The Coexistence and Distribution of Seed-dispersing Animals

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Ecology, Evolution, and Conservation Biology

By

Jacob W. Dittel

Dr. Stephen B. Vander Wall/Dissertation Advisor

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We recommend that the dissertation prepared under our supervision by

JACOB W. DITTEL

Entitled

The Coexistence And Distribution Of Seed-Dispersing Animals

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DOCTOR OF PHILOSOPHY

Stephen B. Vander Wall, Advisor

William S. Longland, Committee Member

Marjorie D. Matocq, Committee Member

Chris R. Feldman, Committee Member

Scott A. Mensing, Graduate School Representative

David W. Zeh, Ph. D., Dean, Graduate School

May, 2016
ABSTRACT

This dissertation set out to answer two questions of seed-dispersing animals; what is the distribution of seed-dispersing animals across North America and whether a specific behavior can support the observed diversity in a subset of seed dispersers, scatter-hoarders. I begin with a broad introduction of food-hoarding and the importance of the behavior for both the animals hoarding food, as well as the plants having their seeds hoarded. In Chapter 1, I investigated how one particular behavior, cache-pilfering, may support diversity in species rich rodent communities despite differences in food-hoarding behavior. In Chapter 2, I examined whether rodent community structure influenced the rate of cache-pilfering. Specifically, I was interested in whether community composition or rodent abundance affected the frequency of cache pilfering across western Nevada. Finally, in Chapter 3 I was the first to elucidate the distributional patterns of two seed-dispersing guilds across North America. In addition to describing the distribution of seed dispersers, I also investigated whether or not the distribution of the plants they were dispersing or climatic variables could predict species richness and distribution.

In Chapter 1, I was able to determine that cache-pilfering is reciprocal among scatter-hoarding species, but species that larder-hoard are unable to pilfer. This reciprocal pilfering could negate any harvesting advantages one species has over another, allowing for the coexistence and maintenance of species diversity witnessed in many rodent communities. In Chapter 2, I discovered that cache-pilfering is highly correlated with rodent abundance and not rodent richness. These results suggest that individuals of different species pilfer at similar rates, further supporting reciprocal cache-pilfering.
Finally, in Chapter 3, I was able to determine the distribution of all North American seed dispersers; richness of these animals is highest in the southwestern portions of North America and decrease with an increase in latitude and in eastern North America. This work was the first to describe the distributional patterns of seed dispersers in North America, and recognize an apparent mismatch in richness between animals and the plants they disperse.
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INTRODUCTION

Seeds are a limited resource both temporally and in quantity. Seeds are only available seasonally and in quantities often fewer than necessary to support granivorous animal populations. In order to prepare or mitigate the limited quantities of food, many granivorous animals exhibit food hoarding behaviors. Food hoarding, or more specifically seed-caching, is an important behavior for many granivorous animals because it allows them to preserve food when it is plentiful, for future consumption when food is limited (Vander Wall 1990). Food stores may be used to help the animal survive winters when they are unable to leave their dens to forage or when food is unavailable. Food stores can also be used in the spring to prepare for the breeding season. In addition to preserving food, seed-caching also allows individuals to sequester food away from inter-and intraspecific competitors. Sequestering food from competitors may give individuals advantages because they will have greater access to food when it is scarce, potentially increasing their fitness over others. The sequestering and storing of food often leads to cache pilfering, when individuals steal caches from one another. Cache pilfering can have detrimental effects on individuals; if an individual loses too many caches they may die from starvation.

Seed-caching animals have adapted two broad behaviors, larder-hoarding and scatter-hoarding, in order to reduce or prevent cache pilfering. Larder hoarding is typically a defense strategy, where an animal places their entire cache in a central location that they defend. Species that utilize this strategy are often physically and behaviorally dominant to conspecífics, allowing them to fend off potential pilferers (Clarke and Kramer 1994). Scatter-hoarding can broadly be viewed as a deceptive tactic
to storing food (Stapanian and Smith 1984, Dally et al. 2006). Animals will create multiple small caches across their range that cannot be defended, but are much more difficult to detect. In addition to spacing caches out, many animals will exhibit behaviors that will further decrease the chances of pilfering. These behaviors include caching away from competitors, caching in locations not frequented by competitors, caching in locations that have increased chances of predation, and even creating sham caches when individuals believe they are being watched (Dally et al. 2006, Steele et al. 2013, 2015, Zhang et al. 2013, 2014). These scatter-caching behaviors result in many unique behaviors between competitors that may help explain their coexistence and diversity (Leaver and Daly 2001, Vander Wall et al. 2009).

In addition to the interactions described above, scatter-caching often forms a mutualism between scatter-hoarders and plants. In these interactions seed-cachers act as seed dispersers, potentially moving seeds long distances away from the parent plant. This is important from the plants perspective for two reasons, dispersal away from the parent plant can reduce Janzen-Connell effects and scatter-hoarding may disproportionately place seeds in locations favorable to germination, or so-called “directed dispersal.” In plant species that suffer high Janzen-Connell effects, offspring survival is near zero when seeds are under or near the parent plant (Janzen 1970 and Connell 1971). This is because parent plants act as “magnets” for seed predators and pathogens, disproportionately increasing the chance of seed death near the parent. Therefore, dispersal away from the parent plant or conspecifics increase the chance of survival by decreasing predation. Secondly, seed dispersers may prefer seed-cache locations that are also positive for seed germination (Howe & Smallwood 1982). These sites include microhabitats that favor
germination (e.g. increased light, increased moisture) or decrease predation (e.g. decreased detection). The preferential selection of these sites by seed dispersers therefore increases survivorship of seeds.

