2006). However, further observations revealed that *P. salinus* becomes a seed predator of *L. papilliferum* once flowering is complete and fruits are maturing on the plant. A study was therefore conducted to explore the extent to which *P. salinus* removes seeds from *L. papilliferum*, and to determine the fates of those seeds once they are removed from plants.

Materials and Methods

Study sites

The study was conducted in 2007 at three populations of *L. papilliferum* located near Boise, Idaho: Big Gulch (BG: 43°44'13.34"N / 116°26'22.66"W), Kuna Butte (KB: 43°23'14.49"N / 116°28'44.59"W), and Powerline (PL: 43°22'15.34" / 116°10'35.68"W). Within the last 10-15 years both BG and KB have experienced livestock grazing and disturbance by fire, and both sites are dominated by *Artemisia tridentata* (big sagebrush), *Poa secunda* (Sandberg bluegrass), *Ranunculus testiculatus* (bur buttercup), and the invasive grass *Bromus tectorum* (cheatgrass). By contrast, PL is considered to be in a more natural state because it is dominated by *A. tridentata* and *P. secunda*, with little or no *R. testiculatus* and *B. tectorum* present.

Seed predation experiment

Experiments were conducted to quantify seed loss caused by *P. salinus*. At each study site up to five slick spots with flowering *L. papilliferum* were selected, each being located within 10 m of an active *P. salinus* colony. Within each slick spot two plants were selected and matched for size, flowering phenology, and distance from the ant colony. One plant was randomly assigned to the treatment group and the other to the control group. Early in the flowering season, prior to the formation of fruits, a 15 cm high, 60-75 cm diameter plastic barrier was placed 2 cm deep in the soil around the base of each treatment plant. Ants could not ascend the barriers or travel beneath them, and

thus were denied access to treatment plants. The barriers were open at the top to allow access by insects that pollinate the plant (Fig. 1.1). No barrier was placed around control plants.

The treatment and control plants were visited weekly for the duration of the experiment. Because the large numbers of fruits produced by each plant made it impractical to assess total seed loss to predation, each plant was divided into six equal quadrants from above, and a random number table was used to select two inflorescences from each quadrant based on their height from the ground. Using these 12 inflorescences, the number of flowers, fruits, depredated fruits, and dehiscid fruits were counted. Distinguishing between depredated fruits and a dehiscid fruit was easy early in the season. When ants removed fruits they snipped the entire fruit from the plant, leaving behind a cleanly cut pedicel (Fig. 1.2a). By contrast, in the case of naturally dehiscid fruits either the fruit husk and/or ovary remained attached to the pedicel, or the entire pedicel withered and broke free from the plant. However, later in the season it became increasingly difficult to distinguish depredated fruits from dehiscid fruits. As fruits matured and dried out, ants changed their foraging behavior by opening the fruit and removing the seeds directly, leaving behind the husk and/or ovary in a manner similar to that found for naturally dehiscid fruits. At this point no inference about the fate of seeds was possible based on the appearance of plants, so the quantitative aspect of the experiment was replaced by direct observations of ants removing seeds from the plants.

The effect of site (BG, KB, PL) and treatment (exposed to ants [controls] *versus* shielded from ants) on amount of seed predation was analyzed using ANOVA with 3 x 2 factorial treatment structure (JMP in 5.1 SAS Institute Inc., 2004). The data for the three

sites and two treatments met all assumptions of the ANOVA, except in the case of the control group at KB, which was not normally distributed (Wilkes λ , $p = 0.007$). In that particular instance, the control plant of one pair was discovered by *P. salinus* approximately three weeks later than other plants at the site. As a result, this plant had only lost a small proportion of seed when the experiment was stopped. Because ants discovered this plant late in the experiment, both plants in the pair were excluded from the analysis, and all assumptions of the ANOVA were then met.

To establish whether animals other than *P. salinus* remove fruits from *L. papilliferum*, five fruiting *L. papilliferum* more than 25 m from the nearest *P. salinus* nest were selected at KB. (According to Jorgensen and Porter [1982] and Burris [2004], harvester ants will travel a maximum of 15-20 m from their colonies to forage.) These plants were monitored weekly for signs of fruit loss to predators. Statistical comparisons of seed loss between these plants and five plants that were surrounded by ant proofs barriers at the same site were made using a Mann Whitney U Test (JMP in 5.1, SAS Institute Inc., 2004).

Seed removal from the ground

Because *L. papilliferum* seeds that drop to the ground can also be harvested, an experiment was conducted at BG and KB to quantify how many seeds on the ground ants remove. Using the same treatment and control plants from the experiment described above ($n = 10$ pairs), 10 *L. papilliferum* seeds were placed on the ground in a 10 cm x 10 cm grid beneath each plant. The seeds were added early in the morning, prior to active foraging by *P. salinus*. The numbers of seeds remaining 3 h later were counted. The

experiment was repeated several weeks later at the same locations. Any differences in seed number between control and treatment plants were attributed to harvester ant foraging because no other insects were ever observed carrying or consuming *L. papilliferum* seeds. Statistical comparisons were made using a Mann-Whitney U test (JMP in 5.1, SAS Institute Inc., 2004).

Fate of depredated seeds

To determine the fate of seed-bearing fruits collected by *P. salinus*, 50 ants each at Big Gulch and Kuna Butte were observed from the time they collected a mature fruit on a plant until the fruit was either discarded or taken inside the ant nest (Fig. 1.2b). In addition, the middens of 15 ant colonies at these two sites were examined for signs of *L. papilliferum* seed predation (i.e., discarded fruit husks), as well as for the presence of intact fruits or seeds. Intact *L. papilliferum* seeds found in middens were to be returned to the laboratory to determine whether they were capable of germination; however, none were found.

Results

Seed predation experiment

Data collected in this study showed that plants exposed to harvester ants suffered higher levels of fruit loss than plants shielded from ants. The differences in total percent fruit loss between treatment and control plants were statistically significant (Fig. 1.3, table 1.1; two-factor ANOVA $F_{1,18} = 71.03$, $p < 0.0001$). There was no significant

interaction between the site and treatment group ($F_{2,18} = 0.28$, $p = 0.79$), nor was there a significant effect of site on seed predation ($F_{2,18} = 0.75$, $p = 0.49$). Determining the fate of seeds after they dehisced from plants was hampered when ants changed their foraging behavior (see Methods). Therefore, direct assessment of seed loss caused by harvester ant foraging was concluded as soon as this change in behavior was observed. The 40% cumulative fruit loss shown in Fig. 1.3 is conservative because ants continued to remove fruits from plants after quantitative measurements were stopped.

Lepidium papilliferum located at least 25 m from a *P. salinus* nest showed no signs of seed predation, and there was no significant difference in seed loss between plants that were more than 25 m from an ant nest and those that were surrounded by ant-proof barriers (Mann-Whitney U test, $n = 10$, $p = 0.91$). Thus, at KB at least, *P. salinus* was the only major seed predator of *L. papilliferum*.

Seed removal from the ground

Ants were efficient scavengers of *L. papilliferum* seeds placed on the ground. More than 90% of seeds placed on the ground and exposed to ants disappeared within 3 h, whereas less than 10% of seeds placed on the soil within ant-proof barriers went missing over the same period of time (Fig. 1.4; Mann Whitney U Test, $n = 20$, $p < 0.0001$). Wind cannot explain the difference between treatment and control because the experiment was conducted on calm days.

Fate of depredated seeds

Of the 100 ants observed carrying an *L. papilliferum* fruit from a plant, 10 dropped the fruit at some point before reaching their nest. However, in all 10 cases the fruits were quickly recovered and successfully transported to the nest. Ultimately, all 100 ants carried the fruits into their nests, after which time the fate of the fruits is unknown. Ants were frequently observed leaving their nests and depositing empty *L. papilliferum* fruit husks on the midden, along with debris from other plants. Despite intensive searching, no intact fruits or *L. papilliferum* seeds were found in any of the 30 middens sampled.

Discussion

Harvester ants are widely recognized as important seed consumers in low nutrient and dry environments (Morton, 1985; Beattie & Hughes, 2002). Their influence may become particularly relevant for rare and endangered plant species where high predation rates can have a major influence on a species' survival (Albert *et al.*, 2005). Indeed, the high rates of seed predation imposed by *Pogonomyrmex salinus* on the rare mustard *Lepidium papilliferum* may represent a significant threat to the plant's long-term viability. Harvester ant colonies are a prominent feature of many *L. papilliferum* populations, and this study has shown that *P. salinus* are capable of removing large numbers of fruit and seed, leaving affected plants with few seeds to contribute to the next generation.

At least 40% of seed-bearing fruits were removed directly from *L. papilliferum* before it became difficult to distinguish between depredated seeds and those that had dehisced naturally from their fruits. However, seed loss attributable to *P. salinus* was not completely reflected in the amount of fruits or seeds removed from plants; the ants also collected and returned to their nests many fruits and seeds lying on the ground. More than 90% of *L. papilliferum* seeds placed on the ground were lost within 3 h when *P. salinus* were allowed access to them. By contrast, almost no seeds were lost over the same period of time when *P. salinus* were denied access to the seeds, suggesting that *P. salinus* are efficient scavengers. The direct loss of seeds from plants, combined with those scavenged off the ground, suggest that at least some *L. papilliferum* experience nearly complete seed loss to *P. salinus*. Such a high level of seed predation by harvester ants is not unprecedented when a particular plant species is a preferred food source, as is the case for *P. occidentalis* foraging on the seeds of *Alyssum desertorum* (Crist & MacMahon, 1992). The intensity of seed predation by *P. salinus* on *L. papilliferum* may be exacerbated by the plant's clumped distributions within sagebrush-steppe habitat. Because *L. papilliferum* is more-or-less restricted to growing within the boundaries of slick spots, dense aggregations of seeds are created. By creating a profitable and predictably available resource, dense aggregations of seeds create resource rich patches that may facilitate rapid removal by harvester ants (Hughes & Westoby, 1990; Gorb & Gorb, 2000).

High levels of seed loss may be sufficient to drive a rare species such as *L. papilliferum* to extinction (see Carlson and Whitford [1991] for other examples), or it may put such species at a competitive disadvantage to species less affected by seed

predation (Inouye *et al.*, 1980). In arid environments, seed predation may alter the local abundance and distribution of semelparous species (Beattie & Hughes, 2002). For example, Brown *et al.* (1979) documented a 50% increase in desert annuals within two years of excluding harvester ants from the area, demonstrating that these ants can play a significant role in determining local plant abundance. Given the limited distribution, specific habitat requirements, and declining numbers of *L. papilliferum*, similar efforts to limit seed predation by *P. salinus* may be warranted.

Although seed removal by predators is generally viewed as being detrimental to plants, in some cases it may also serve as an effective seed dispersal mechanism (Janzen, 1971; Crawley, 2000), including instances when secondary dispersers move seeds abandoned by seed predators (Dean & Yeaton, 1992). However, in the case of *L. papilliferum* it is unlikely that harvester ants or some secondary mechanism serve as effective seed dispersers. Of the 100 ants observed carrying fruits to their nests, all arrived at their nests successfully and carried the fruit below ground. Although the ultimate fates of those seeds are not known, harvester ants are granivores and thus likely consumed them. Although others have reported that viable seeds collected by harvester ants sometimes escape consumption and end up in middens (MacMahon *et al.*, 2000), no intact *L. papilliferum* fruits or seeds were found in *P. salinus* middens in our study. Moreover, even if *L. papilliferum* seeds are occasionally lost or discarded by ants, the narrow habitat requirements of *L. papilliferum*, combined with the nest-clearing habits of *P. salinus*, make the likelihood of successful germination and survival unlikely. Any plant that germinates on a midden would be quickly destroyed because *Pogonomyrmex* ants clear all herbaceous vegetation growing within approximately 1 m of their nests

(MacMahon *et al.*, 2000; personal observations). Moreover, although many types of plants germinate and grow on the middens of abandoned *Pogonomyrmex* colony mounds (Coffin & Lauenroth, 2000; Gordon, 2000), most *P. salinus* colonies lie outside of slick spots and thus would not offer the proper habitat for *L. papilliferum* to thrive. The same constraint on survival would be true for seeds dropped in transit to ant colonies once the ants left slick spots.

Owyhee harvester ants appear to be the only seed predators of *L. papilliferum*. There was no evidence of seed predation occurring beyond 20 m from a *P. salinus* colony, which is consistent with the maximum foraging distance previously described for harvester ants (Burris, 2004). Moreover, during eight years of study no other animals have been observed removing or consuming *L. papilliferum* fruits or seeds (personal observations). Although *L. papilliferum* is susceptible to other forms of herbivory, these do not appear to have significant population-level consequences for the plant. For example, florivory by chrysomelid beetles reduces the effectiveness of insect-mediated pollination by up to 50% (Leavitt & Robertson, 2006); however, these beetles are usually found only late in the season when most pollination has already taken place (Robertson *et al.*, 2004). Likewise, plutellid moth larvae feed on the leaves of *L. papilliferum*, but they are patchily distributed and seldom encountered (Robertson *et al.*, 2004). Thus, *P. salinus* appears to be the only numerically significant herbivore, seed predator or otherwise, of *L. papilliferum*. Nevertheless, one should be mindful that herbivore numbers often fluctuate, so species that currently seem innocuous may become problematic in the future.

