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Colony Dynamics and Plant Community Associations of the Harvester Ant, *Pogonomyrmex salinus* (Hymenoptera: Formicidae) in Sagebrush-Steppe Habitat

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Abstract

We present the results of a five-year field study on colony dynamics and plant community associations of Owyhee harvester ants, *Pogonomyrmex salinus* Olsen, in sagebrush-steppe habitat in southwestern Idaho. Over a five-year period, the total number of ant colonies across 16 sites increased from 843 to 878 (4.15%) as a result of 315 colony deaths and 350 colony initiations. Up to 7.1% of colony initiations may have been instances of nest relocation. Colonies had a higher rate of failure in their first year than in subsequent years (12.4% versus 4.6-8.4% over the next three years). Of the 11 sites analyzed for colony dispersion, one was significantly clumped and the others did not differ from random. Population density in the final year of study ranged from 0.1-62.9 colonies per hectare, and was best described by an inverse relationship with sagebrush cover and positive relationship with coverage of non-*Bromus* (non-cheatgrass) understory vegetation. We interpret these results both in terms of (1) food resources – harvester ants avoid cheatgrass seeds in their diet, preferring instead small-seeded grasses and forbs, and (2) habitat structure – harvester ants prefer nesting in open areas where the ground is exposed to sun and they can clear vegetation from the vicinity of their nests. Given the habitat associations we report, the transition from sagebrush-dominated habitat to open grasslands that is occurring rapidly throughout much of the western United States may prove costly to native plant species whose seeds are readily consumed by harvester ants.

Keywords: harvester ant, seed predation, habitat preferences, population density

Distribution of resources such as food and shelter, presence or absence of predators and competitors, and the nature and intensity of habitat disturbance can all play a role in how animals perceive and respond to local habitat quality. Variation in one or more of these parameters can influence habitat selection, survival, or both, resulting in changes in population density (Pulliam 1988, Morris 2003, Krauss et al. 2005). In mobile organisms, habitat selection can be a dynamic process throughout an organism's life, with individuals or groups dispersing from one area to another in response to competition, predation risk, and resource availability (Boinski and Garber 2000, Mayer et al. 2007, Morris and MacEachern 2010). In organisms that are sessile for much of their life (e.g., plants, corals, bivalves, and most ants), dispersal is limited to specific stages of the life cycle. In such cases, the locations where individuals settle, either through passive dispersal or habitat selection, can have long-lasting fitness consequences for the disperser. When recruitment to specific locations is not limited by propagule supply, variation in habitat quality is expected to have a density dependent effect on populations. However, when propagules are in short enough supply to prevent saturation of the habitat, density dependence will not be observed (e.g., Cole and Wiernasz 2002, Billick et al. 2004). Here we report on the colony dynamics of Owyhee harvester ants, *Pogonomyrmex salinus* Olsen (Hymenoptera: Formicidae), and investigate whether their population density is related to habitat quality as defined by the local plant community and its associated effects on nesting suitability and food resources.

Pogonomyrmex ants are large-scale collectors and consumers of plant seeds throughout arid and semi-arid ecosystems of the Americas (MacMahon et al. 2000). Their nesting and foraging activities have the capacity to alter the composition and dynamics of plant communities (Reichman 1979, Carlson and Whitford 1991, MacMahon et al. 2000). In the western United States, the large, conical nests of harvester ants typically range in density from 10-80 colonies/ha (MacMahon et al. 2000). Although harvester ants collect seeds from a wide range of plant species, they tend to specialize on abundant, small-seeded species (Crist and MacMahon 1992, Pirk and Lopez de Casenave 2011, Schmasow and Robertson 2016). Because harvester ant colonies often occur in high density, and because many species aggressively defend the borders of their foraging ranges (Gordon and Kulig 1996, Howell and Robertson 2015), harvester ants are often viewed as a group whose population density is limited by space or food resources (MacMahon et al. 2000). Recruitment limitation as a function of distance to mating aggregations may also be important in determining population density (Cole and Wiernasz 2002, Billick et al. 2004).

Like many ants, *P. salinus* has a life cycle that is defined by a brief mating and dispersal phase followed by an extended sessile adult stage. Newly produced queens fly from their natal colonies to mating aggregations on hilltops (Anderson and Keyel 2006) or in open areas above tall shrubs (Rust 1988). Mating flights are triggered by midsummer precipitation (Anderson and Keyel 2006, see also Nagel and Rettenmeyer 1973, Mull and Crist 1993). After mating, female *P. salinus* disperse and commence solitary colony founding (Anderson and Keyel 2006). Once established, *Pogonomyrmex* colonies may survive 15-20 years or longer (MacMahon et al. 2000).