Despite seed acquisition and dispersal being well studied, ecologists have barely scratched the surface on how species interactions and the plants they disperse effect community composition. In the first two chapters of this dissertation I examined how one seed caching behavior, pilfering, influences and is influenced by rodent community structure. The third chapter took a broader focus on seed dispersal and looked at the relationship animal disperser richness has with the diversity of the plants they disperse, as well as abiotic variables across North America. Chapter one examined how the pilfering ability of four co-occurring rodent species may support their coexistence. I conducted a series of trials to determine the rate of pilfering among the species to determine if it was equal (i.e. reciprocal) or if there were differences among the species. This is important because any large differences in pilfering ability could result in species extirpation, while near equal pilfering ability among species may better explain the observed co-existence seen in many seed-caching rodent communities. The second chapter attempted to determine how community structure may influence pilfering, and if pilfering levels can be predicted across habitats based on the rodent community present. Lastly, in chapter three I was the first to describe the geographic pattern of seed dispersing animals as a guild as well as describe broad variables that could predict either “hot-spots” or “cold-spots” of seed disperser diversity across North America. Overall, this work attempted to delve deeper into seed-caching animal behavior and distribution in order to obtain a better understanding of the patterns of species distribution and coexistence.
Literature Cited


Zhang, M. M. Z. Shen, G. Q. Liu, and X. F. Yi. 2013. Seed caching and cache pilferage by three rodent species in a temperate forest in the Xiaoxinganling Mountains. 

Chapter 1: Differential hoarding behavior and reciprocal pilfering support species coexistence in a seed-caching rodent community

Jacob W. Dittel¹², Ramon Perea³, and Stephen B. Vander Wall¹²

¹Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV, 89557; ²Department of Biology, University of Nevada, Reno, NV, 89557; ³Department of Biology, Stanford University, Stanford, CA, 94305

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Introduction

The underlying mechanisms of competitor coexistence have enthralled ecologists since Darwin first described the phenomenon in his book, *The Origin of Species* (Darwin 1859). Competition has long been thought of as a bitter rivalry between ecologically similar species for a shared resource ending in extirpation or niche change of one or both species, releasing both species from the competition (Grinnell 1904, Gause 1934). Competitive exclusion was initially considered a battle between species at the source of a resource, but more recently competition has been considered a balance of niche (MacArthur 1972, Tilman 2004) or resource partitioning (Basset 1995). That is, competition for a resource can happen away from the source both temporally and spatially in how resources are used (Chesson 2000).

North American seed-caching rodent communities are especially species rich in the southwestern United States (Dittel 2016, Chap. 3) and the stable coexistence of these ecologically similar rodents has perplexed ecologists (e.g., Brown et al. 1979, Price et al. 2000). Extensive work has been conducted investigating resource use "trade-offs" that would allow for coexistence (Price 1978, Brown 1988, Longland and Price 1991, Vander Wall 1993, Thayer and Vander Wall 2005), but no study to date has provided sufficient evidence to adequately explain coexistence of rodent communities (Leaver and Daly 2001, Price and Mittler 2006). Price et al. (2000) suggested that differences in seed-caching behavior among species may support coexistence by allowing some species to specialize at harvesting and storing food, while others could specialize at pilfering caches.
Cache pilfering is a common behavior in seed-caching rodent communities (Vander Wall and Jenkins 2003, Steele et al. 2011, Jansen et al. 2012, Zhang et al. 2013). This is not surprising as one type of seed-caching, scatter-hoarding, has long been thought of as a tactic to reduce pilferage (Macdonald 1976). Scatter-hoarding is generally characterized as the creation of multiple diffuse and small caches throughout a home range as opposed to larder-hoarding which is the creation of a single or few large caches. However, high rates of pilferage are not sustainable if an individual cannot replace or reduce cache loss. Therefore, asymmetrical pilferage among individuals would force a change in caching or foraging behavior to reduce pilferage or lead to elimination from the community of the individual that is disproportionately pilfered from. The high rodent richness in seed caching communities suggests the effects of pilfering are being reduced to some extent. However, very little work has been published on how different caching behaviors and the ability of species to pilfer from one another can support coexistence.

In the eastern Sierra Nevada there exists a rich community of scatter-hoarding rodents that overlap greatly in resource use. Rodents compete over temporally limited food sources (e.g. seeds of Jeffrey pine, bitterbrush, manzanita, and chinquapin) to survive the winter months where food is scarce evidenced in their similar larder contents (Kuhn and Vander Wall 2008, 2009). These highly diverse communities are primarily composed of rodents with a range of scatter-hoarding behavior such as intense scatter-hoarders such as chipmunks (Tamias spp.), intermediate scatter-hoarders such as deer mice (Peromyscus spp.), and infrequent scatter-hoarders such as golden-mantled ground squirrels (Callospermophilus lateralis). Additionally, these rodents overlap in the locations they choose to store their food (under shrubs and light litter) and caching
behavior (Briggs et al. 2009). Previous work has tested the ability of two species to pilfer from another in pairwise trials (T. amoenus & P. maniculatus: Vander Wall 2000, Cyanocitta stelleri & T. amoenus: Thayer and Vander Wall 2005, and C. lateralis & T. amoenus: Vander Wall et al. 2009). Tamias amoenus and P. maniculatus were able to pilfer effectively from all species they were tested against while, C. lateralis and C. stelleri are unable to pilfer caches (Vander Wall 2000, Thayer and Vander Wall 2005, Vander Wall et al. 2009). However, no study to date has investigated pilfering at the community level and whether scatter-hoarding behavior correlates with pilfering ability. Additionally, it is unknown whether or not all members of the community can compensate for pilfering by pilfering in return or how pilfering is tolerated.