The overall significance of seed predation for *L. papilliferum* populations remains an open question. Although *P. salinus* can exact a large toll on offspring production by individual *L. papilliferum*, the implications of seed predation to the long term viability of the plant requires information about the extent to which *P. salinus* and *L. papilliferum* overlap throughout the plant's range, and whether specific habitat attributes provide conditions that would promote further proliferation of ants in the future. Throughout the plant's range, as well as the western United States in general, disturbance events such as fire are facilitating the replacement of natural sagebrush-steppe habitat with annual grassland (Rosentreter, 1992; Hilty *et al.*, 2003). While we are unsure about historical distributions of harvester ant colonies and how disturbance may affect them, the shift in vegetation may allow harvester ants to colonize or expand their numbers within areas that historically were not favorable for nesting. For example, habitat disturbance by humans has contributed to the expansion of both range and nesting densities in *P. occidentalis* (DeMers, 1993), a close relative of *P. salinus* according to Shattuck (1987). Understanding the factors that contribute to colonization and nesting success by *P. salinus* in areas where *L. papilliferum* grows may prove critical to the development of a meaningful approach for managing and conserving this rare mustard endemic to southwestern Idaho.

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Figure 1.1. Design of the seed predation experiment. A plastic barrier was placed around treatment plants to prevent access by harvester ants. By contrast, control plants were vulnerable to seed predation by ants.

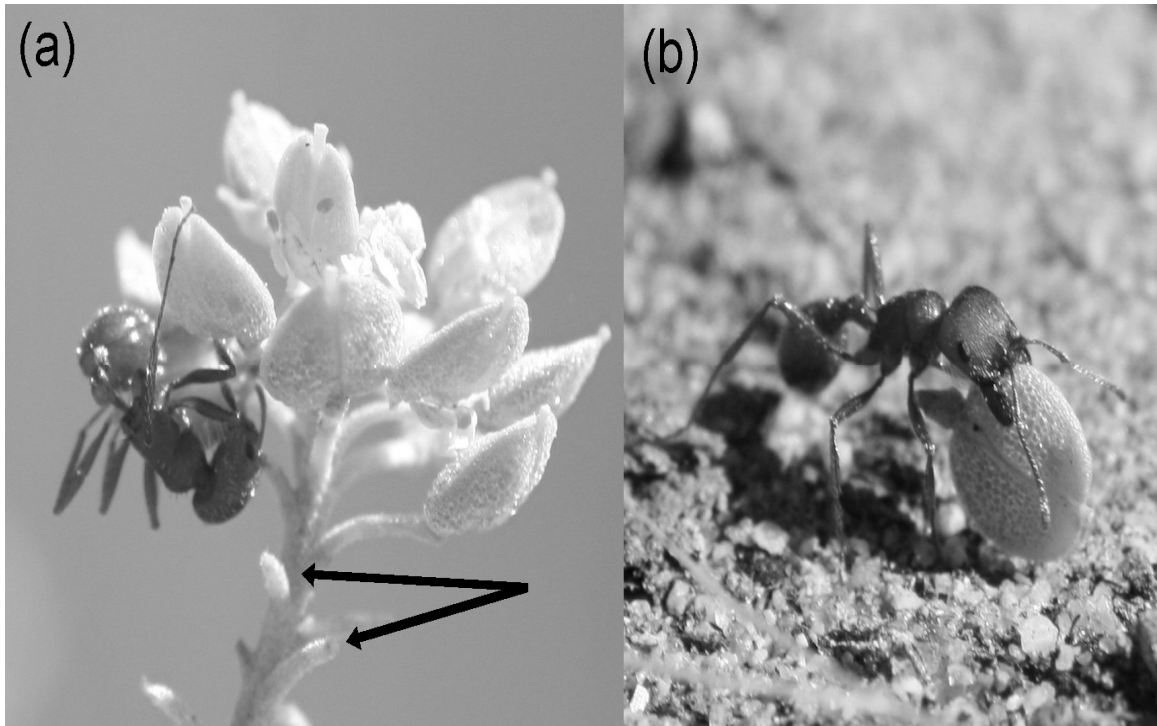


Figure 1.2. (a) *P. salinus* removing a mature fruit from *L. papilliferum*. The arrows show locations of fruits that were excised earlier by ants. (b) *P. salinus* returning an *L. papilliferum* fruit to its colony.

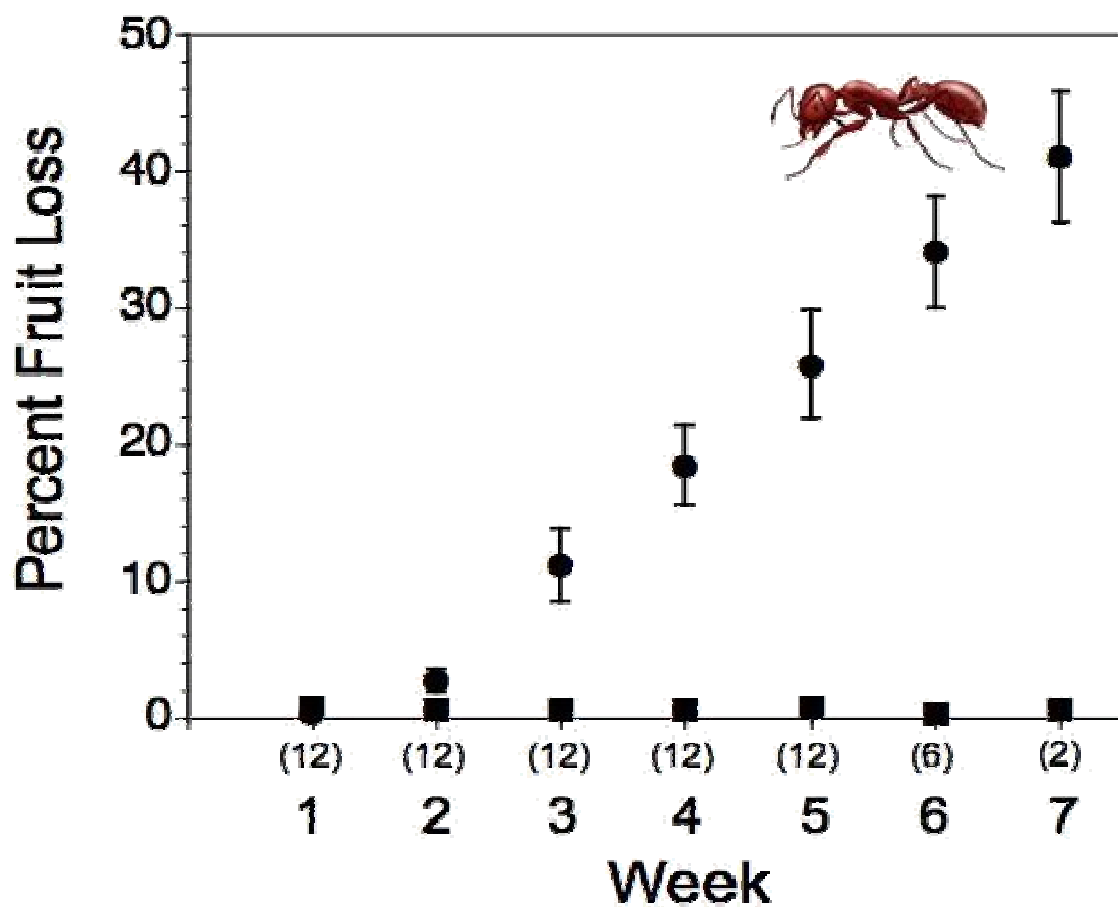


Figure 1.3. Graph showing the results of the seed predation experiment. The points represent the mean percent fruit loss to harvester ants \pm SE. Circles represent plants exposed to ants, whereas squares represent plants with an ant barrier surrounding them. Sample sizes are shown in parenthesis. There was a significant difference in fruit loss when comparing the total amount lost between the two groups ($F_{1,18} = 71.03$, $p < 0.0001$) the treatment group lost less than 1% of its fruits (and seeds) while the control group lost $> 40\%$ of its fruits and seeds.

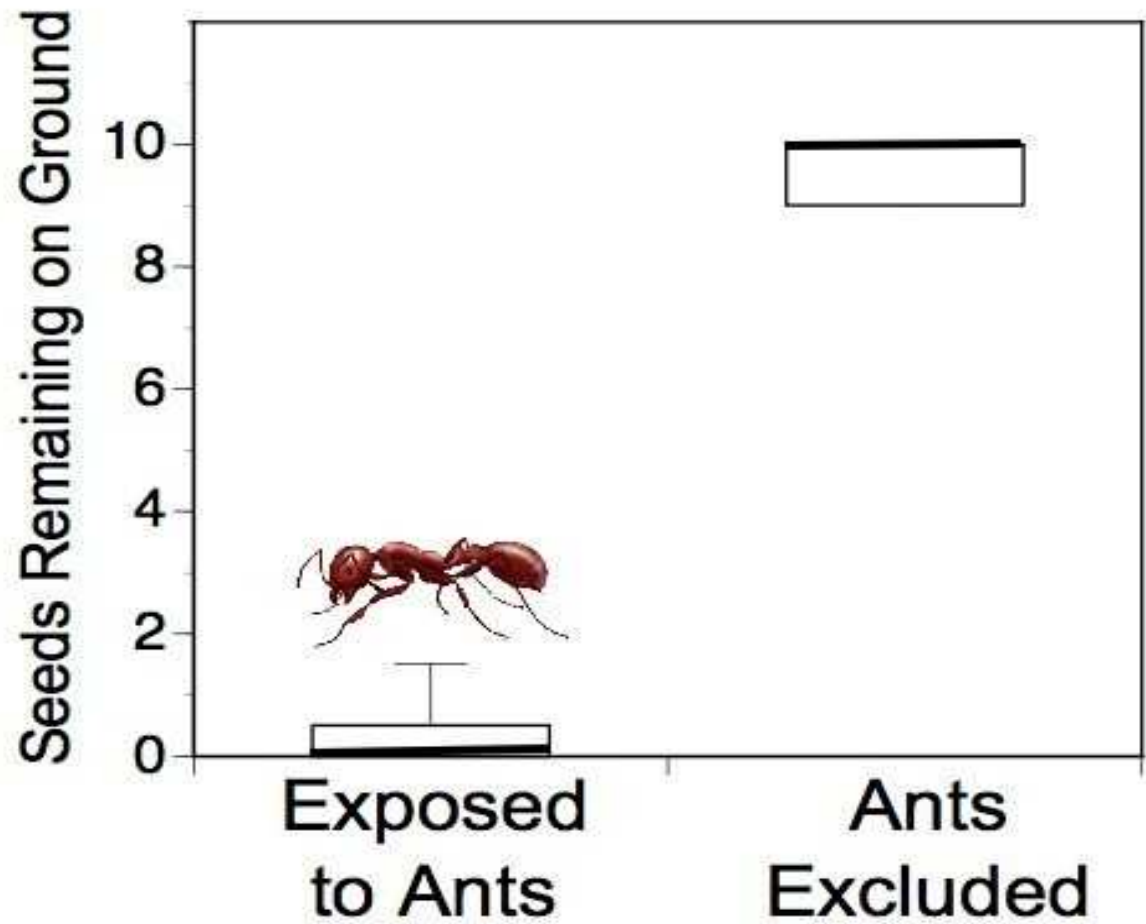


Figure 1.4. Box plot chart showing the difference between the numbers of seeds foraged from the ground in both the treatment and control groups. Less than 1 out of 10 seed was remaining in the control group while more than 9 out of 10 were left in the treatment group. This difference is significant using the non-parametric Mann-Whitney U test ($n = 20$, $p < 0.0001$).

Table 1.1. Source Table for the Two-factor ANOVA Examining Differences in Seed Loss from the Individual Plants.

Source	DF	Sum of Squares	Mean Square	F Value	P Value
Treatment	1	0.61172366	0.61172366	71.03	<0.0001
Site	2	0.01286296	0.00643148	0.75	0.4880
Treatment X Site	2	0.00480474	0.00240237	0.28	0.7598
Error	18	0.15501028	0.00861168		
Total	23	0.78882342			

CHAPTER 2: INCREASED SEED PREDATION
BY OWYHEE HARVESTER ANTS THREATENS
THE SURVIVAL OF SLICKSPOT PEPPERGRASS, A RARE
MUSTARD IN SOUTHWEST IDAHO

Abstract

- (1) Anthropogenic disturbance is responsible for shifts in the composition and structure of many biotic communities. Disruptions to communities can promote the success of non-indigenous species, and they can shift the roles of native species in ways that parallel exotic species invasions. Within southwest Idaho, the conversion of sagebrush-steppe habitat to areas dominated by grasses may be fueling the expansion of the Owyhee harvester ant, *Pogonomyrmex salinus*, a native granivore that can remove and destroy large quantities of seed from many plant species, including the rare mustard slickspot peppergrass, *Lepidium papilliferum*.
- (2) Ten sites with flowering *L. papilliferum* were mapped to show the distribution of *P. salinus* colonies relative to slick spots occupied by *L. papilliferum*. In total, 110 slick spots contained *L. papilliferum*, 69 of which were located within 20 m of a *P. salinus* colony. Of those 69 slick spots, 52 (75%) showed signs of seed loss to the ants.
- (3) Across 29 *L. papilliferum* populations there was a significant inverse relationship between the number of *P. salinus* colonies and the abundance of big sagebrush, *Artemisia tridentata* ($\beta = -1.07$, $p = 0.0017$). Conversely, there was a positive

correlation between the number of *P. salinus* colonies and Sandberg bluegrass, *Poa secunda* ($\beta = 39.73$, $p = 0.036$).