Some species of *Pogonomyrmex*, including *P. salinus*, clear understory vegetation within 1-2 m of their nest mounds (Sharp and Barr 1960, Willard and Crowell 1965, Sneva 1979). Removal of vegetation increases moisture levels within nests (Rogers and Lavigne 1974, Laundré 1990) and raises soil temperature through increased surface exposure to sun, thereby increasing the time window available to foragers during cooler periods (Bucy and Breed 2006). The benefits of nest clearing may help explain why harvester ants in sagebrush-steppe habitat tend to colonize open grasslands more than shrub-dominated areas (Willard and Crowell 1965, Sneva 1979, Ostoja et al. 2009, Holbrook et al. 2016). Shrubs decrease soil exposure to sun, have extensive root systems that disrupt soil and alter moisture levels (Friese and Allen 1993), and are generally difficult or impossible for ants to clear from the vicinity of their nests.

To address whether vegetation influences population density in *P. salinus*, and to increase our knowledge of colonization and nest mortality in this species, we monitored 16 populations of *P. salinus* annually over a five-year period and quantified the plant community at each site as it related to sagebrush, grasses and forbs. Previous research found that *P. salinus* foragers tend to ignore the seeds of cheatgrass, *Bromus tectorum*, an exotic annual grass, focusing instead on smaller-seeded grasses such as Sandberg's bluegrass, *Poa secunda*, and various native and exotic mustard species (Schmasow and Robertson 2016). The aversion of harvester ants to cheatgrass seeds is thought to reflect the difficulty ants have transporting cheatgrass seeds and their long, bristled awns (Kelrick et al. 1986, Crist and MacMahon 1992, Schmasow and Robertson 2016). Based on the foraging preferences of *P. salinus*, and the assumption that *P. salinus* queens are more likely to settle and persist in habitats with abundant food resources, we predicted that habitats rich in small-seeded (i.e., non-*Bromus*) understory vegetation would support higher densities of harvester ant colonies than habitats dominated by cheatgrass. We also predicted that *P. salinus* nesting densities would be negatively associated with sagebrush cover, as earlier studies found that harvester ants are more abundant in grasslands than in sagebrush-dominated habitat.

Materials and Methods

Site Selection

We conducted annual surveys of Owyhee harvester ant colonies at 16 sites in southwestern Idaho from mid-June through mid-July 2010-2014. Three of the sites were first surveyed in 2009, and those data are included in our analysis of colony survival. The sites ranged in size from 0.5-19.1 ha (mean \pm SE = 8.5 \pm 4.0 ha) and were separated by 3.0-14.5 km in all but one case. The one exception was Kuna Butte SW, a site we divided into two separate regions. We considered these regions distinct in our analyses because region 1 burned in the late 1990s and was converted from sagebrush to grassland, whereas region 2 did not burn and continues to be dominated by sagebrush and a mixture of grasses in open interspaces. A common feature of all 16 sites, and the factor that defined their selection and boundaries, was the presence of *Lepidium papilliferum*, a rare species of mustard that was the focus of a separate study on seed predation by harvester ants. Apart from the limited and patchy abundance of *L. papilliferum* (i.e., <<1%

coverage), vegetation at the 16 sites was typical for the region and included *Bromus tectorum* (cheatgrass), *Poa secunda* (Sandberg's bluegrass), *Artemisia tridentata* (big sagebrush), and *Sisymbrium altissimum* (tall tumbled mustard), as well as limited and variable numbers of other grass and forb species.

Surveying Harvester Ant Colonies

Using a hand-held Garmin® GPS, observers walked narrow, overlapping parallel transects and recorded the locations of all active harvester ant nests detected within the boundaries of each site. Surveys were conducted between 0900 h and 1300 h, which corresponded with the timing of peak ant activity outside the nest. Newly discovered nests were marked with a uniquely numbered aluminum tag staked to the ground within 1 m of the colony entrance. In cases where ants were not active on the nest mound, the observer disturbed the upper 10 cm of the nest to provoke a defense response by workers. If ants did not emerge from the nest, the observer would return one or two days later to test in a similar manner whether it was active.

Vegetation Sampling

Vegetation was sampled at each site in late June or early July in 2010 and 2014. We used the line-intercept method (Canfield 1941, Bonham 1989) to measure percent coverage of big sagebrush, *Artemisia tridentata*. We conducted ten, 100 m long parallel transects spaced equidistant within the survey area of each site. Along each transect, the observer recorded the cumulative distance (in meters) occupied by sagebrush at a height of 1 m. Sagebrush coverage was calculated as the mean value of the 10 transects.