In this paper, we investigate the possible roles of pilfering in allowing for coexistence in a community of ecologically similar rodents in the eastern Sierra Nevada. Based on previous work (Vander Wall 2000, Vander Wall et al. 2009) we predict that pilfering is not equal among rodents and a rodent’s ability to pilfer will be based on their seed caching strategy. Species that primarily scatter-hoard seeds should be effective pilferers, whereas species who do not scatter-hoard (i.e. larder-hoard) should be poor pilfers. Poor pilfering may be a result of behavioral constraints (spending majority of time defending larders), physiological (inability to detect olfaction cues), or both. Additionally, we predict that species that are good pilferers should be able to pilfer from other good pilfering species at nearly equal rates. If pilfering is not nearly equal amongst pilferers, the best pilfering species would have a competitive advantage and be able to extirpate less effective pilfering species.
Methods

Study area and species

We conducted this study in Whittell Forest and Wildlife Area, University of Nevada – Reno, in Little Valley, Washoe County, Nevada (39° 14’ 49” N, 119° 52’ 38” W, elev. 1990 m) during the spring, summer, and fall months of 2009, and 2012 - 2015. Little Valley is located in the Carson Range of the eastern Sierra Nevada approximately 30 km south of Reno, NV and 5 km northeast of Lake Tahoe. Little Valley's forests are primarily dominated by Jeffery Pine (*Pinus jeffreyi*) with extensive stands of lodgepole pine (*Pinus contorta*) along valley meadows. The understory is predominantly antelope bitterbrush (*Purshia tridentata*) and greenleaf manzanita (*Arctostaphylos patula*) on decomposed granite soils. Little Valley has a semi-arid climate with most precipitation falling in the form of snow during the winter months. Approximately 50% of the annual precipitation (87.5 cm) falls as snow, the remaining precipitation primarily falls during late spring and early fall thunderstorms.

We studied four species of seed-caching rodents: yellow-pine chipmunk (*Tamias amoenus*), long-eared chipmunk (*Tamias quadrimaculatus*), golden-mantled ground squirrel (*Callospermophilus lateralis*), and deer mouse (*Peromyscus maniculatus*). These four species primarily compose the seed-caching rodent community found in Whittell Forest and Wildlife Area. While a few vagrants such as the lodgepole chipmunk (*Tamias speciosus*) and the Piñon mouse (*Peromyscus truei*) may wander into Little Valley, they are uncommon and no individuals were caught during the study. The two species of *Tamias* are active scatter-hoarders, *P. maniculatus* is an intermediate scatter-hoarder, and
C. lateralis, primarily larder-hoards in their nest burrow (Vander Wall 2000, Vander Wall et al. 2009).

**Experimental design**

Rodent foraging trials were conducted in one of four 10 × 10 m rodent-proof enclosures (see Vander Wall 2000 for enclosure details). Vegetation and soil type inside the enclosures matched the vegetation and soils outside of the enclosures and that of Little Valley. Inside each enclosure there was a buried 20-liter plastic bucket with PVC tubing allowing for entry from the surface. PVC tubing was 34 mm in diameter for Tamias species and P. maniculatus or 50 mm in diameter for C. lateralis. These nest buckets provided refuge for all rodents and were readily accepted by most individuals used during trials. In addition to the buckets, each enclosure also contained a dish with water for rodents and a wooden feeder box that allowed access to seeds for rodents but excluded birds.

We conducted sixty-six trials from 2009 – 2015. Each trial consisted of two phases: (1) caching and (2) search for caches (i.e. pilfering) by naïve forager of the same species as cacher, or search for caches by a naïve forager of a species different than the cacher. We conducted trials in a manner similar to Vander Wall (2000). We used small mammal traps to capture individuals from the study area (Little Valley) for use in trials. All individuals were weighed, sexed, and marked with a serially numbered ear tag. No individual was used more than once during trials or across years. Only adult rodents were used for trials. Juveniles and pregnant or lactating females were not used. During caching trials, we placed a captured individual into the enclosure for 24 h with 150 radioactively
labeled *P. jeffreyi* seeds in the feeder box. All seeds were marked with Fe-59 so cached seeds could be found within the enclosure. After 24 h we removed the rodent from the enclosure and released it at its capture location. Some *P. maniculatus* individuals did not remove enough seeds from the feeder box in 24 h and were allowed 48 h to cache. At the end of phase 1, we removed all remaining seeds in the feeder box, as well as any seeds placed in the nest bucket and seed hulls from consumed seeds. We used a Geiger counter to search the enclosure for seed caches hulls of consumed seeds. We excavated caches and recorded the cache size and depth. Additionally, we recorded the Cartesian coordinate of each cache along with the distance from the nearest shrub edge and substrate data. After all seeds were excavated from the enclosure, we replaced all caches at the exact same location, depth, and number of seeds originally found in caches.

Phase 2 began with the introduction of a naïve individual from one of the four study species of rodent. An individual of each species of rodent was given the opportunity to forage inside the enclosure for caches made by an individual from phase 1. The order of species used was randomized. When a naïve individual was captured, we placed the individual inside the nest bucket in the enclosure and allowed it to forage and pilfer caches for 24 h. The only pine seeds available to naïve individuals were those in caches, and the only other food sources available were “natural” foods (e.g. arthropods and seeds of forbs), and 10 sunflower seeds. We placed individual sunflower seeds randomly within the enclosure and counted their removal by subjects as verification test subjects were foraging for food. It has been shown that the rodents used for this study are only able to detect seeds under moist soil conditions (Vander Wall 2000), so phase 2 trials were only conducted after rain events, when possible, or the enclosure was
artificially wetted using ~350 L of water. After 24 h, we removed the naïve individual from the enclosure and released it at the location where it was captured. The original caches were then checked to determine if pilfering occurred. If any caches were removed, the enclosure was re-checked for new caches made by the naïve individual and for seed hulls. We recorded the proportion of caches pilfered for each phase 2 trial. We replaced all pilfered caches and removed any new caches or seed hulls from the enclosure. This process was repeated four times for each species of rodent. After the four phase 2 trials, all seed caches and seed hulls were removed from the enclosure, "resetting" it, and phase 1 was repeated. Because *C. lateralis* is such an infrequent scatter-hoarder we were unable to get any individuals to create enough scatter-caches to use in trials. Therefore, we replicated *C. lateralis* caches within the enclosures using data from this study and Vander Wall *et al.* (2009), conducted inside the same enclosures, for all trials where *C. lateralis* was the scatter-hoarder.