- (4) Given the large amount of overlap in habitat between *P. salinus* and *L. papilliferum* across the plant's range, and the extent to which *P. salinus* eliminates *L. papilliferum* seeds from contributing to future generations, the presence of big sagebrush appears critical to the plant's prospects for survival. Therefore, a premium must be placed on restoration and rehabilitation of sagebrush steppe to conserve the natural community structure and minimize the risk to native plants from seed predation by harvester ants.

Introduction

Anthropogenic disturbances can cause dramatic changes in the composition and structure of biological communities (Hannah *et al.*, 1994; Laurance *et al.*, 1998; Hooper *et al.*, 2005). Human development and agriculture, altered fire regimes, as well as the introduction of exotic species can affect the species composition of many communities, shifting them to a less diverse state (D'Antonio & Vitousek, 1992; Vitousek *et al.*, 1997; Smart *et al.*, 2006; Krezewski & Waller, 2008). This modification of community structure, known as biotic homogenization (McKinney and Lockwood, 1999), is characterized by a decrease in diversity and abundance of native species (D'Antonio & Vitousek, 1992; Fukami *et al.*, 2001), and an increase in exotic invasive species (Elton, 1958; Levine & D'Antonio, 1999). Disruptions to communities can also result in shifts in the role of native species in ways that parallel exotic species invasions (Knops *et al.*,

1999; Naeem *et al.*, 2000). The benefactors of such releases have been termed “winning” species because of specific characteristics that allow them to succeed in disturbed homogenized communities (McKinney & Lockwood, 1999). Winning species often effect changes in disturbed communities in ways that resemble those of exotic species, including increased predation, competition, and habitat alteration, all of which may serve to further degrade the natural composition of the community (Goodrich and Buskirk 1995).

Biotic homogenization is occurring at an unprecedented rate in the Great Basin of the western United States (West, 1999; Hemstrom *et al.*, 2002; Dahlgren *et al.*, 2006; Hemstrom *et al.*, 2007). Less than 20% of natural sagebrush-steppe habitat within this region remains unaltered by human activity (West, 1999). Sagebrush dominated habitat in many areas has given way to herbaceous grasses such as cheatgrass, *Bromus tectorum*, an invasive exotic species (Mack, 1981; Rosentreter, 1992; Prater & DeLucia, 2006). Such shifts in community composition and structure, while detrimental to sagebrush-obligate species like the greater sage grouse (*Centrocercus urophasianus*) and pygmy rabbit (*Brachylagus idahoensis*) (Crawford *et al.*, 2004; Gabler *et al.*, 2001), may provide other native species with opportunities for expansion. The Owyhee harvester ant, *Pogonomyrmex salinus* Olsen, may be a species that is “winning” in response to biotic homogenization. Grasslands provide these ants with a large seed base for foraging, as well as ideal habitat for nesting because the *Pogonomyrmex* ants can easily clear all herbaceous vegetation in a 1-2 m radius around their nests (MacMahon *et al.*, 2000). The removal of vegetation is critical to colony success, perhaps through its effects on the

temperature of colonies (Cole, 1994; Bucy & Breed, 2006), the reduction of cover for predators (Mackay, 1982), and/or the reduction of roots that break up underground chambers (Wu, 1990).

The success of *P. salinus* may represent a threat to the long-term viability of native plant species, including slickspot peppergrass, *Lepidium papilliferum* [(L.F. Hend.) A. Nels. and J.F. Macbr], a rare mustard (Brassicaceae) endemic to sagebrush-steppe habitat in southwest Idaho. Within sagebrush-steppe habitat, as well as the grasslands that have supplanted sagebrush in many areas, *L. papilliferum* is restricted to microsites known as slick spots. Slick spots have higher levels of clay, salt, and water retention than surrounding areas, and are generally devoid of other plant species (Meyer, 1995; Quinney, 1998). Flowering in *L. papilliferum* typically extends from early May to late June. The plant reaches 10 to 40 cm in height and has numerous, multi-flowered inflorescences that terminate at the branches. Its small, white cruciferous flowers, which number from a dozen or so to several thousand per plant, are reliant on insects for pollination (Robertson & Klemash, 2003). Mature fruits dehisce their seeds to the substrate below in late summer, and may persist in a seed bank for up to 12 years (Meyer *et al.*, 2005). Over the past several decades, *L. papilliferum* has declined dramatically in numbers in response to habitat fragmentation, human disturbance, fire, and invasion by exotic plant species (Moseley, 1994). High levels of seed predation by Owyhee harvester ants may compound the problems for survival already faced by *L. papilliferum*. When *P. salinus* colonies are located within 20 m of fruiting *L. papilliferum*, the ants are capable of collecting, removing, and destroying more than 90% of an individual plant's fruits and seeds (Chapter 1).

Although it is clear that *P. salinus* can collect and destroy large numbers of *L. papilliferum* seeds, it is less certain whether the ants represent a significant threat to the plant's survival because the extent to which the two species overlap has not been clearly established. Therefore, in the present study I surveyed *L. papilliferum* populations throughout the plant's range and measured the abundance of *P. salinus* colonies within each population. Also, within all populations I measured under-story and over-story vegetation in relation to the abundance of harvester ant colonies. Because harvester ants clear vegetation from the vicinity of their nest mounds, I hypothesized that the ants would be more abundant in areas with herbaceous vegetation that could easily be cleared than in areas with woody vegetation such as sagebrush. Finally, because seed predation may have a significant influence on *L. papilliferum*'s prospects for survival, I examined the spatial relationships among *L. papilliferum* and *P. salinus* colonies to establish, at a local scale, the extent to which *L. papilliferum* are currently at risk of seed predation.

Materials and Methods

Site selection and mapping

The study was conducted from June through mid August 2008. I selected a total of 29 *L. papilliferum* populations located throughout that plant's range (Fig. 2.1). Within each of the selected sites I conducted a thorough, systematic search for active *P. salinus* colonies and for slick spots with flowering *L. papilliferum*. A hand-held GPS was used to record the locations of ant colonies and *L. papilliferum* at each site. In populations where Owyhee harvester ants and slickspot peppergrass co-occurred, I searched for signs

of *L. papilliferum* seed predation by noting instances in which ants were seen carrying the plant's fruits, and by noting the presence of discarded *L. papilliferum* fruit husks in the middens (refuse piles) of ant colonies. Using the locations of *L. papilliferum* and *P. salinus* mounds I used ARC-Map (ARC GIS 9.1) to create a map of each site. The boundaries of sites were chosen to ensure that they encompassed all slick spots populated by *L. papilliferum*, and that the site encompassed an area of at least 10,000 m².

Vegetation analysis

I used the line-intercept method (Canfield, 1941; Bonham, 1989) to measure percent coverage of big sagebrush, *Artemisia tridentata*, at each of my study sites. Big sagebrush is the dominant over story species throughout much of the region especially in areas inhabited by *L. papilliferum* (personal observation). At each site I conducted 10, 100 m long parallel transects spaced equidistant within each study area to ensure complete coverage. Along each transect I recorded the cumulative distance occupied by sagebrush. Percent over-story coverage at a site was calculated as the mean percent coverage across the 10 transects.

To measure percent under-story canopy coverage at each of the sites I used the quadrat plot frame technique (Gauch, 1982; Scheller & Mladenoff, 2002). Using a 1 m² quadrat frame, sectioned into smaller squares (20 cm²), at a randomly determined location along each line transect. I visually estimated the percent coverage for each herbaceous plant species as the amount of the plot frame covered by each species. Percent under-story coverage was calculated as the mean percent that each species covered within the plot frame across the 10 samples taken at a site.

Statistical analysis

Analysis of the relationship between ant mound abundance and habitat attributes was conducted using the Fit Model platform in JMP in 5.1 (SAS Institute Inc. 2004). For the model I considered three kinds of vegetation: big sagebrush, *Artemisia tridentata* (over-story percent cover), Sandberg bluegrass, *Poa secunda* (under-story percent cover), and cheatgrass, *Bromus tectorum* (under-story percent cover). Other types of under-story vegetation were excluded from the analysis because they were numerically rare relative to the two dominant grasses. Variables retained in the model were selected using a stepwise forward procedure. The probability to enter the model was set at 0.250 and the probability to exit the model was set at 0.100. Before running the model I tested the assumptions of non-correlation between variables and multi-collinearity using JMP in 5.1.

Results

Of the 29 sites included in this analysis, only 10 contained slick spots with flowering *L. papilliferum* in 2008. These 10 sites, which contained a total of 110 slick spots occupied by flowering *L. papilliferum*, were mapped to show the spatial relationships among *P. salinus* colonies and *L. papilliferum* (refer to Appendices A1-A10 for a map of each site). Although each site was unique in terms of the abundance and distribution of ant colonies and flowering *L. papilliferum*, a clear pattern emerged from the data: few slick spots located within 20 m of an Owyhee harvester ant colony (or colonies) escaped seed predation. Of the 110 slick spots across the 10 sites that contained flowering *L. papilliferum*, 69 were located within 20 m of an ant colony (Table 2.1). Of

those 69 slick spots, 52 (75%) showed direct evidence of seed predation by *P. salinus*. It is also clear from the data that *P. salinus* colonies do not require *L. papilliferum* seeds in order to survive. Many successful ant colonies were situated more than 20 m from *L. papilliferum* and showed no evidence of *L. papilliferum* seeds in their middens (e.g., Fig 2.2). Seeds from Sandberg bluegrass and cheatgrass dominated the middens of all Owyhee harvester ant colonies, regardless of their proximity to *L. papilliferum*.

The abundance of ant colonies was significantly correlated with both over-story and under-story vegetation as described by the equation:

$$AB = 39.63 - OSC(1.07) + USC(39.73) \quad [\text{Eqn. 1}],$$

where AB is the number of ant mounds per ha, OSC is percent over-story cover, and USC is percent under-story cover represented by Sandberg bluegrass ($F_{2,26} = 18.59$, $r^2 = 0.42$, $p < 0.05$). The abundance of ant colonies showed a significant inverse correlation with the abundance of big sagebrush (Fig. 3, $\beta = -1.07$, $p = 0.0017$) and a significant positive correlation with Sandberg bluegrass (Fig. 4, $\beta = 39.73$, $p = 0.036$). Cheatgrass was not retained by the model likely because of its significant inverse correlation with sagebrush (Spearman's Rank Correlation, $Rho = -0.416$, $p = 0.025$) which violates an assumption of the model. Details of the over-story and under-story vegetation coverage at each of the 29 sites sampled are provided in Appendix B.

Discussion

Human mediated habitat disturbance can alter biological communities by upsetting the balance among native species (Hobbs & Huenneke, 1992). In the case of the Owyhee harvester ant, loss of big sagebrush appears to create ideal habitat for successful colony formation, perhaps exemplifying McKinney and Lockwood's (1999) notion of a native species that is "winning" in the face of biotic homogenization. For *L. papilliferum*, habitat shifts that promote the expansion and success of a seed predator like *P. salinus* add to the list of problems faced by the plant as a result of habitat degradation. Given the large amount of overlap in habitat between *P. salinus* and *L. papilliferum* across the plant's range, and the extent to which *P. salinus* eliminates *L. papilliferum* seeds from contributing to future generations (Chapter 1; Table 2.1), the presence of big sagebrush may be critical to the plant's continued survival.

The significant inverse relationship between big sagebrush and the abundance of ant colonies is consistent with the general observation that ants in the genus *Pogonomyrmex* prefer to nest in areas where vegetation and debris can be cleared from the immediate vicinity of nests (MacMahon *et al.*, 2000). Harvester ants obviously are ill-equipped to remove sagebrush, so either they are avoiding nesting in areas with sagebrush or they are failing in their attempts to nest there. In the few cases in which ant colonies were found in sagebrush-dominated habitat, the colonies were located in relatively open areas (personal observation).

While the loss of sagebrush removes a structural impediment to colonization by harvester ants, the subsequent transition to grasses presents the ants with little structural barriers and an abundant food source. Sandberg bluegrass was the dominant plant

species in the under-story at many of our study sites, reaching coverages of up to 75%. This species is often included in native plant seed mixes (Biondini & Redente, 1986; Cotts *et al.*, 1991) for reclamation of disturbed sagebrush habitat and the restoration of native rangeland. However, because disturbance (e.g., rangeland fires) generally benefits *P. secunda*, the amount of this grass may be increasing (Tueller, 1962; Daubenmeyer 1975). An unintended consequence of this action is that *P. secunda* may provide harvester ants with an abundant source of food that will not affect the ant's ability to clear the area around nest mounds. Further, Downs et al. (1995) found that post-fire restoration of sagebrush from seed was more successful when sites were pretreated with herbicide to remove herbaceous vegetation like *P. secunda*, and that the early germination and growth of sagebrush may be restricted by large amounts of under-story vegetation. Thus, the seeding of Sandberg bluegrass may be an impediment to sagebrush restoration and lead to an increase in harvester ant colonies. On the other hand, in the absence of Sandberg bluegrass the sites would likely become dominated with *B. tectorum*, which would probably also serve the needs of Owyhee harvester ants. The more pressing problem is the lack of sagebrush recovery following disturbance.