We used the quadrat frame technique (Gauch 1982) to measure understory coverage. At one randomly selected point along each of the 10 line transects described above, the researcher placed a 1m² frame (with 25 equal subdivisions marked by string) on the ground and estimated the percent coverage of each plant species within the frame. If the point we selected was occupied by sagebrush, we moved the sample to the next open space along the transect. For the purposes of analysis, under-story coverage was calculated separately for *Bromus* (cheatgrass) and non-*Bromus* vegetation based on the mean percent coverage of each category across the 10 samples taken at a site.

In 2010, we selected Kuna Butte SW-2 for an analysis of vegetation in the immediate vicinity of harvester ant colonies. Specifically, we compared the vegetation present within a 3-m radius of 20 active ant nests to the vegetation present within a 3-m radius of 20 randomly selected points. If a randomly selected point fell within 3 m of an active nest, a new point was selected. This site was ideal for the comparison because it contained a large number of harvester ant colonies within a matrix of big sagebrush and open patches populated by *B. tectorum* and *P. secunda*.

Analysis of Ant Colony Associations with Vegetation

We used general linear models to examine whether ant colony density across the 16 sites in 2014 was explained by *Artemisia*, *Bromus*, and non-*Bromus* vegetation. These variables were selected *a priori* based on knowledge that Owyhee harvester ants tend to (1) avoid nesting in areas with dense overstory vegetation (Sneva 1979, White 2009), and (2) avoid foraging on *Bromus tectorum* seeds, focusing instead on small-seeded species such as *Poa secunda* and *Sisymbrium altissimum* (Schmasow and Robertson 2016). We ensured that the data met test assumptions through visual examination of residuals and testing for collinearity among predictor variables. We used an information-theoretic approach to select the model with the most support. Competing models were ranked using Akaike's Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson 2002). Models within 2.0 Δ AICc of the top model were considered informative (Burnham and Anderson 2002). We calculated 95% confidence intervals to estimate the effect of each predictor. Analyses were conducted using R (R Core Development Team 2017).

Results

Colony Dynamics

A summary of ant colony numbers across all sites from 2010 to 2014, including annual losses and gains, is provided in Table 1. In the first year of the study, we located and tagged 843 colonies across the 16 sites. From that time forward until the end of the study, we recorded 315 colony losses and 350 colony initiations. Twenty-five of the 350 newly initiated colonies (7.1%) were located within a few meters of colonies that had been newly listed as inactive,

and 12 nests recorded as inactive (i.e., dead) were found to be active the following year. We assumed that our initial determinations of nest failure in these 12 cases were incorrect and revised the data accordingly. In no cases did a nest 'reactivate' after two or more years of inactivity.

Colony numbers across the 16 sites peaked at 956 in 2012, but by 2014 had declined to 878 following an extended period of drought in spring and summer 2013 that severely limited the amount of vegetative growth and seed production that year. Overall, there was a 4.15% increase in the number of ant colonies between 2010 and 2014; 11 sites experienced a net increase, whereas four had net losses, and one remained constant at a single colony (Figure 1). The number of new colonies per hectare relative to the number of colonies lost per hectare at sites decreased significantly from 2011 to 2014 (Figure 2; Friedman test, $\chi^2 = 22.39$, $p < 0.0001$). All sites combined, colonization events exceeded colony failures in 2011 and 2012, whereas colony failures exceeded colonizations in 2013 and 2014 (Table 1, bottom row).

To test whether ant colonies were more likely to fail within their first year compared to subsequent years, we calculated the probability of nest failure in each of four age categories for which we have data (i.e., 0-1, 1-2, 2-3, and 3-4 years). We fit a logistic regression using nest survival as the outcome (i.e., survive or fail) in an intercept-only model, and added site as a random effect to capture any site-related correlations in survival. Because these models included subsets of the same nests, we could not create independent statistical tests directly by comparing survival probabilities. Instead, we noted whether the probability estimate of colony failure for a given age group fell within the 95% confidence interval of the previous age group. We found that 12.4% of nests ($N=362$) failed within their first year, whereas 7.0% of active nests failed between their first and second year ($N=258$). The probability estimate of colony failure between years 1-2 fell outside the 95% confidence interval of the year 0-1 estimate (Table 2). By contrast, probability estimates for years 2-3 and 3-4 did not fall outside the 95% confidence intervals of their respective previous age group, which suggests that survival probabilities were similar after the first year. When year was treated as a time-varying covariate in a Cox proportional hazards regression (Hosmer et al. 2008) with site as a random effect, we found no significant difference in survival of colonies among years of the study.