*Data analysis*

Hoarding behavior differences between the two *Tamias* spp. and *P. maniculatus* were analyzed using ANOVA and Tukey’s Post-hoc analysis (*α* = 0.05) for cache size, depth, and distance from shrub edge. Whether each species was more likely to create caches under bare soil or under light litter (substrate type) was analyzed using chi-squared tests. Because the *C. lateralis* caches in this study were a compilation of caches made in other studies by *C. lateralis*, they were not included in these analyses.

Cache pilfering data were analyzed using ANOVA and Tukey’s Post-hoc analysis (alpha = 0.05) to determine differences, if any, between species ability to pilfer and
frequency they are pilfered from. Both mean proportion of caches pilfered and mean number of seeds pilfered were the dependent variables. To better quantify the pilfering ability of a species we created a simple “pilfering effectiveness” metric. This metric is the ratio between the number seeds gained via pilfering versus the number of seeds lost via pilfering (n seeds gained divided by n seeds lost). Numbers greater than one indicate a species has an advantage over interspecific competitors, a value of one would indicated that a species has neither an advantage or disadvantage to interspecific competitors, while a value of less than one would suggest a species is at a disadvantage to interspecific competitors. All data were analyzed in program R (R Core Team 2015).

Results

The two species of Tamias and P. maniculatus differ in their caching behavior in cache size (F_{2, 336}=21.74, p < 0.001), depth (F_{2, 336}=85.74, p < 0.001), distance from shrub edge (F_{2, 336}=19.03, p < 0.001), and preference in whether there was leaf litter or not (X^2= 37.60, df= 2, p< 0.001, table 1). On average, T. quadrimaculatus had larger cache sizes (mean ± SD = 3.2 ± 2.4) than both T. amoenus (2.4 ± 1.6) and P. maniculatus (1.6 ± 0.6). Additionally, T. quadrimaculatus created deeper caches (16.5 mm ± 12.52), than both T. amoenus (8.3 mm ± 5.2) and P. maniculatus (2.8 mm ± 2.5). Peromyscus maniculatus on average cached underneath shrubs (-0.4 cm ± 11.1), while T. amoenus (11.7 cm ± 20.5) and T. quadrimaculatus (10.9 cm ± 15) cached further away but not statistically different from one another. Lastly, each species differed in their preference in substrate type; P. maniculatus preferred to cache under leaf litter (76% of caches), T.
*Tamias amoenus* preferred to cache under bare soil (65% of caches), and *T. quadrimaculatus* did not favor either during this study (51% of caches in leaf litter).

In every trial used for analysis, the pilfering species foraged within the enclosure, minimally removing at least 5 sunflower seeds (6.4 ± 1.1). Three out of the four study species (both *Tamias* spp. and *P. maniculatus*) were effective pilferers, on average pilfering 28 ± 26% of the caches within an enclosure in 24 h. *Tamias amoenus* on average pilfered 36 ± 30%, *T. quadrimaculatus* pilfered 28 ± 26%, and *P. maniculatus* pilfered 25 ± 19% of scatter-caches in 24 h. However, there is no significant difference between their ability to pilfer seeds (F$_{2,57}$ = 1.09, p = 0.34, Fig. 1). *Callospermophilus lateralis* did not pilfer in this study during 6 trials. Additional results from Vander Wall *et al.* (2009) supported our results and no additional phase 2 trials with *C. lateralis* were performed beyond the six. Because *C. lateralis* was unable to pilfer any caches it was not included in statistical analysis as a pilferer but was included as a cacher. There was also no difference in how much a species was pilfered (F$_{3,57}$ = 1.539, p = 0.214, Fig. 2). On average *T. amoenus* lost 35 ± 28%, *T. quadrimaculatus* lost 32 ± 26%, *P. maniculatus* lost 34 ± 28%, and *C. lateralis* lost 16 ± 14% of their caches in 24 h within the enclosures. A two-way ANOVA of pilfering ability and caches lost shows no difference in the total amount of caches pilfered or loss between species (F$_{11,48}$ = 1.09, p = 0.39, Fig. 3). However, if *P. maniculatus’* pilfering ability is looked at individually it pilfers from *C. lateralis* significantly less than from other rodent species (F$_{3,16}$ = 6.066, p = 0.006). There is no difference between *T. amoenus’* ability to pilfer between species (F$_{3,16}$ = 0.26, p = 0.85) nor *T. quadrimaculatus’* ability (F$_{3,16}$ = 0.86, p=0.48)
When looking at the number of seeds received from pilfering during a 24 h trial there was a difference between species \( (F_{3,57} = 3.9, p = 0.03, \text{Figure 4}) \). Tukey’s post-hoc results showed a difference between the number of seeds \( T. amoenus \) (27.3 ± 20.7) and \( P. maniculatus \) (13.2 ± 9.6) found, but the number of seeds found by \( T. quadrimaculatus \) (17.6 ± 16.5) did not statistically differ from either \( T. amoenus \) nor \( P. maniculatus \). There were no differences between how many seeds a cacher lost between species \( (F_{3,57} = 0.25, p = 0.86, \text{Figure 5}) \). During the 24 h time period, on average \( T. amoenus \) lost 18.3 ± 12.1 seeds, \( T. quadrimaculatus \) lost 17.9 ± 13.8 seeds, \( P. maniculatus \) lost 18.4 ± 13.7 seeds, and \( C. lateralis \) lost 25.71 ± 22.73 seeds. A two-way ANOVA with the pilferer and cacher interaction is significant \( (F_{3,16} = 2.0, p=0.05, \text{figure 5}) \). There are no differences between the three pilfering species \( (\text{Tamias spp. and } P. maniculatus) \), but the ability of the \( \text{Tamias} \) spp. to pilfer from \( C. lateralis \) causes the significant interactions between cachers and pilferers. If \( C. lateralis \) is removed from the analysis there is no longer a significant difference between the number of seeds each pilfering species gains \( (F_{3,42} = 1.54, p=0.24) \). The pilfering effectiveness ratios for each species were: \( T. amoenus = 1.47 \), \( T. quadrimaculatus = 0.98 \), \( P. maniculatus = 0.72 \), and \( C. lateralis = 0 \). The complete pilfering network is presented in Fig. 6.