Within habitats dominated by grasses, *P. salinus* colonies ranged from uncommon to very common. Sites dominated by grasses but with low numbers of *P. salinus* likely represent areas recently disturbed where ants have yet to fully colonize. Alternatively, these sites maybe unsuitable for *P. salinus* for reasons other than vegetation. Regardless, it is clear that at least some areas without sagebrush, in contrast to those with sagebrush, have the capacity to sustain large numbers of harvester ant colonies. This relationship raises a concern for the conservation of *L. papilliferum* because throughout the plant's

range, as well as the western United States in general, disturbance events such as fire are causing natural sagebrush steppe habitat to be replaced by grasslands (Rosentreter, 1992; Hilty *et al.*, 2003). The shift from sagebrush to grasses may allow harvester ants to colonize areas that historically were not suitable for nesting. Such influxes of ants could have a profound effect on the plants remaining in those areas because the ants can remove and destroy large numbers of seeds. Seed predation has been linked to significant decreases in both abundance and species richness within plant communities (Inouye *et al.*, 1980; Carlson & Whitford, 1991; Samson *et al.*, 1992), which can spell disaster for native species that are already rare or in decline (Albert *et al.*, 2005).

To illustrate the risk that harvester ants pose even to populations of *L. papilliferum* that currently suffer little or no seed predation, consider the “Red Tie” population shown in Fig. 2.5. This population is dominated by basin big sagebrush, with *L. papilliferum* interspersed throughout. There is little contact between *L. papilliferum* and *P. salinus* throughout most of the site. However, at the eastern edge of the site the vegetation transitions from sagebrush to more open, grassy areas. Three *P. salinus* colonies are located in this area. Given the proximity of these ant colonies to *L. papilliferum*, a fire or other disturbance event that removes sagebrush and promotes growth of herbaceous vegetation may create suitable conditions for the rapid expansion of *P. salinus* into the ant-free areas currently occupied by *L. papilliferum*. Because similar scenarios are likely repeated throughout *L. papilliferum*'s range, resource managers should place a premium on preserving and rehabilitating sagebrush habitat within *L. papilliferum* populations to keep *P. salinus* numbers in check, and they should monitor areas surrounding *L. papilliferum* habitat that may serve as sources of harvester

ants when conditions favor expansion. Goodrich and Buskirk (1995) suggest that habitat restoration should be the focus of efforts to control pest species within disturbed habitats, while active control measures (such as eradication and exclusion) should only be considered to buy time in the short term or as a final option because of monetary costs, possible unacceptable social responses, and unpredicted affects on native community structure. Active control measures should only be attempted after there has been careful assessment of the possible consequences for non-target organisms.

It should be noted that although *P. salinus* has the capacity to remove substantial amounts of seed from *L. papilliferum* (Chapter 1), the consequences for *L. papilliferum* recruitment may be difficult to detect in the short term if the overlap in habitat between *P. salinus* and *L. papilliferum* is a relatively new phenomenon, or if the high intensity of predation is new owing to recent increases in ant populations. (Although *P. salinus* is native to southwest Idaho, it is unclear whether their numbers have increased dramatically in recent years in response to altered habitat.) Because *L. papilliferum* within slick spots produce seed banks that can last up to 12 years (Meyer *et al.*, 2005), new plants may continue to germinate for some time even if seed predation is preventing the seed bank from being replenished. In areas where predation pressure on seeds remains high year after year, *L. papilliferum* numbers will likely decline drop precipitously once the seed bank is depleted – analyses of population structure suggest that the plant has limited capacity for seed dispersal among slick spots (Robertson & Ulappa, 2004; Billinge & Robertson, 2008). Thus, although rehabilitation of basin big sagebrush should remain the ultimate goal of conservation efforts, in the short term it

may be necessary to consider the control of *P. salinus* colonies located within 20 m of flowering *L. papilliferum* because these ants represent an immediate danger to the plant's survival.

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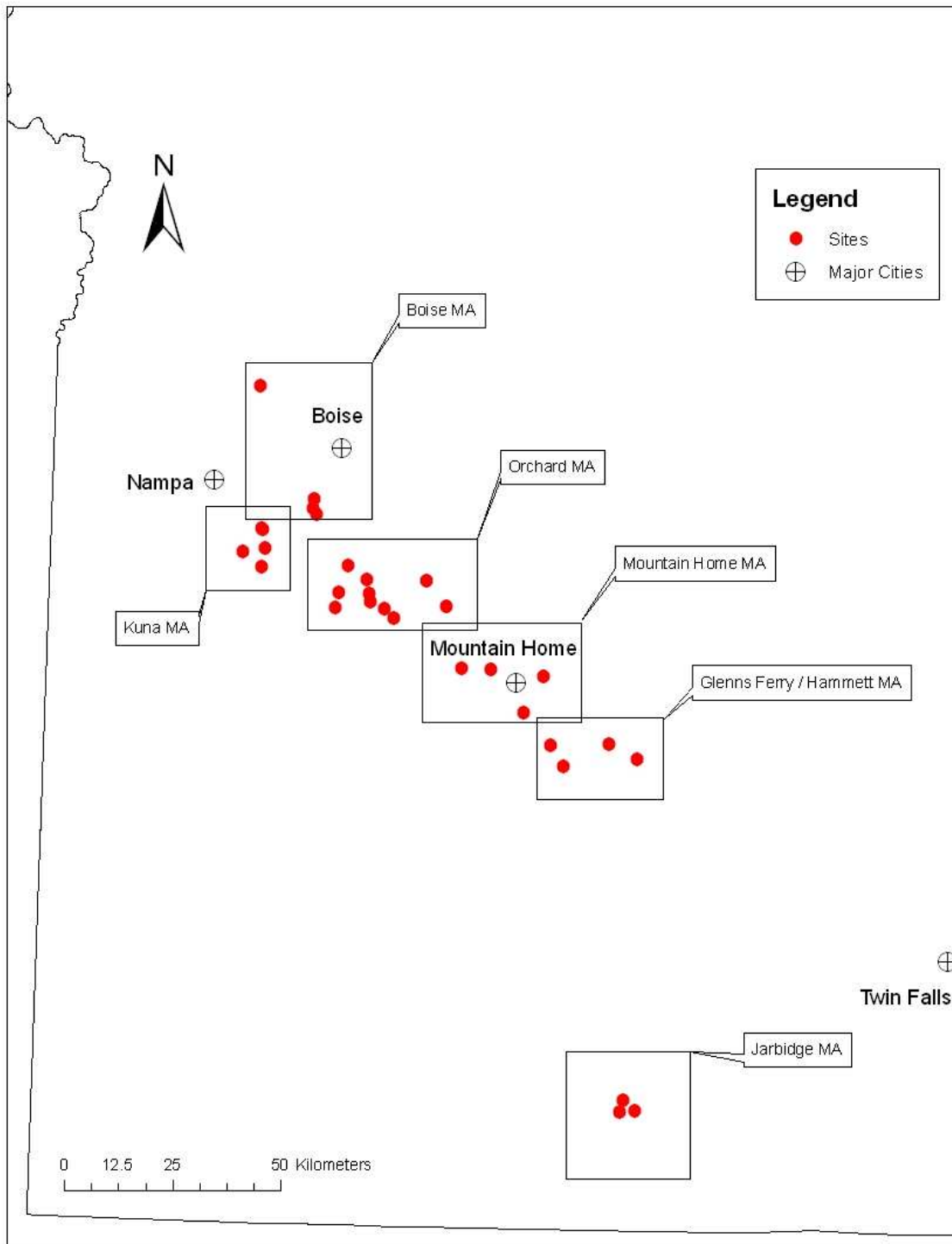


Figure 2.1. Map of Southwest Idaho showing 29 study sites. MA's are management areas as delineated by the Idaho Conservation Data Center 2005.

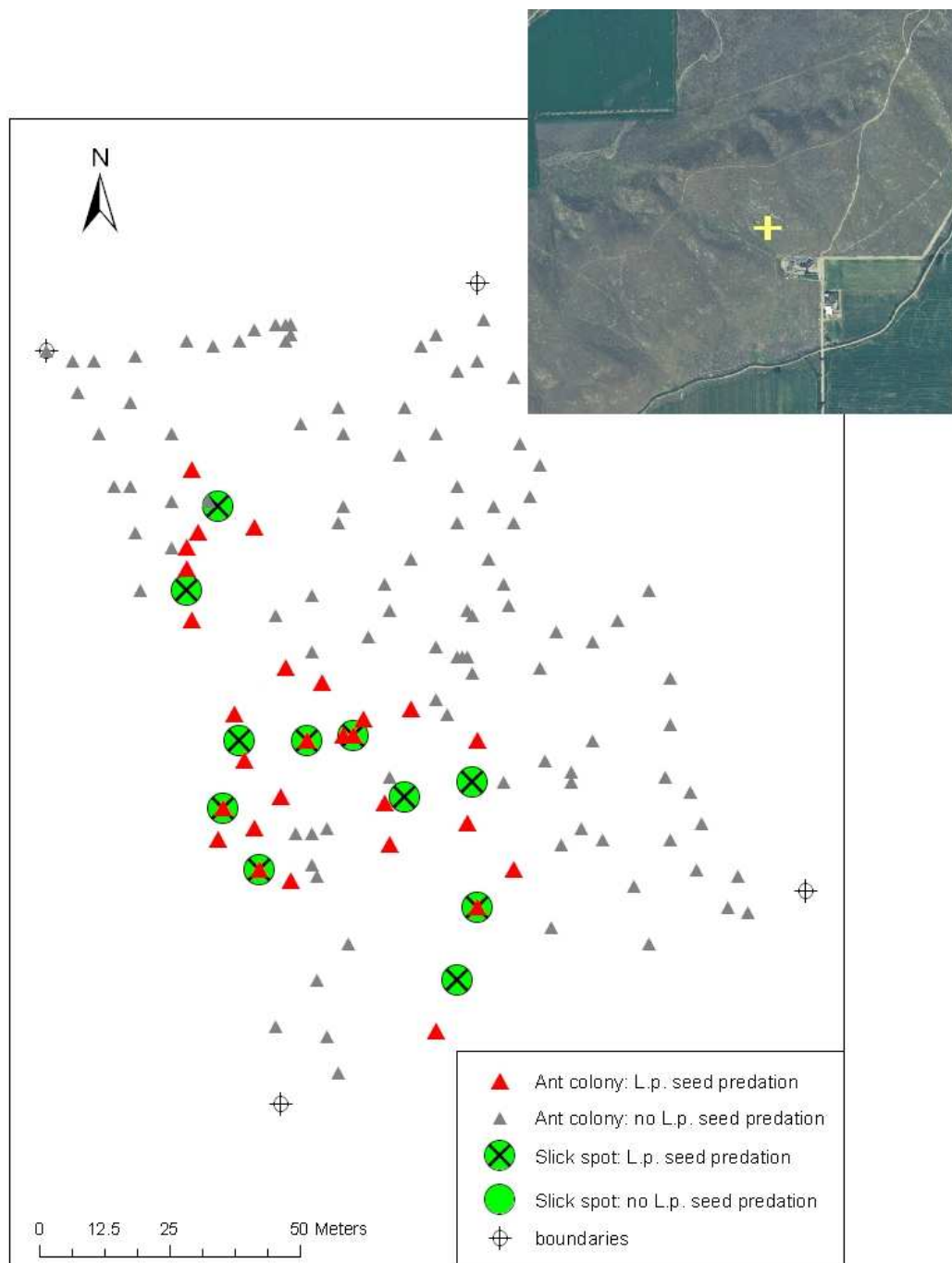


Figure 2.2. Map showing the abundance of harvester ant nests within a *L. papilliferum* site (Big Gulch). As is evident from this figure harvester ants survive well even without proximity to *L. papilliferum*.

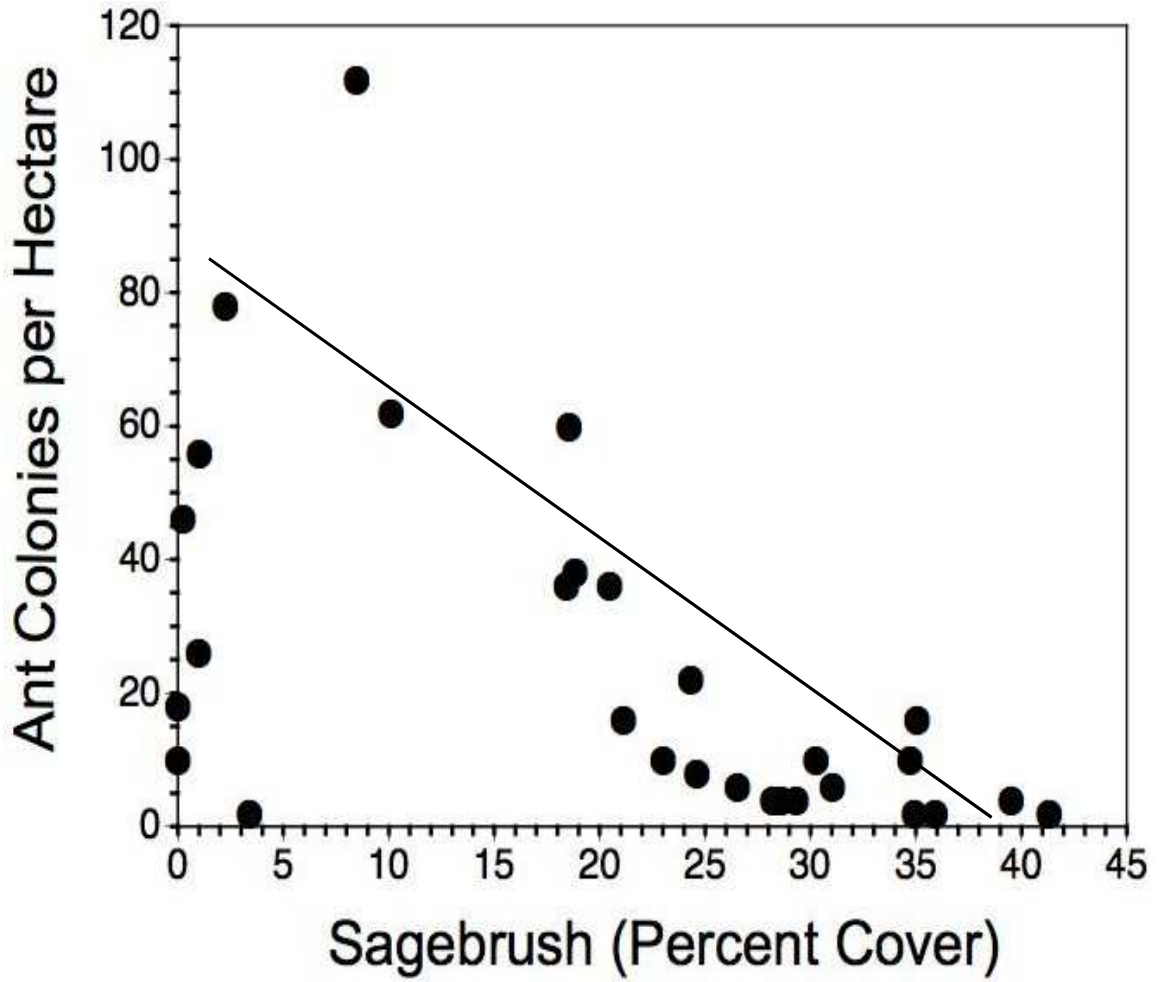


Figure 2.3. The relationship between percent cover of big sagebrush and harvester ant colony abundance at 29 element occurrences of *L. papilliferum*. There is a significant inverse relationship ($\beta = -1.07$, $p = 0.0017$) between amount of sagebrush cover and harvester ant nest abundance showing that as sagebrush cover decreases the number of harvester ant nest mounds increases.