We also tested whether colonies that died within their first year were located closer to established colonies than those that survived their first year. We included sites that had at least four colonies die within their first year between 2011 and 2013 ($N=6$ sites, range=4-11 deaths). The corresponding number of colonies that survived their first year ranged from 12-52. Proximity to an established nest did not differ significantly between colonies that died in their first year and those that survived (t-tests with Holm-Bonferroni adjustment for multiple comparisons, $N=6$, all Adj. $P > 0.67$).

Colony dispersion at sites in 2014 was determined using nearest neighbor analysis (Clark and Evans 1954) with edge correction (Sinclair 1985). We excluded sites that had fewer than 15 colonies ($N=5$), of which three had fewer than five colonies. The distribution of colonies (Figure 3) did not differ significantly from random at 10 of the 11 sites we analyzed (Table 3). Colonies at Red Tie South were significantly clumped.

Ant Colony Associations with Vegetation

Because site-specific vegetation profiles did not differ appreciably between sampling years, except at Glens Ferry, where a wildfire in August 2011 destroyed most of the sagebrush, we focused our analysis of vegetation and ant colony associations on data collected in 2014. Table 4 provides a summary of the characteristics of each site in 2014, including area surveyed, ant colony density, and vegetation.

Of the seven competing models to describe the relationship between vegetation at a site and the number of ant colonies per hectare, the top model included the predictors "*Artemisia*" and "*non-Bromus understory*" (Table 5). All other models were $>2 \Delta AICc$ from the top model, and were thus considered uninformative (Burnham and Anderson 2002). The three lowest ranked models included *Bromus* (cheatgrass) cover, either alone or in combination with other vegetation. Based on the top model, harvester ant colony density was negatively associated with sagebrush cover (95% CI = -0.65, -0.04) and positively associated with availability of *non-Bromus* understory (95% CI = 0.45, 4.44; Figure 4) as described by the equation:

$$\text{Ant Colony Density} = 12.36 - 0.35(\text{Artemisia}) + 2.45(\% \text{ non-Bromus understory})$$

Consistent with the top AICc model, analysis of vegetation at Kuna Butte SW-2 revealed that the areas within 3-m of ant colonies had significantly less sagebrush coverage and more non-*Bromus* (primarily *Poa secunda*) coverage than similarly defined areas around randomly selected points that lacked harvester ant colonies (Table 6).

Discussion

Colony Dynamics

Most studies of harvester ant population densities report values of 10-80 colonies/ha (MacMahon et al. 2000), consistent with the range of densities we found for *P. salinus*. Conditions known to influence settlement in harvester ants include vegetation and food availability (Sharp and Barr 1960, Bernstein 1975, Sneva 1979, Blom et al. 1991), topography and soil features (Blom et al. 1991, Crist and Wiens 1996, Johnson 2001), precipitation and soil moisture (Johnson 1998, Dibner et al. 2015), and recruitment limitation (Cole and Wiernasz 2002; Billick et al. 2004). Thus, while our study focused on the importance of vegetation (and by extension, food availability) on population density, other factors may have contributed the variation in ant colony densities we found among sites.

Despite a net increase of 4.51% in the number of harvester ant colonies between 2010 and 2014, most of the populations we monitored experienced relatively minor changes in population density. Nevertheless, perturbations in habitat quality, such as changes in soil moisture and food supply, may have influenced annual recruitment and survival. Between 2013 and 2014, the total number of harvester ant colonies dropped from 941 to 878. This net loss of 63 colonies (a 7.2% drop in population size) was the result of 101 colonies being lost and only 38 being added. Increases in mortality and decreases in colonization, also noted between 2012 and 2013, may have been a consequence of drought and its effects on foundress survival (Johnson 1998) and food supply (Wagner and Gordon 1999). During the summer of 2013, we observed very little growth and seed production by *P. secunda* and *B. tectorum* at our study sites. Likewise, a survey of *Lepidium papilliferum* (the rare mustard present at all of our sites) revealed that the plant's numbers were lower in 2013 than in any of the preceding eight years (Kinter et al. 2014). Thus, higher colony mortality and fewer successful colonization events in 2013 and 2014 compared to previous years may have been responses to low precipitation, reduced food supply, or both.

Numerous studies report that *Pogonomyrmex* colonies are more likely to die within their first year than in the years that follow as the colony matures (Gordon 1991, Keeler 1993, Wiernasz and Cole 1995), and that mortality of foundresses attempting to initiate colonies is higher still (Gordon and Kulig 1996, Cole and Wiernasz 2002). However, once a colony survives its first year it can often survive 15-20 years, sometimes longer (MacMahon et al. 2000). Our study provides further support for differential colony survival as a function of age. Specifically, the percentage of nests that failed within their first year was higher than in subsequent years.