**Discussion**

Rodents pilfered on average 28% of caches in 24 h during this study. This removal rate is within the range found by Vander Wall and Jenkins (2003) in their review of the literature. More recently, Jansen et al. (2012) recorded cache removal rates at 57% in the first week or about 11% daily for the first week and within the range of this study.
for agoutis (*Dasyprocta punctata*). The two species of *Tamias* and *P. maniculatus* pilfered at the same rates statistically (Fig. 1). *Callospermophilus lateralis* was the only species unable to pilfer caches, this result is similar to Vander Wall *et al.* (2009) where they concluded the inability of *C. lateralis* to detect caches was due to poor olfactory abilities. Poor olfaction seems to be the cause of *C. lateralis*’ inability to pilfer in this study as well. *Callospermophilus lateralis* readily found single sunflower seeds within the enclosures on top of the soil (presumably visually) yet were apparently incapable of finding caches of Jeffery pine seeds buried a couple of millimeters deep or in the case of *P. maniculatus* caches just below the surface or underneath plant litter. An alternative explanation is that *C. lateralis* individuals can detect buried caches but determine it is not worth the effort to dig them up. This seems unlikely, as individuals had a limited food source (10 sunflower seeds) for 24 h and the caches are shallow. Especially since *C. lateralis* are significantly larger than *Tamias* spp. and *P. maniculatus*, who readily dig up caches, so the amount of energy to dig up caches should be less for *C. lateralis*.

Overall, the four study species were also pilfered from at statistically equal rates (Fig. 2). However, individual comparisons showed that *C. lateralis* was pilfered from *P. maniculatus* significantly less than either *Tamias* species. There were caching behavior differences between both *Tamias* spp. and *P. maniculatus* (Table 1), but these differences are small and our results suggest that the differences do not prohibit competitors from finding caches as they are all similar in size, depth, and location. One exception where caching behavior may reduce pilferage may be deep caches of *C. lateralis*. These deep caches could prevent pilferage by *P. maniculatus*. *Peromyscus maniculatus* individuals are able to detect at least some *C. lateralis* caches, evidenced by some pilfering. The two
caches found by *P. maniculatus* were 32 and 34 mm deep, on the shallow end of *C. lateralis* caches created in this study (mean = 46.4 ± 9.7 mm). It is possible that *P. maniculatus* are unable to detect deeper caches but even if *P. maniculatus* could detect them, excising these caches is likely very energetically costly especially when other food sources are available (Vander Wall *et al.* 2009). In addition to energy costs, excising these caches likely also take significant amount of time, leaving the mice exposed to predators.

Despite pilfering relatively the same amount of caches from each other, the reward of pilfering is not equal for each species. Because both *Tamias* spp. frequently pilfered from *C. lateralis* and *P. maniculatus* did not, *T. amoenus* received more seeds on average than *P. maniculatus*. This gives a large pilfering advantage to *T. amoenus* (1.47) over *P. maniculatus* (0.72). This difference would also would infer a fitness advantage to *T. amoenus* over *P. maniculatus* because they would have more access to stored food. However, it is important to note that if *C. lateralis* is removed from the analyses the advantage for *T. amoenus* disappears. With out *C. lateralis* there is no difference between the number of seeds each species pilfers and the pilfering effectiveness changes for each species: *T. amoenus* = 1.24, *T. quadrimaculatus* = 0.81, and *P. maniculatus* = 0.94. *Tamias amoenus* in this scenario still has a pilfering advantage over the other species, but it is significantly reduced compared to *P. maniculatus*. *Callospermophilus lateralis* is such an infrequent scatter-hoarder the true value of pilfering effectiveness for each species is probably closer to the results without *C. lateralis*. Because we were testing the ability of rodents to detect caches, our study design required making multiple caches in the relatively small area of our enclosures, creating high densities of *C. lateralis* caches.
These high densities of caches are unlikely to exist in the wild. Thus while *T. amoenus* can detect *C. lateralis* caches as effectively as other caches, it is unlikely they encounter them in natural settings anywhere near as frequently as other species caches. An intermediate pilfering effectiveness value between our results seems to be supported by observed populations of rodents in Little Valley. *Tamias amoenus* is by far the most abundant rodent, followed by *P. maniculatus*, and *T. quadrimaculatus* being the least abundant of the three.