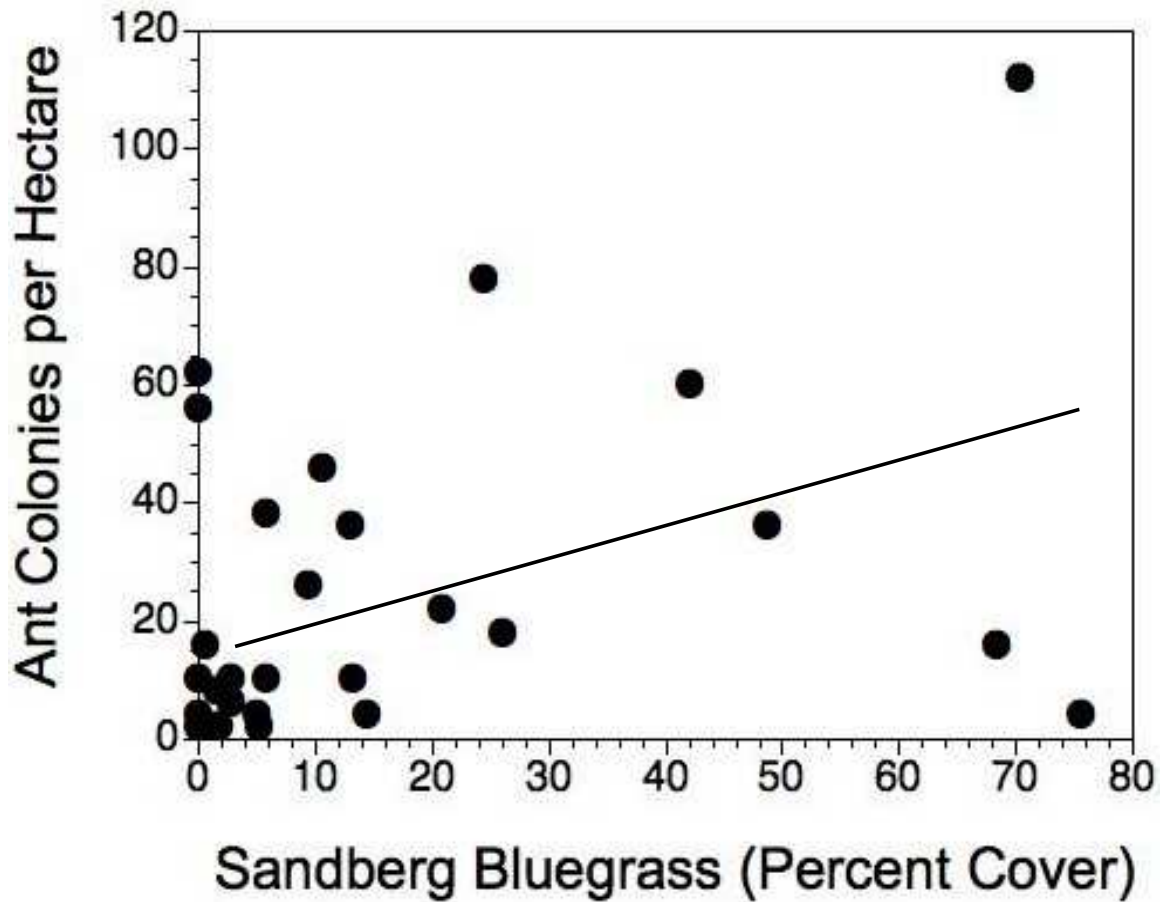


Figure 2.4. The relationship between percent cover of Sandberg bluegrass and harvester ant colony abundance at 29 element occurrences of *L. papilliferum*. There is a significant positive relationship ($\beta = 39.73$, $p = 0.036$) between harvester ant nest abundance and under-story cover of Sandberg bluegrass showing that as cover of Sandberg bluegrass increases so does the number of harvester ant nest mounds.

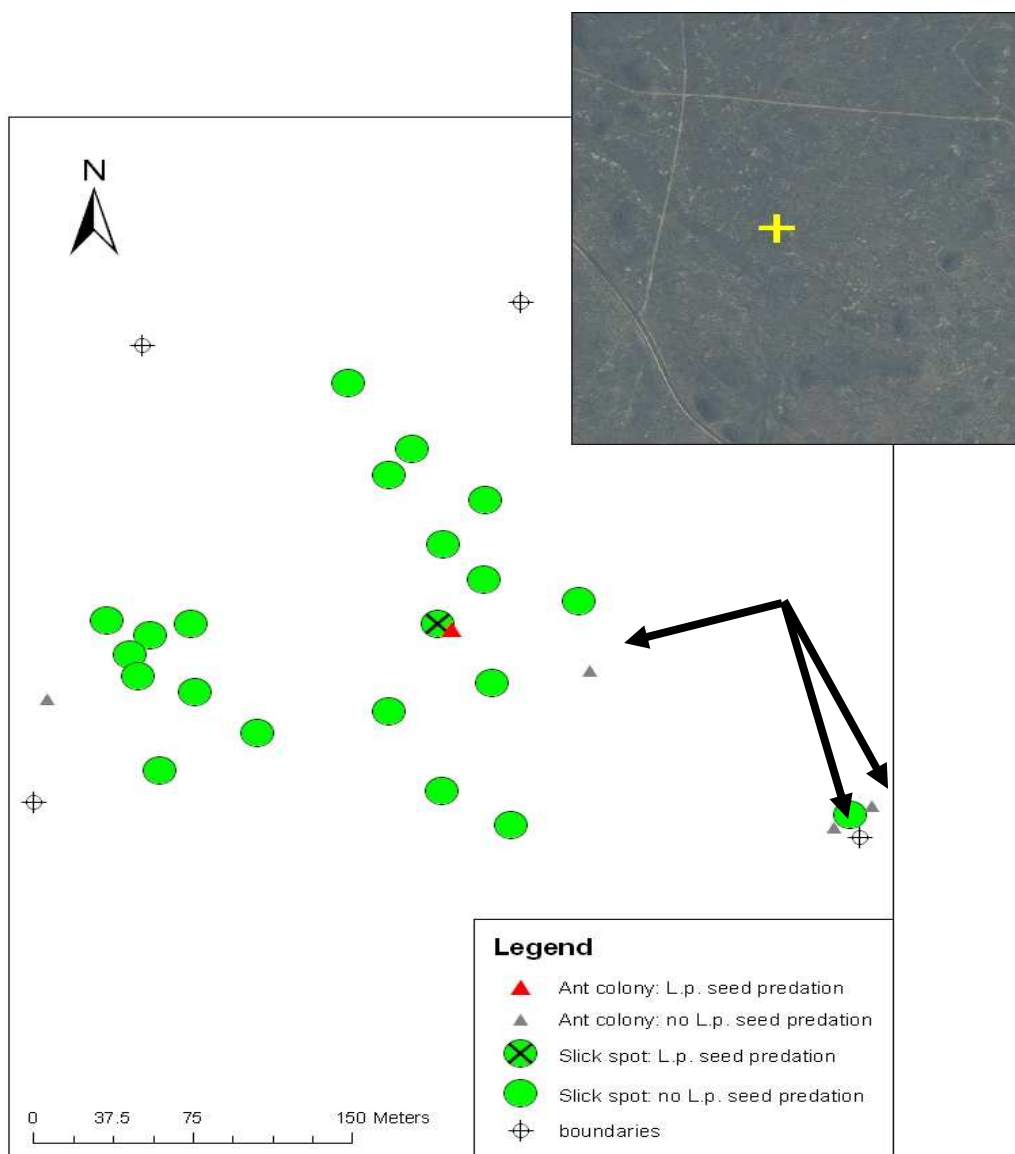


Figure 2.5. Map showing the abundance of harvester ants within a *L. papilliferum* site. This site (Red Tie) is one of the most pristine and undisturbed sites in this study. Note the low numbers of harvester ants within this site, and the few colonies near the Southeastern boundary (shown by the black arrows). Within 100 m of this boundary the habitat changes from a sagebrush dominated one to a community dominated by herbaceous grass. It is from this direction that expansion of harvester ants into this site will likely come.

Table 2.1. Table Showing the Site-Specific Vulnerability of *L. papilliferum* to Seed Predation by Harvester Ants.

Site (Element Occurrence)	Number of ant colonies	Number of Slick spots with flowering <i>L. papilliferum</i>	Number of slick spots with flowering <i>L. papilliferum</i> as a function of distance from a harvester ant colony. (Number of slick spots with signs of seed predation [†])		Percentage of slick spots ≤20m from an ant colony	Total percentage of slick spots with signs of seed predation
			≤20 m	>20 m		
Big Gulch (076)	129	11	11 (11)	0 (0)	100	100
Red Tie (027)	5	21	2 (1)	19 (0)	10	5
Powerline (067)	12	5	2 (2)	3 (0)	40	40
Glenn's Ferry (058) ^δ	9	9	1 (1)	8 (0)	11	11
Christmas Mtn. (053)	5	8	2 (1)	6 (0)	25	13
Initial Point (019)	10	6	5 (3)	1 (0)	83	50
Kuna Butte (018)	96	27	23 (18)	4 (0)	85	67
Mountain Home (061)	36	11	11 (3)	0 (0)	100	27
Nicholson Road	2	1	1 (1)	0 (0)	100	100
Simco Road (015)	57	11	11 (11)	0 (0)	100	100
TOTALS	361	110	69 (52)	41 (0)	Mean=65.4	Mean=51.3

[†] based on direct observations of ants removing fruits from slick spots, or the presence of *L. papilliferum* fruit in the midden of the closest harvester ant colony.

^δ because of the large size of this element occurrence, only a section was surveyed.