Settlement patterns and competition for food among neighboring colonies may influence mortality of newly established harvester ant colonies. For example, in *P. occidentalis*, colonies that failed in their first year were located closer to established nests than those that survived (Wiernasz and Cole 1995). Similarly, one-year-old *P. barbatus* colonies were more likely to appear near 2- and 3-year-old nests than near older nests, which may indicate that older, larger colonies outcompete newly founded ones for food (Gordon and Kulig 1996). In our study, proximity of new colonies to established colonies did not affect whether new colonies survived their first year. However, in many cases we do not know whether the neighboring colony was 2-3 years of age or older because the ages of colonies discovered in the first year of study are unknown.

Twelve colonies we scored as 'dead' were recorded as 'active' the following year. These colonies were either misdiagnosed or the nests were recolonized by new foundresses. Because harvester ants tend to move deeper underground when surface temperatures rise beyond tolerance (Anderson and Munger 2003, Cole et al. 2010), we concluded that these colonies were likely incorrectly scored as having failed. Although there may be benefits of occupying failed nests (e.g., untapped food stores, limited availability of alternative nesting sites), these benefits might be outweighed by costs associated with the conditions that caused colony failure in the first place. Nevertheless, Porter and Jorgensen (1988) reported that 25% of new colonies in their study of *P. salinus* represented recolonization events (assuming they were not misdiagnosed), so the possibility of recolonization of failed nests in our study cannot be discounted.

Twenty-five of 350 new colonies discovered over the course of our study (7.1%) were located within a few meters of failed colonies that had been active the year before. It is likely that at least some of these new colonies represent instances of nest relocation. Nest relocation is known for several *Pogonomyrmex* species, including *P. salinus*, although rates of relocation vary among species. For example, in *P. badius* and *P. barbatus*, nest relocation is relatively common (~10-80% of nests per year: Van Pelt 1976, Harrison and Gentry 1981, Gordon 1992), whereas in *P. occidentalis* and *P. owyheeii* (= *P. salinus*), nest relocation is described as infrequent (~1% of nests: Porter and Jorgensen 1988, Cole and Wiernasz 2002). Our results suggest that nest relocation in *P. salinus* may be higher than what was reported by Porter and Jorgensen (1988), at least in some circumstances.

The availability of suitable nesting sites is likely an important factor in the dispersion patterns of *Pogonomyrmex* colonies (Gordon 1991) and other types of seed-harvesting ants (Blanco-Moreno et al. 2014). Overdispersion may indicate intense competition among colonies when suitable nesting sites are uniformly available within the sampling area (Harrison and Gentry 1981, Ryti and Case 1986, Cushman et al. 1988), or when recruitment is sufficiently intense to occupy areas that have high colony turnover. However, like *P. salinus* in our study, many populations of *Pogonomyrmex* exhibit random or clumped dispersion of colonies (Whitford et al. 1976, Gordon 1991), at least at some scales (Crist and Wiens 1996, Schooley and Wiens 2003). At Red Tie South, for example, *P. salinus* colonies were generally found in open, grassy patches within a much larger matrix of sagebrush. Similarly, at Kuna Butte SW-2, nests were positioned in areas with significantly less sagebrush coverage and more Sandberg bluegrass coverage than random points within the site. While clumped and random dispersion patterns may reflect the early stages of a lengthy colonization process that leads to overdispersion (Wiernasz and Cole 1995), interpretation of dispersion patterns should consider the spatial distribution of critical resources (e.g., food, soil conditions) within populations.

Ant Colony Associations with Vegetation

Population densities of *P. salinus* were inversely related to the amount of sagebrush at a site and positively related to coverage of non-*Bromus* understory vegetation, both at the scale of individual sites (Figure 4) and the vegetation around nests within sites (Table 6). The association between vegetation and colony density could be a result of habitat selection by queens dispersing from their mating sites or random settlement with differential survival of queens during the early stages of nest founding. While Gordon and Kulig (1996) suggest that the physical attributes of locations did not influence the position of new colonies of *P. barbatus*, more research is needed to determine whether dispersing queens are selective about where they attempt to found a colony.