This experiment was not able to fully test the entire community of seed cachers found at our study site. Most notably we were not able to determine the ability of rodents and corvids to pilfer from each other. However, this interaction is likely asymmetrical. Thayer and Vander Wall (2005) showed that the Steller's jay (*Cyanocitta stelleri*) is an ineffective pilferer of *T. amoenus*, but *T. amoenus* can effectively pilfer from *C. stelleri*. Similar results have been found in other corvids (Kamil and Balda 1985). Corvid species in this community recover caches using spatial memory and lack the olfactory acuity that the rodent species have which makes them poor pilferers (Vander Wall 1982, Kamil and Balda 1985). To pilfer, jay species would have to actively watch rodents or conspecifics cache in order to pilfer the cache. This method of pilfering does not appear to be energetically efficient and is unlikely an effective method of foraging (Thayer and Vander Wall 2005). Corvid seed-caches resemble rodent caches in in size and depth (Lanner and Vander Wall 1980, Hutchins and Lanner 1982, Tomback 1982, Thayer and Vander Wall 2005) so rodents with the olfactory acuity to find caches under the right conditions, are likely to find bird caches with similar success as rodent caches. However, corvids may be able to reduce pilferage by caching in locations where rodents seldom
forage or populations are small (Thayer and Vander Wall 2005, Dittel 2016 Chap. 2). Further evidence of rodents pilfering from corvids was found in a study by Kuhn and Vander Wall (2009) that investigated the contents of *T. amoenus* winter larders. When the larders were excavated, seeds from whitebark pine (*Pinus albicaulis*), which does not occur in Little Valley, were found in *T. amoenus* caches. Clark’s Nutcrackers (*Nucifraga columbiana*) collect whitebark pine at higher elevations and scatter-hoard them in little valley, therefore the only way for *T. amoenus* to get these seeds is to pilfer from Clark’s Nutcrackers.

There are also three additional species of rodent that we were unable to study; *Tamias speciosus*, *Tamiascurus douglasii*, and *Otospermophilus beecheyi*. It is unlikely *T. douglassii* and *O. beecheyi* are effective pilferers as they are almost universally larder hoarders. It is also unlikely that they are pilfered from frequently because both species create larders / middens, which they defend from competitors. *Tamias speciosus* is a transient species in Little Valley, rarely occurring at the study site. There absence is unlikely due to competitive exclusion via cache pilferage but likely physiological as Little Valley is at the lower edge of *T. speciosus*’ range. Little Valley may be too arid for *T. speciosus*, as *T. amoenus* and *T. speciosus* co-occur in nearby sites a few kilometers west of Little Valley (Chappell 1978, personal observation).

The results of this study, specifically the ability of both *Tamias* spp. and *P. maniculatus* to pilfer from each other more or less equally, support the hypothesis of reciprocal pilfering proposed by Vander Wall and Jenkins (2003). This hypothesis states that despite high levels of cache pilferage scatter-hoarders are able to tolerate pilferage because the pilferers are also likely to be scatter-hoarders and therefore pilfered
individuals have the opportunity to “pilfer back” seeds. This hypothesis is an alternative to the theory of food hoarding put forth by Andersson and Krebs (1978), which stated that food hoarding would only evolve if caching individuals had a distinct advantage in recovering their own caches. With such high levels of pilfering being observed in scatter-hoarding communities, any recovery advantage an individual has in finding their own caches is small or transient as caches are pilfered and recached frequently (Vander Wall and Jenkins 2003, Perea et al. 2015). Furthermore, the presence of interspecific pilferage supports that reciprocal pilfering is a unique behavior and not a mischaracterization of reciprocal altruism (Vander Wall and Jenkins 2003). Evidence against reciprocal altruism can be found in studies where scatter-hoarding rodents exhibit behavior to reduce pilfering by not caching in the presence of potential pilferers (Burnell and Tomback 1985, Steele et al. 2008, Pravosudov et al. 2010), caching in locations without competitors (Thayer and Vander Wall 2005), caching in high-risk predation sites (Perea et al. 2011, Steele et al. 2013, 2015) or by hyper dispersing caches (Waite and Reeve 1992, 1994, 1995, but see Male and Smulders 2006).

However, it has been suggested that these cache pilferage prevention tactics are evidence against the reciprocal pilfering hypothesis (Leaver et al. 2007, Pravosudov et al. 2010). Generally, arguments against reciprocal pilfering assert that if the hypothesis is true that animals should not bother reducing pilferage or should even share their caches because food can be seen as communal. These arguments are a misinterpretation of the reciprocal pilferage hypothesis. Reciprocal pilferage was framed with the assumption that individuals are acting solely in their own selfish interests (Vander Wall and Jenkins 2003) and the behaviors described above to reduce cache pilferage clearly suggest that
scatter-hoarding animals are acting in selfish ways. Under the reciprocal pilferage hypothesis, scatter-hoarding individuals still have an advantage in finding their own caches via spatial memory over naïve individuals. In fact, individuals prefer to retrieve their own caches before others (Vander Wall et al. 2008, Steele et al. 2011), and foraging for hidden caches without any prior knowledge of their location is less efficient than creating caches and retrieving them later via memory. In this study area, scatter-caches are rarely available to naïve individuals during most of the time seeds spend in caches due to the inability of rodents to detect caches in dry conditions (Vander Wall 2000). During this time, the cacher has a distinct advantage over other individuals at cache recovery using spatial memory (Vander Wall 2000). In the fall, when the soil becomes consistently moist, is when scatter-caches are most likely to be pilfered. Therefore, any scatter-hoarding species of scatter-hoarder that may have a foraging advantage over the others has this advantage negated when caches are temporarily available to all scatter-hoarding species. Cache pilferage is likely an opportunistic foraging strategy that has the highest benefit when seed availability is low and individuals need to supplement their own caches. Fall rains are highly variable and irregular. If fall rains do not come, or are too light to sufficiently moisten the soil, scatter-caches cannot be detected easily. Therefore, any individuals who do not produce their own scatter-caches will have a larder that is insufficient to survive the winter during years when conditions are not sufficient.