APPENDIX A

**Gis Maps Showing the Spatial Relationships
Between Occupied Slick Spots
and Harvester Ant Colonies
within *Lepidium papilliferum* Population**

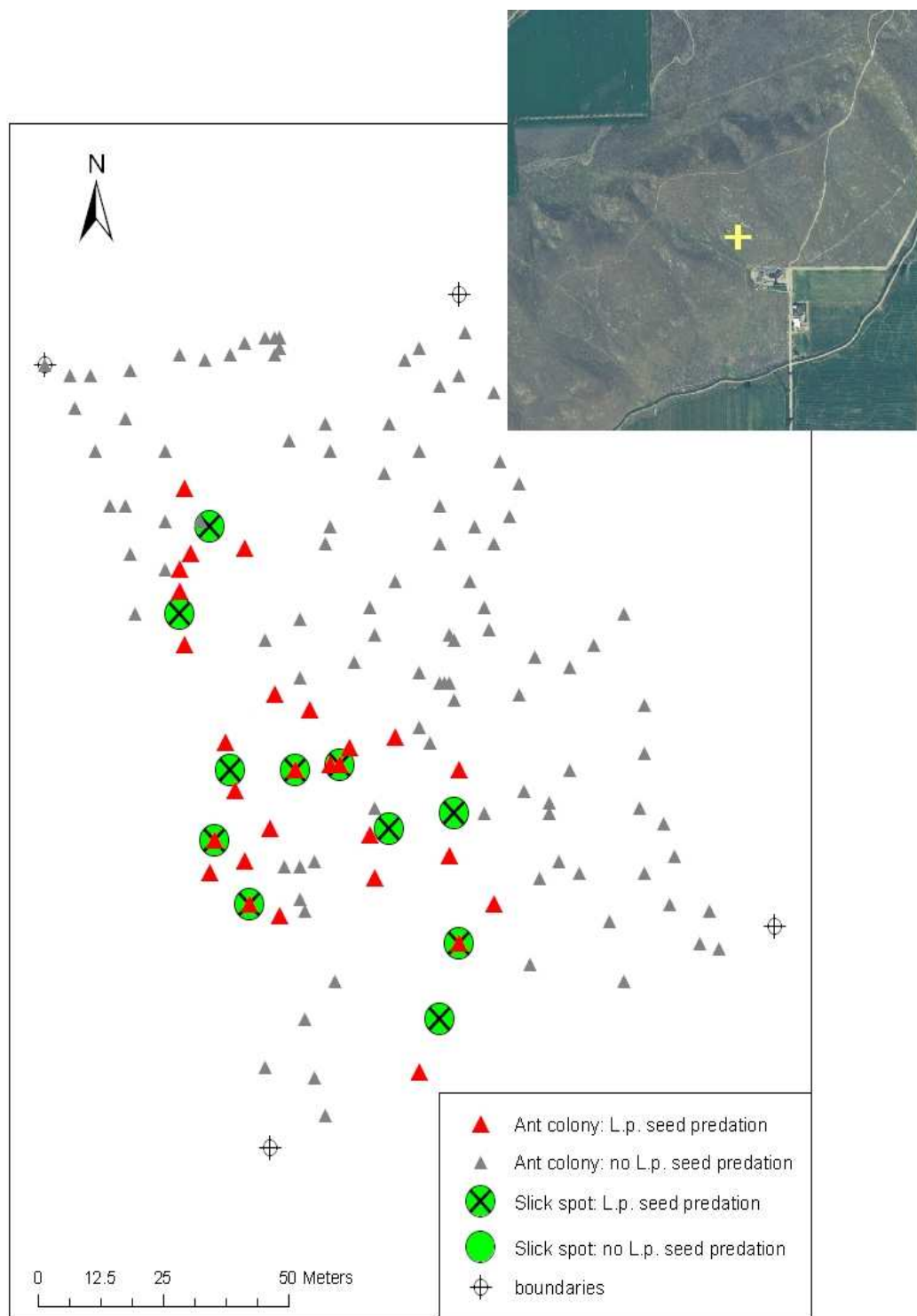


Figure A.1. Map of slick spots and ant colonies at Big Gulch (EO 076)

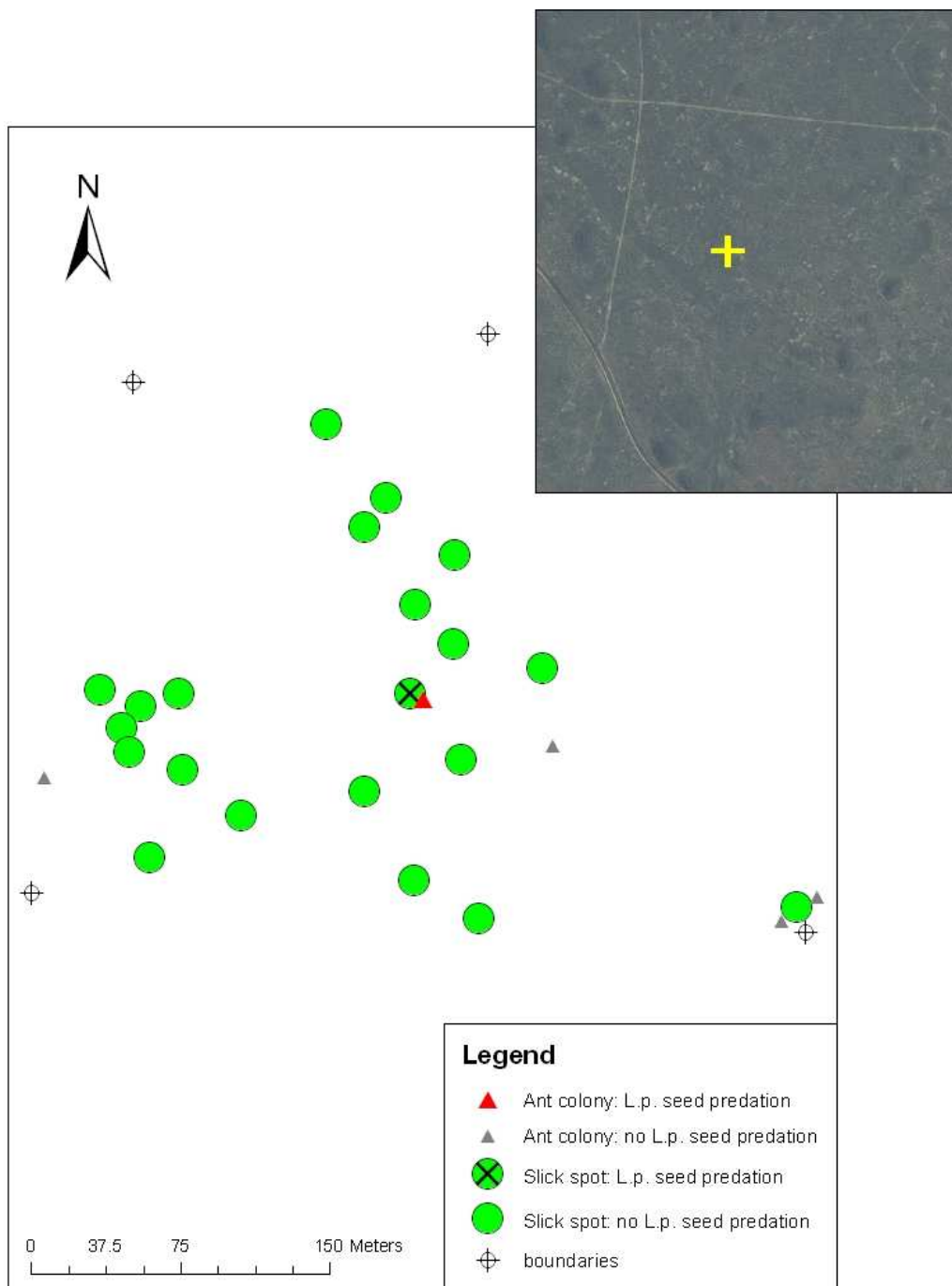


Figure A.2. Map of slick spots and ant colonies at Red Tie (EO 027)

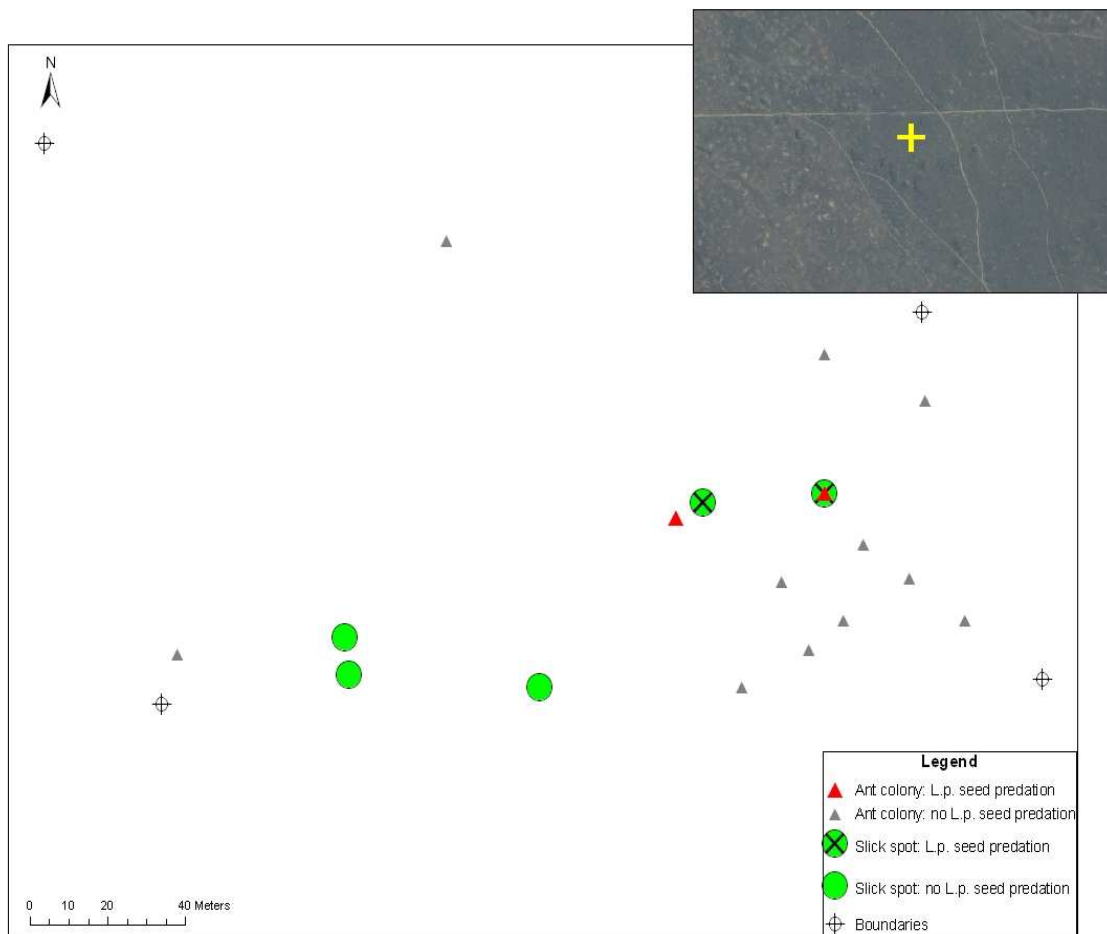


Figure A.3. Map of slick spots and ant colonies at Powerline (EO 067)

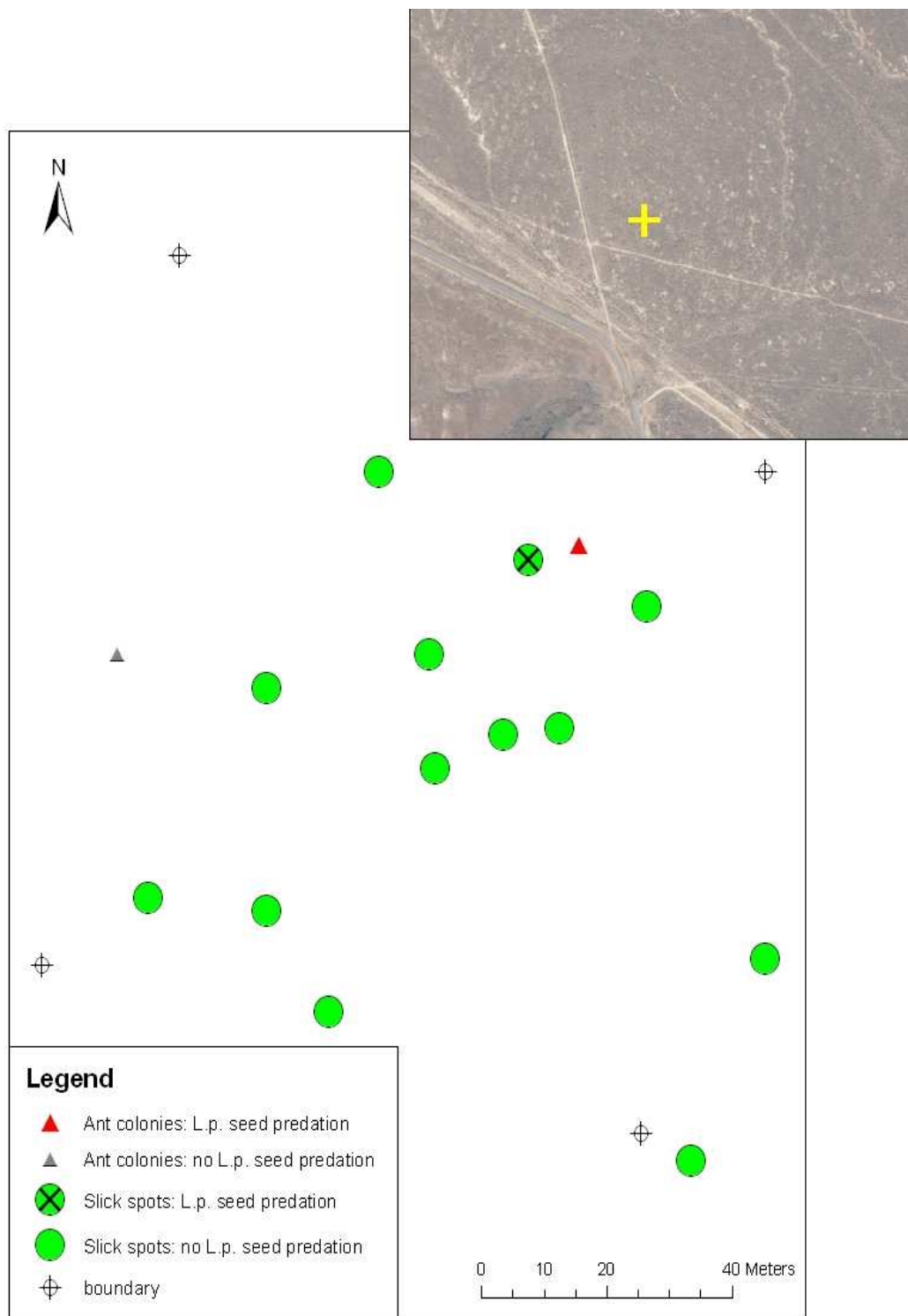


Figure A.4. Map of slick spots and ant colonies at Glenns Ferry (EO 054)