Regardless of the mechanism responsible for patterns of colonization, survival of individual colonies depends, at least in part, on the presence of adequate food resources. The relationship we found between vegetation and colony density is consistent with descriptions of habitat associations and diet preferences of *Pogonomyrmex* ants. As seed consumers, harvester ants are typically associated with open grasslands where food is plentiful (MacMahon et al. 2000, Ostoja et al. 2009). Although harvester ants consume a wide variety of seeds, they generally prefer smaller seeds that are easily transported back to the nest (MacMahon et al. 2000). *P. salinus* prefer the smaller seeds of *Poa secunda*, *Sisymbrium altissimum* and *Lepidium papilliferum* to the larger and more cumbersome seeds of *Bromus tectorum* (Schmasow and Robertson 2016), which likely explains why the inclusion of *B. tectorum* in the AICc model, either alone or in combination with other vegetation, did not help describe colony density (Table 5). Clearly, not all grasslands are alike to harvester ants. Thus, descriptions of habitat preferences of harvester ants, or their habitat associations if settlement patterns arise for reasons other than habitat selection, need to delve deeper than broad scale classifications that ignore key functional variables such as food resources.

Many studies report lower densities of harvester ants in sagebrush-dominated areas compared to open grasslands (this study, Willard and Crowell 1965, Sneva 1979, Soule and Knapp 1996, Brown et al. 1997, Ostoja et al. 2009, Holbrook et al. 2016). The negative association between sagebrush cover and harvester ant population density likely indicates that sagebrush stands are less suitable than grasslands for nesting and food gathering. Relative to grasslands, sagebrush stands may have fewer seeds and a greater abundance of rodents that directly compete with ants for seeds (Ostoja et al. 2009). Edaphic characteristics could also contribute to the relatively low abundance of harvester ants in sagebrush. Sagebrush decreases the soil's exposure to sun, and in at least one harvester ant species, shade increases the incidence of nest relocation (Carlson and Gentry 1973, Harrison and Gentry 1981). Moreover, the root systems of sagebrush can extend laterally for many meters (Friese and Allen 1993), which may disrupt soil and moisture levels in and around ant nests.

Although colony densities of *P. salinus* were related to coverage of sagebrush and non-*Bromus* vegetation, variation in recruitment potential within and among sites may also be important to the dynamics of colonization. Because recruitment tends to be highest near mating sites, at least in *P. occidentalis* (Cole and Wiernasz 2002, Billick et al. 2004) but probably *P. salinus* as well given its similar mating system, chronic and consistent limitation of recruitment at locations more distant from mating sites may maintain population densities below the level that available resources can support (Cole and Wiernasz 2002). By contrast, areas close to mating sites likely receive sufficient recruits to saturate the environment (Cole and Wiernasz 2002). Although we did not identify the locations of mating sites in our study, the strong relationship between vegetation and population density suggests that recruitment limitation was not the primary determinant of population densities. Nevertheless, recruitment limitation may help explain why a site like Red Tie South supported only 16 harvester ant colonies even though many open areas populated by *Poa secunda* and other small-seeded species remained uncolonized. Experimental introduction of mated queens to areas where low recruitment is suspected, followed by the monitoring of new colonies that result (Cole and Wiernasz 2002), would help clarify the extent to which recruitment limitation and density dependence are responsible for observed population densities.

Conservation and Management Implications

Throughout sagebrush-steppe habitat in the western United States, synergy between fire and exotic annual grasses has shortened fire cycles and converted sagebrush-dominated stands into grasslands, disrupting many native grass and forb species in the process (Balch et al. 2013). The shift from sagebrush to grassland may allow harvester ants to colonize areas that historically were unsuitable for nesting by providing open spaces with a rich food supply, except in areas where cheatgrass overwhelmingly dominates. The relationship we found between vegetation and harvester ant population density in sagebrush-steppe communities could prove useful when addressing a site's potential for colonization by *P. salinus* or other *Pogonomyrmex* species, particularly in cases of recent disturbance (e.g., fire) where the carrying capacity for ants is likely in a state of flux while the plant community settles on a new equilibrium (e.g., Holbrook et al 2016). Vegetation state transitions that benefit colonization by harvester ants, such as the transition from shrub-dominated areas to grassland, may prove costly to native plant species whose seeds are readily consumed by ants. Indeed, seed predation has been linked to significant decreases in both abundance and species richness within many plant communities (Andersen 1988, Carlson and Whitford 1991, Samson et al. 1992). These effects may have particularly serious consequences for native species that are already rare or in decline (Ancheta and Heard 2011). Thus, understanding habitat associations and the dynamics of colonization in harvester ants may prove important to the conservation, management, and restoration of native plant species in sagebrush-steppe communities.

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Figure Legends

Fig. 1. Harvester ant colony densities at each of the 16 sites as a function of year. Each line represents one site.