Despite the inability of C. lateralis to reciprocate pilferage, it is able to coexist with pilfering species of rodents. This is likely due to differences in foraging behavior. Callospermophilus lateralis primarily larder-hoard seeds and rarely scatter-hoard them
(Vander Wall 1992, Vander Wall et al. 2009). To avoid the high levels of cache pilferage present in these communities, it is possible *C. lateralis* adapted larder-hoarding behavior, allowing it to aggressively defend single larders. A distinct size difference likely gives *C. lateralis* an advantage both physically and behaviorally over smaller heterospecifics across its range. Additionally, in Price and Mitler's (2003) models of coexistence in heteromyid rodents, a non-caching consumer species increased the likelihood of coexistence of competitors. The consumer species facilitates coexistence by reducing competition between caching species and is able to coexist itself by having a harvesting advantage. *Callospermophilus lateralis* seemingly occupies this role in the rodent community and likely has a harvesting advantage over *P. maniculatus* and *T. amoenus* because it can harvest seeds directly from pine cones by cutting them before they open.

This study is the first to investigate reciprocal pilfering at the community level and is consistent with the hypothesis of reciprocal pilfering and helps explain the maintenance of relatively high richness of ecologically similar heterospecifics. Further study of cache pilfering is needed to include scatter-caching corvids as pilferers and cachers, to better understand the apparent asymmetry in pilferage between corvids and rodents. Similar studies should also be performed on a wide variety of scatter-caching communities across a magnitude of environments to better understand if reciprocal pilferage is a widespread phenomenon for seed-cachers or if it is limited to the semi-arid ecosystems of the Sierra Nevada.
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<table>
<thead>
<tr>
<th>Cache Characteristics</th>
<th>Rodent Species</th>
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<tr>
<td></td>
<td><em>Peromyscus maniculatus</em></td>
</tr>
<tr>
<td>Cache size (number of seeds)</td>
<td>1.6 ± .6&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Cache depth (mm)</td>
<td>2.8 ± 2.5&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Distance from shrub edge (cm)</td>
<td>-0.4 ± 11.2&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Most used substrate</td>
<td>Litter</td>
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</table>

Table 1: Cache descriptor for each species that cached within the enclosures. Table lists the average number of seeds a cache, cache depth (mm), distance of cache from a shrub’s edge (cm), and substrate preference (litter or bare soil) for each species. Letters next to cache size, depth and distance values indicate results of Tukey’s post-hoc analysis (alpha = 0.05). Different letters indicate means are statistical different. The asterisk signifies that *Callospermophilus lateralis* was not included in these analyses because they did not cache enough to test statistically during this study. The results given are the averages for the caches we made based on Vander Wall *et al.* (2009).
**Figure 1:** Mean percent of caches pilfered in 24 h by each rodent species, bars indicated 95% confidence intervals. *Callospermophilus lateralis* did not pilfer any caches during this study and were not included in the analysis. There were no significant differences between the means ($F_{2,57} = 1.09$, $p = 0.34$).

**Figure 2:** Mean percentage of caches pilfered in 24 h from each rodent species, bars indicate 95% confidence intervals. There was no significant difference between the means ($F_{3,57} = 1.539$, $p = 0.214$).

**Figure 3:** Mean percentage of caches pilfered in 24 h for each species pair. There were no differences between *T. amoenus*’ ability to pilfer between species ($F_{3,16} = 0.26$, $p = 0.85$) nor *T. quadrimaculatus*’ ability ($F_{3,16} = 0.86$, $p=0.48$) However, *P. maniculatus*’ ability to pilfer from *C. lateralis* was significantly less than from other rodent species ($F_{3,16} = 6.066$, $p = 0.006$). *Callospermophilus lateralis* did not pilfer any caches in 6 trials during this study and were not included in the analysis as pilferers.

**Figure 4:** Mean number of seeds pilfered in 24 h by each rodent species, bars indicated 95% confidence intervals. *Callospermophilus lateralis* did not pilfer any caches in 6 trials during this study and were not included in the analysis. There were no significant differences between the means ($F_{3,57} = 3.9$, $p = 0.03$).
**Figure 5:** Mean number of seeds pilfered in 24 h from each rodent species, bars indicate 95% confidence intervals. There was no significant difference between the means (F\(_{3,57} = 0.25, p = 0.86\)).

**Figure 6:** Mean number of seeds pilfered in 24 h for each species pair. There was no difference between how many seeds *T. amoenus* pilfered between species (F\(_{3,16} = 0.98, p = 0.43\)) nor the number of seeds *T quadrimaculatus* pilfered (F\(_{3,16} = 1.13, p = 0.37\)). However, *P. maniculatus* pilfered significantly less seeds from *C. lateralis* than other rodent species (F\(_{3,16} = 9.44, p < 0.001\)). *Callospermophilus lateralis* did not pilfer any caches in 6 trials during this study and were not included in the analysis as pilferers.

**Figure 7:** Interaction network showing reciprocal pilfering of caches of the study species in Little Valley. The width of the connecting lines indicates the pilferers (top row) ability to pilfer from the caching species (bottom row). Thicker lines indicate more pilferage. Bars indicate the total mean pilferage ability of a species (top row) or total mean percentage of caches loss of a species (bottom row). Note, *C. lateralis* was incapable of pilfering caches so it was not included in the top row (pilferers) but it was pilfered from so it is included in the bottom row (cachers).
Figure 1:

![Graph showing percentage of caches pilfered by different species.]

- **P. maniculatus**
- **T. amoenus**
- **T. quadrimaculatus**

- n=20 for each species.
Figure 2:

Percentage of caches pilfered

- P. maniculatus
- C. lateralis
- T. amoenus
- T. quadrimaculatus

Caching species
Figure 3:

- **Pilfering species**
  - Peromyscus maniculatus (○)
  - Tamias amoenus (◇)
  - Tamias quadrimaculatus (×)
  - Spermophilus lateralis (●)

- **Caching species**
  - P. maniculatus
  - C. lateralis
  - T. amoenus
  - T. quadrimaculatus

- **Percentage of seeds pilfered**
  - 0
  - 20
  - 40
  - 60
  - 80
  - 100

The graph shows the percentage of seeds pilfered by different caching species under the influence of pilfering species.
Figure 4:

Number of seeds pilfered

- P. maniculatus (n=20)
- T. amoenus (n=20)
- T. quadrimaculatus (n=20)

Pilfering species
Figure 5:

![Graph showing the number of seeds pilfered by different caching species.]