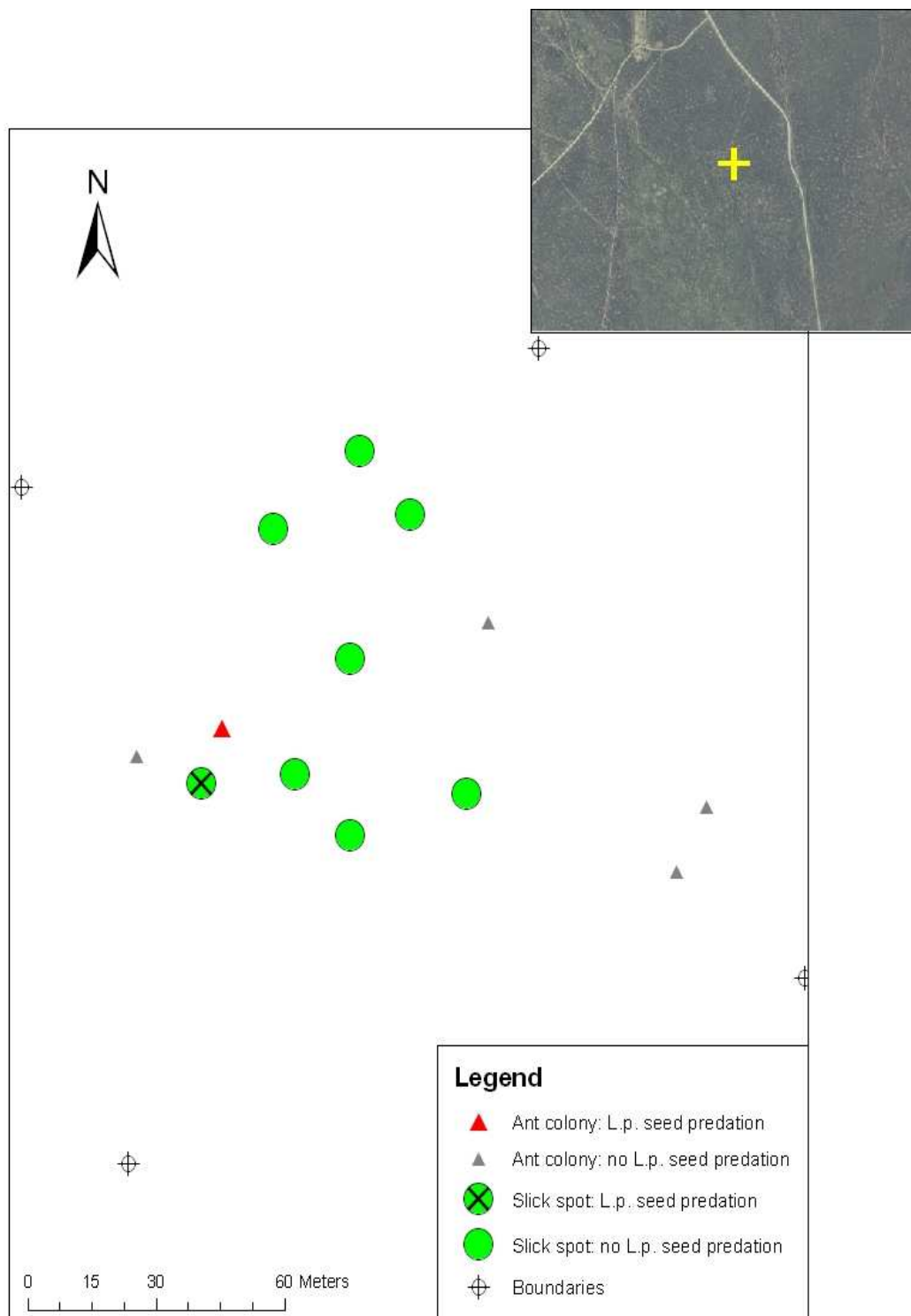


Figure A.5. Map of slick spots and ant colonies at Christmas Mountain (EO 053)

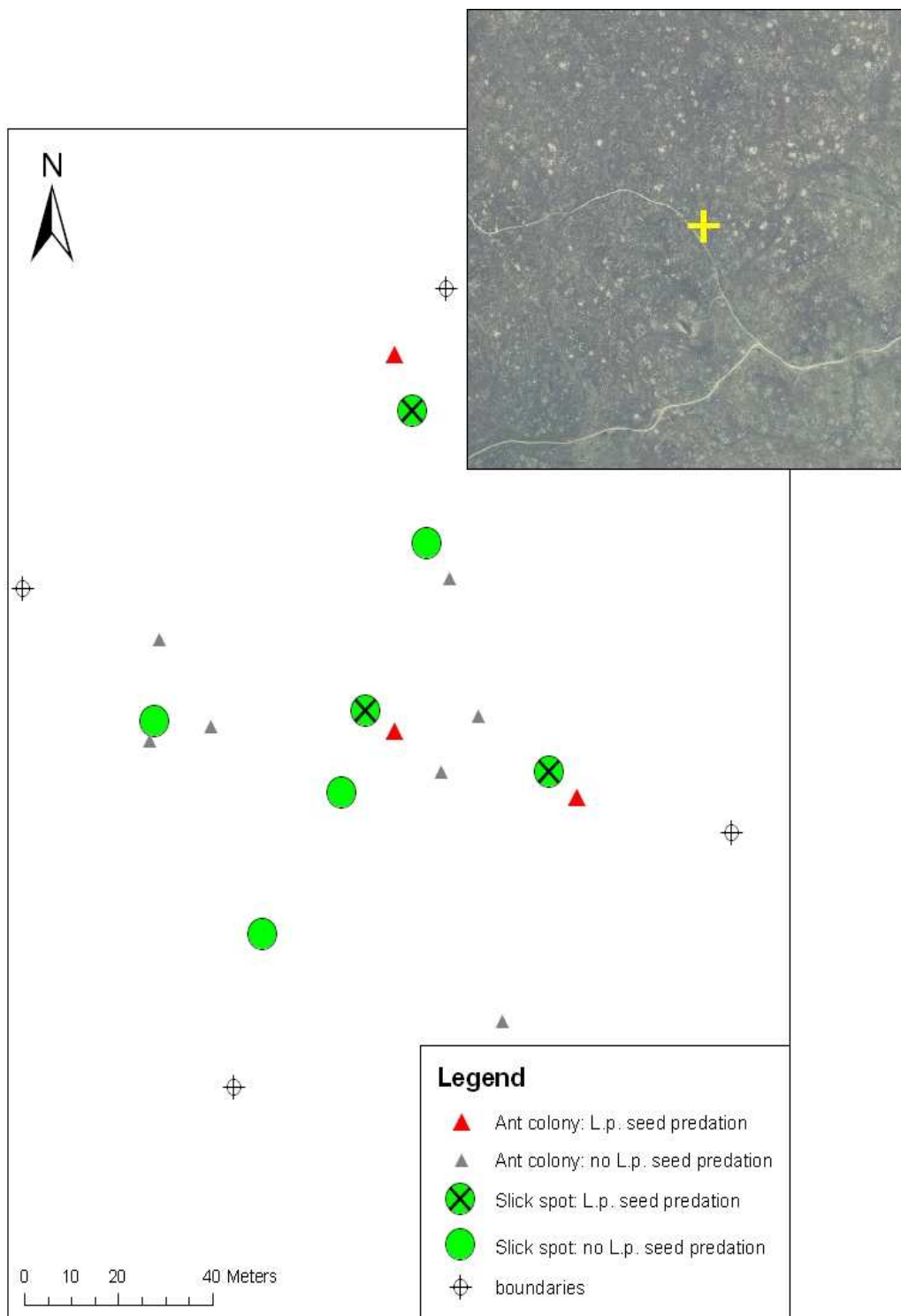


Figure A.6. Map of slick spots and ant colonies at Initial Point (EO 019)

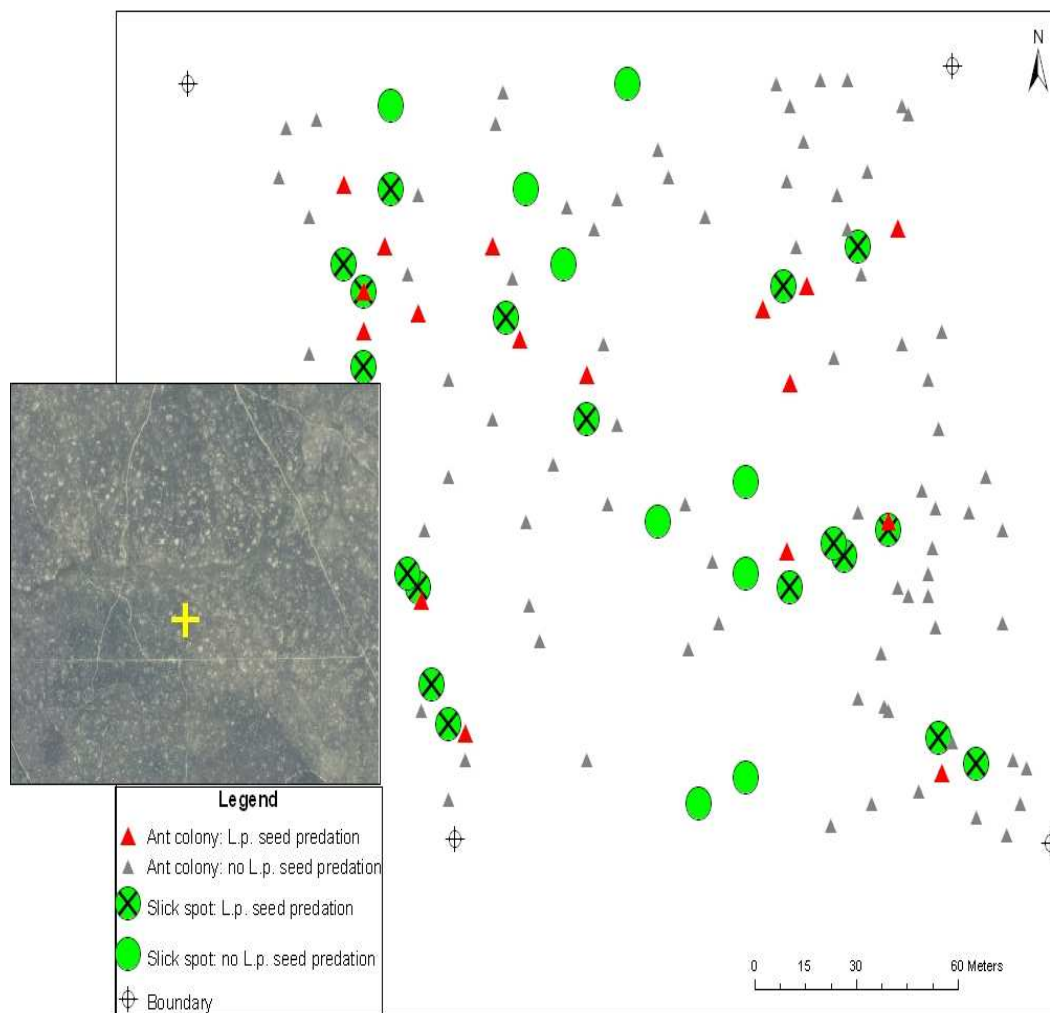


Figure A.7. Map of slick spots and ant colonies at Kuna Butte (EO 018A)

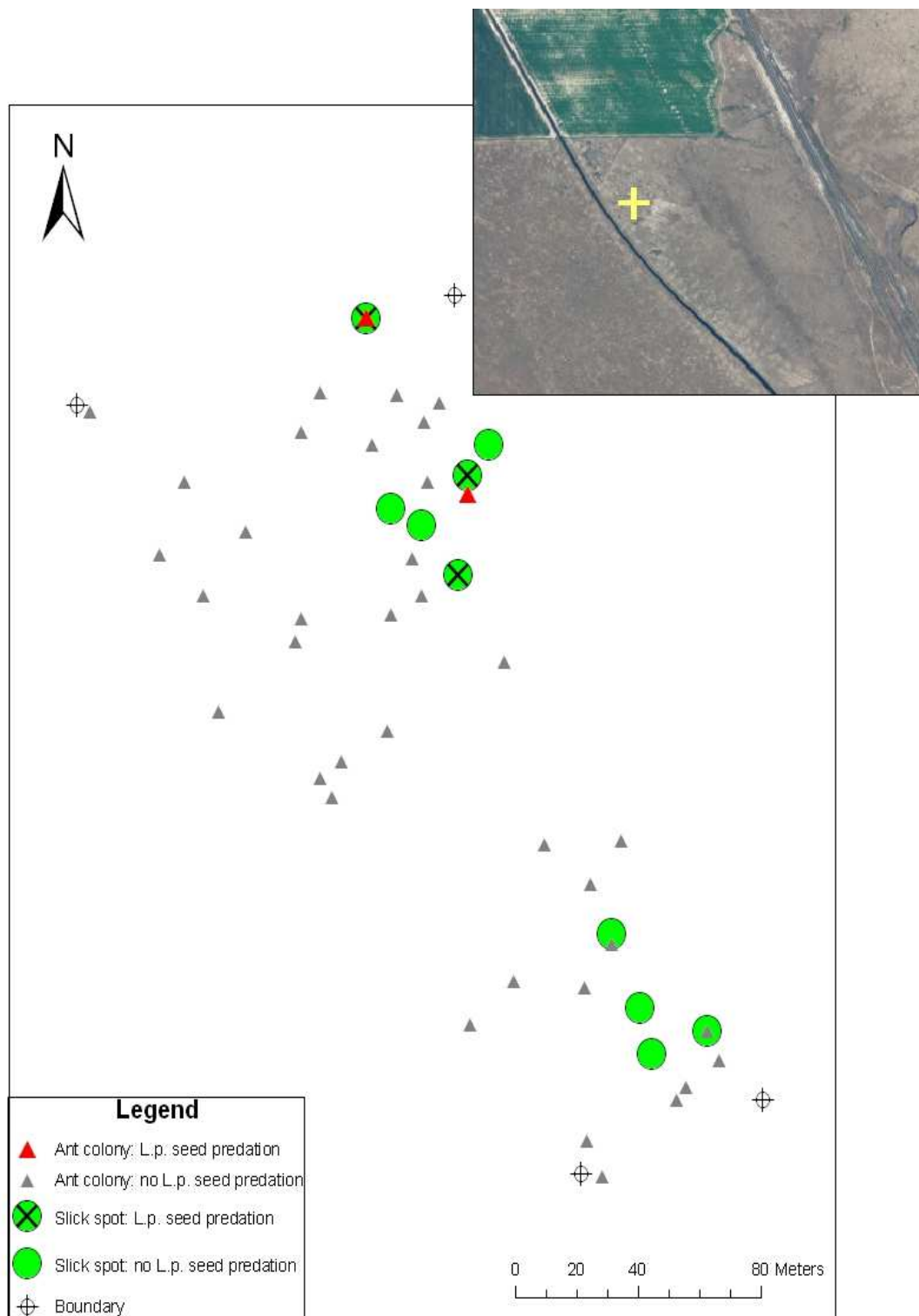


Figure A.8. Map of slick spots and ant colonies at Mountain Home (EO 068)