Fig. 2. Box plot chart summarizing the net change in the number of colonies per hectare across the 16 sites as a function of year. The horizontal line within each box represents the median. The upper and lower limits of each box represent the 75th and 25th quartiles, respectively. The upper and lower whiskers represent the 90th and 10th quartiles, respectively. Filled circles are values beyond the range of the whiskers.

Fig. 3. Distribution of harvester ant colonies in 2014 at the 11 sites included in dispersion analyses. KB = Kuna Butte.

Fig. 4. Relationship between harvester ant colony density, sagebrush cover, and the percent cover of non-*Bromus* understory plants in 2014 (N = 16 sites). Both predictor variables are present in the top AICc model (Table 5).

Table 1 – Harvester ant colony numbers from 2010-2014. Values in parentheses represent the loss and gain (-,+) of individual colonies within a site during a given year.

Site	Area surveyed (ha)	No. of Ant Colonies (- losses, + gains)					Net No. colonies/ha added or lost 2010-2014
		2010	2011	2012	2013	2014	
Glenns Ferry	1.75	17	24	32	36	38	+12.0
			(-2,+9)	(-1,+9)	(-4,+8)	(-4,+6)	
Hammett Hills	4.53	87	93	101	107	100	+2.9
			(-2,+8)	(-3,+11)	(-2,+8)	(-11,+4)	
Hartley Road	2.83	226	228	217	208	178	-17.0
			(-9,+11)	(-23,+12)	(-18,+9)	(-38,+8)	
Initial Point	1.50	25	38	42	43	40	+10.0
			(-1,+14)	(-6,+10)	(-2,+3)	(-4,+1)	
Kuna Butte (lower)	0.62	22	23	23	21	18	-6.4
			(-0,+1)	(-1,+1)	(-7,+5)	(-3,+0)	
Kuna Butte (upper)	0.66	1	2	2	2	2	+1.5
			(-0,+1)	(-0,+0)	(-0,+0)	(-0,+0)	
Kuna Butte SW - 1	5.15	169	175	199	187	183	+2.7
			(-6,+12)	(-13,+37)	(-28,+16)	(-9,+5)	
Kuna Butte SW - 2	5.13	76	88	115	123	124	+9.4
			(-6,+18)	(-4,+31)	(-5,+13)	(-5,+6)	

Site	Area surveyed (ha)	No. of Ant Colonies (- losses, + gains)					Net No. colonies/ha added or lost 2010-2014
		2010	2011	2012	2013	2014	
Nicholson Road	0.50	8	10	11	11	11	+6.0
			(-0,+2)	(-1,+2)	(-0,+0)	(-0,+0)	
Pleasant Valley	1.36	0	3	4	4	4	+2.9
			(-0,+3)	(-0,+1)	(-0,+0)	(-1,+1)	
Powerline	8.34	24	29	28	28	27	+0.4
			(-1,+6)	(-3,+2)	(-2,+2)	(-1,+0)	
Red Tie South	19.09	14	14	15	15	16	+0.1
			(-0,+0)	(-0,+1)	(-0,+0)	(-0,+1)	
SE of Reverse	3.98	60	71	74	74	72	+3.0
			(-3,+14)	(-3,+6)	(-4,+4)	(-6,+4)	
Simco Road	7.01	92	91	72	64	50	-6.0
			(-16,+15)	(-19,+0)	(-10,+2)	(-16,+2)	
Tenmile Creek	6.50	1	1	1	1	1	0
			(-0,+0)	(-0,+0)	(-0,+0)	(-0,+0)	
Willow Creek	1.47	21	21	20	17	14	-4.8
			(-1,+1)	(-3,+2)	(-5,+2)	(-3,+0)	
TOTALS:	70.42	843	911	956	941	878	+0.5
			(-47,+115)	(-80,+125)	(-87,+72)	(-101,+38)	

Table 2 – Percentage of ant colonies that failed as a function of colony age. Model estimates of intercept and probability of colony failure (95% confidence intervals) are provided for each age category.

Age of Colony	% of Colonies that Failed (N = total number of colonies)	Model Estimates	
		Intercept (95% CI)	Probability of Colony Failure (95% CI)
0-1 years	12.4 (N=362)	-1.94 (-2.38, -1.50)	0.126 (0.085, 0.182)
1-2 years	7.0 (N=258)	-2.66 (-3.54, -1.77)	0.066 (0.028, 0.145)
2-3 years	8.4 (N=142)	-2.47 (-3.72, -1.21)	0.078 (0.024, 0.229)
3-4 years	4.6 (N=42)	-3.40 (-10.17, 3.37)	0.032 (0.000, 0.967)

Table 3 – Number of ant colonies, mean nearest neighbor distance (R_A), mean expected nearest neighbor distance based on random dispersion with edge correction (R_E), and dispersion index (R) for 11 of 16 sites in 2014. Only sites with > 15 colonies were included in the analysis.