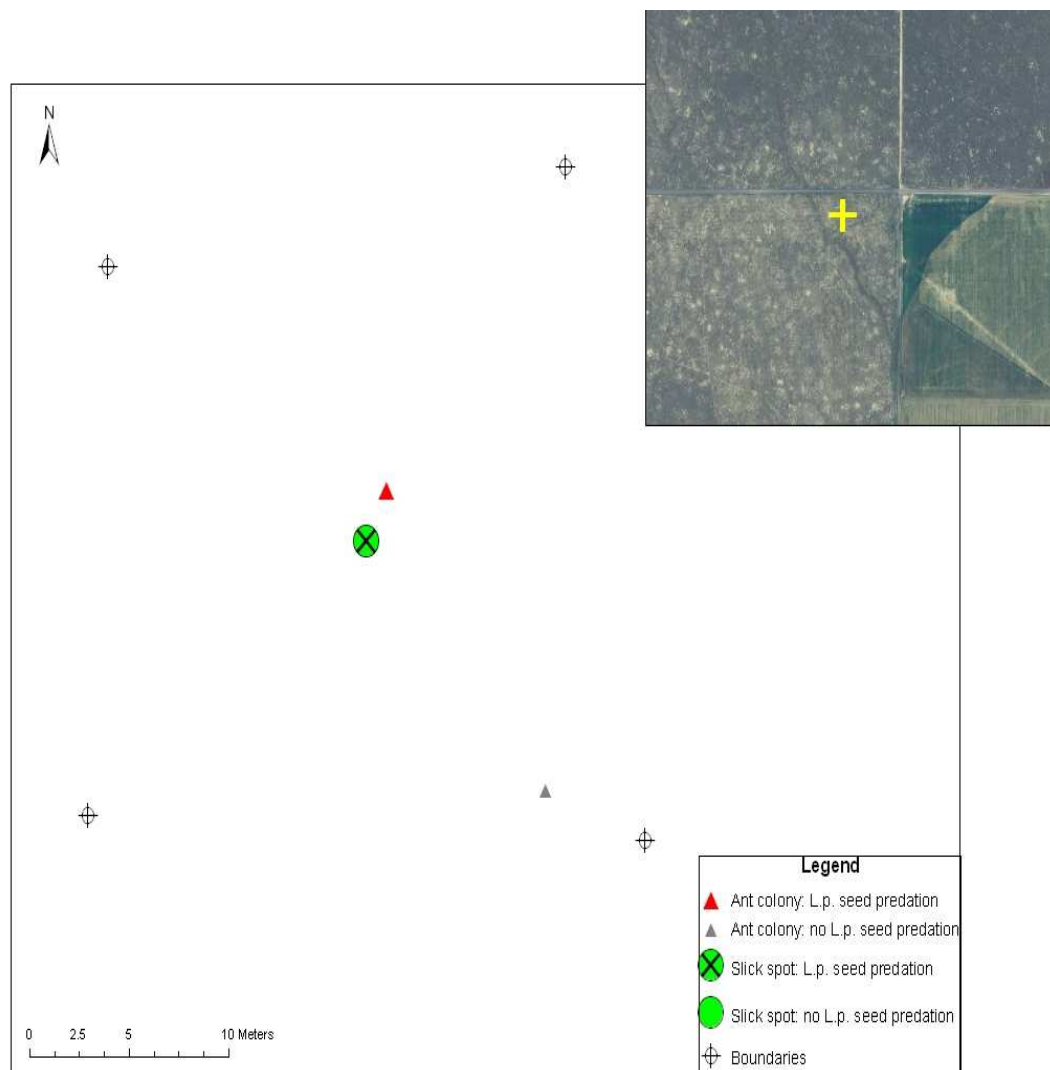


Figure A.9. Map of slick spots and ant colonies at Nicholson Road (EO unknown)

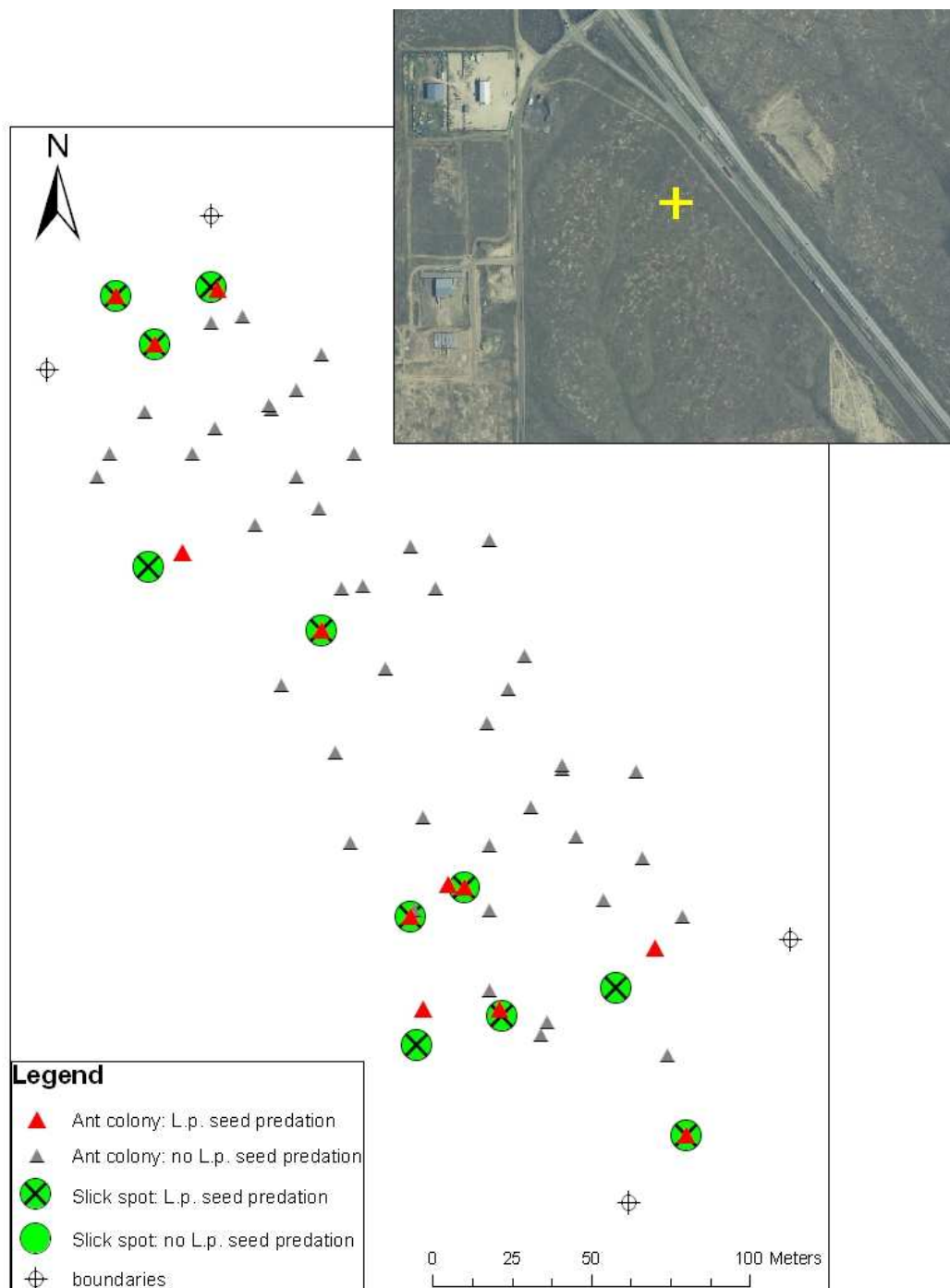


Figure A.10. Map of slick spots and ant colonies at Simco Road (EO 015)

APPENDIX B

**Harvester Ant and Vegetative Data
for 29 *Lepidium papilliferum* sites**

Table B.1. Vegetative characteristics of each of the 29 sites examined. The plants measured were for the over-story sagebrush (*Artemisia tridentata*); and for the under-story the plants were cheatgrass (*Bromus tectorum*), sandberg's bluegrass (*Poa secunda*), tumble mustard (*Sisymbrium altissimum*), blue bunch wheatgrass (*Agropyron spicatum*), and clasping peppergrass (*Lepidium perfoliatum*). Ant density is measured as the number of active ant colonies per hectare.

Site		Ant Density	Overstory Coverage	Understory Coverage					
	EO#*		<i>Artemesia tridentata</i>	<i>Bromus tectorum</i>	<i>Poa secunda</i>	<i>Sisymbrium altissimum</i>	<i>Agropyron spicatum</i>	<i>Lepidium perfoliatum</i>	Total Under-story
Bennett	008	16	35.04%	0.00%	0.50%	1.40%	0.00%	0.00%	1.90%
BG/Hartley	076	112	8.48%	1.10%	70.40%	8.90%	0.00%	0.00%	80.40%
Chalk flats	010	38	18.84%	80.80%	5.70%	0.00%	0.00%	0.00%	86.50%
Christmas Mtn	053	36	20.48%	17.60%	48.80%	3.60%	0.00%	0.00%	70.00%
Christmas Mtn N	028	10	30.26%	0.00%	5.80%	3.80%	0.00%	0.20%	9.80%
Crater ring	002	46	0.25%	0.00%	10.50%	3.70%	0.00%	54.00%	68.20%
Emerald city wash	027E	2	41.32%	21.20%	1.30%	8.20%	0.00%	2.40%	33.10%
Fake raptor rock	059A	4	28.22%	2.80%	75.60%	0.00%	0.00%	8.80%	87.20%
Flat draw res	703	4	24.34%	0.00%	20.80%	0.00%	15.70%	0.00%	36.50%
Fraser res. E	021	22	26.54%	72.40%	2.80%	3.30%	0.00%	0.00%	78.50%
Glenns Ferry NW	058	6	28.62%	79.20%	5.00%	1.80%	0.00%	3.00%	89.00%
Hot creek	051	4	34.94%	0.00%	1.70%	0.70%	0.80%	20.40%	23.60%
Initial point	019	2	0.00%	68.40%	2.80%	4.80%	0.00%	0.00%	76.00%
Juniper butte S	707	10	39.51%	0.00%	14.40%	0.00%	9.60%	0.00%	24.00%
Juniper butte W	709	4	34.72%	0.00%	13.20%	0.00%	8.00%	0.00%	21.20%
Kuna butte N	024	10	0.00%	43.60%	26.00%	3.80%	0.00%	0.00%	73.40%
Kuna butte SW	018	26	2.24%	30.80%	24.40%	10.80%	0.00%	0.00%	66.00%
Orchard corner	027B	78	3.38%	33.20%	0.00%	14.00%	0.00%	51.60%	98.80%
Orchard SW	035A	2	21.12%	27.20%	68.40%	1.10%	2.70%	0.00%	99.40%
Nicholson	?	1	0.00%	48.20%	3.90%	0.00%	0.00%	0.00%	52.10%
Powerline	067	16	31.04%	1.40%	2.80%	1.10%	0.70%	0.90%	6.90%
Red tie	027A	6	35.94%	0.00%	5.10%	1.40%	1.37%	0.00%	7.87%
Mountain Home	061	2	18.42%	1.20%	13.00%	0.00%	12.00%	0.00%	26.20%
Simco Rd	015	36	1.02%	74.80%	0.00%	4.60%	8.80%	0.00%	88.20%
Soles rest Cr	030	56	18.56%	14.40%	42.00%	0.60%	2.50%	0.00%	59.50%
South cole pl	048B	60	23.02%	56.80%	0.00%	2.00%	2.00%	3.60%	64.40%
South cole tm	048A	10	24.60%	77.20%	1.60%	0.00%	1.60%	1.00%	81.40%
Ten mile	032	8	29.30%	48.20%	0.00%	6.00%	2.40%	0.00%	56.60%
West side canal	050	4	10.10%	46.80%	0.00%	11.00%	0.00%	0.00%	57.80%