Site	No. of Ant Colonies	mean R_A (m)	mean R_E (m)	R	z-score	P Value
Glenns Ferry	38	11.50	11.53	1.00	-0.010	0.50
Hammett Hills	100	12.62	11.15	1.13	0.664	0.26
Hartley Road	178	7.12	6.56	1.09	0.332	0.37
Initial Point	40	12.76	10.44	1.22	0.905	0.18
Kuna Butte (lower)	18	9.60	10.65	0.90	-0.393	0.35
Kuna Butte SW-1	183	9.58	8.62	1.11	0.505	0.31
Kuna Butte SW-2	124	11.24	10.67	1.05	0.293	0.39
Powerline	27	25.74	30.33	0.85	-1.121	0.13
Red Tie South	16	35.63	61.07	0.58	-5.96	< 0.001
SE of Reverse	72	13.70	12.44	1.10	0.558	0.29
Simco Road	50	19.15	20.16	0.95	-0.295	0.39

Table 4 – Summary of site characteristics in 2014. Non-*Bromus* understory consisted primarily of *Poa secunda* and *Sisymbrium altissimum*.

Site	Area surveyed (ha)	No. of ant colonies	Density of ant colonies (No./ha)	Vegetation		
				<i>Artemisia</i> (m/100m)	<i>Bromus tectorum</i> (%)	Non- <i>Bromus</i> understory (%)
Glenns Ferry†	1.75	38	21.7	10.0	15.0	8.6
Hammett Hills Road	4.53	100	22.1	54.1	0.9	12.3
Hartley Road	2.83	178	62.9	15.5	1.9	10.5
Initial Point	1.50	40	26.7	0	10.2	3.6
Kuna Butte (lower)	0.62	18	29.0	16.2	14.4	7.1
Kuna Butte (upper)	0.66	2	3.0	54.8	17.5	1.5
Kuna Butte SW-1	5.15	183	35.5	8.2	8.0	6.9
Kuna Butte SW-2	5.13	124	24.2	32.7	7.7	4.8
Nicholson Road	0.50	11	22.0	0	0.7	9.6
Pleasant Valley	1.36	4	2.9	39.0	0	8.2
Powerline	8.34	27	3.2	52.6	0.8	2.4
Red Tie South	19.09	16	0.83	81.6	0	10.9
SE Reverse	3.98	72	18.1	35.0	4.6	3.9
Simco Road	7.01	50	7.1	0.6	10.2	1.2
Tenmile Creek	6.50	1	0.1	7.9	21.6	0.1
Willow Creek	1.47	14	9.5	11.2	3.8	5.8

† Fire killed most of the sagebrush at the Glenns Ferry site in late 2011. Prior to the fire there was 48 m/100m *Artemisia* coverage at this site.

Table 5 – AICc results for seven competing models that assess the influence of vegetation types on the density of ant colonies across 16 field sites. Model 1 showed the strongest support for influencing the density of ant colonies. All other models were $> 2 \Delta AICc$ from the top model, and thus are considered uninformative. “All understory” is the sum of Non-*Bromus* understory and *Bromus*.

	Candidate Model	K	AICc	$\Delta AICc$	AICcWt	Cum. Wt
1	<i>Artemisia</i> + Non- <i>Bromus</i> understory	4	136.15	0.00	0.49	0.49
2	Non- <i>Bromus</i> understory	3	138.56	2.41	0.15	0.64
3	Intercept (null model)	2	139.00	2.85	0.12	0.75
4	<i>Artemisia</i>	3	139.42	3.28	0.09	0.85
5	<i>Artemisia</i> + <i>Bromus</i>	4	141.35	5.20	0.04	0.94
6	All understory	4	141.65	5.50	0.03	0.97
7	<i>Bromus</i>	3	141.79	5.64	0.03	1.00

Table 6 – Comparisons of vegetation surrounding harvester ant colonies versus random points at Kuna Butte SW-2 site in 2010 (two-tailed Student’s t-test). Non-*Bromus* understory was primarily *Poa secunda*.

Vegetation	% cover (\pmSE) in 3m		t (df = 38)	P
	radius around ant colonies (N = 20)	radius around random points with no ant colony (N = 20)		
Sagebrush	9.4 \pm 2.4	31.5 \pm 3.9	4.86	< 0.0001
Non- <i>Bromus</i>	53.2 \pm 5.0	27.0 \pm 3.6	4.24	0.0001