- **P. maniculatus**
- **C. lateralis**
- **T. amoenus**
- **T. quadrimaculatus**

Legend:
- ○: Data point
- |: Confidence interval

Each category has a sample size of 15. (n=15 for each species)
Figure 6:

- **Pilfering species**
  - Peromyscus maniculatus
  - Tamias amoenus
  - Tamias quadrimaculatus
  - Spermophilus lateralis

- **Caching species**
  - P. maniculatus
  - C. lateralis
  - T. amoenus
  - T. quadrimaculatus

- **Number of seeds pilfered**

- Values range from 0 to 50.
Figure 7: Percentage of caches pilfered

Percentage of caches lost

<table>
<thead>
<tr>
<th></th>
<th>T. amoenus</th>
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<td>Percentage</td>
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<th>T. quadrimaculatus</th>
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</thead>
<tbody>
<tr>
<td>Percentage</td>
<td>35%</td>
<td>38%</td>
<td>28%</td>
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Chapter 2: The effects of rodent abundance and richness on cache pilfering across an environmental gradient in western Nevada

Jacob W. Dittel\textsuperscript{1,2}, and Stephen B. Vander Wall\textsuperscript{1,2}

\textsuperscript{1}Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV, 89557; \textsuperscript{2}Department of Biology, University of Nevada, Reno, NV, 89557;

**Keywords:** Seed-caching, scatter-caching, pilfering, rodents, reciprocal pilfering
Introduction

Food hoarding is important for many granivorous animals, particularly rodents, for future consumption during food shortages (Vander Wall 1990). Many of the seeds eaten by food-hoarding granivores are temporally abundant in quantities that exceed the requirements of granivores. Food hoarding, or seed-caching, therefore allows animals to preserve seeds for future consumption during times of food scarcity. Additionally, seed-caching gives a competitive advantage to animals by reducing the amount of food freely available and sequestering seeds from inter- and intraspecific competitors. However, a consequent of seed-caching, cache pilferage, is a phenomenon that seed-cachers have to manage. Cache pilferage can decimate an animal’s food stores leading to reduced fitness or death from starvation. As a result of cache-pilferage, seed-caching animals have evolved a plethora of behavioral strategies to reduce pilferage. Many studies have looked at the effects of cache pilferage on caching behavior (Dally et al. 2006, Steele et al. 2013, 2015, Zhang et al. 2013, 2014), seed fate (Vander Wall 2002, Jansen et al. 2012), and seed cacher community coexistence (Leaver and Daly 2001, Vander Wall et al. 2009, Dittel 2016, Chapter 1).

One form of seed caching, scatter-hoarding, is considered a pilferage avoidance strategy (Stapanian and Smith 1984, Dally et al. 2006), allowing animals who can not create or defend larder hoards to store food. Cache pilferage has also been suggested to facilitate seed dispersal by moving caches further away from parent plants (Howe and Smallwood 1982) and is hypothesized that it helps to support the high richness we see in rodent communities today (Dittel 2016, Chapter 1). Due to this, the majority of cache pilferage studies have focused on scatter-hoarding animals.
Seed cache pilfering is known to be consistently high (2-30% daily removal) for long-term hoarding species (Vander Wall and Jenkins 2003) and it is known that animals alter their caching behavior in response to pilfering (Vander Wall 1990, pg. 90). In the presence of conspecifics and heterospecifics, many animals will exhibit deceptive or secretive behaviors to try to deceive pilferers (Dally et al. 2006). If the risk of cache pilferage is perceived to be high, seed-cachers will alter their behavior by caching out of view of pilferers (Dally et al. 2005b), in hard to view sites (Dally et al. 2004), or by creating sham caches (Steele et al. 2008). Many rodents will seek out specific environmental factors such as vegetation structure (Petit et al. 1989, Swartz et al. 2010), soil moisture (Vander Wall 2000), and soil type (Briggs and Vander Wall 2004) to reduce pilfering rates. Cache pilferage can be devastating to individuals and therefore caching animals put significant effort into protecting their caches from pilferage. Species of heteromyid rodents have been shown to cache in different microhabitats that decrease the likelihood conspecifics can find their caches. Heteromyids will cache seeds in habitats that are not frequented by their conspecific competitors (Swartz et al. 2010) and will change cache microhabitat locations when pilferage occurs (Preston and Jacobs 2001, 2005). Seeds cached in moist soil are more detectable to rodents through olfaction (Johnson and Jorgensen 1981, Vander Wall 1993, 2000). Increased pilferage due to increased detection ability of caches is likely why many rodents (particularly Tamias spp.) in the arid and semi-arid western United States have primarily adopted scatter-caching behaviors while eastern mesic species have adopted larder-hoarding (Vander Wall and Jenkins 2011). Finally, substrate has been shown to have an effect on pilfering ability. Deer mice species (Peromyscus) have been shown to preferentially cache seeds in
small-particle soils because cache pilfering was lower in these soils than large-particle soils (Pearson and Theimer 2004). This is likely associated with soil moisture as well, as large-particle soils next to rocks were found to have higher water content than small-particle soils in the open. Substrate has also been shown to affect detection ability in *Tamias* spp. (Briggs and Vander Wall 2004), with rodents having decreased detection rates in ash substrates as opposed to sand substrates.

Many cache removal studies assume pilfered seeds are eaten and therefore a loss of food for the cacher (Vander Wall *et al.* 2005). This perception has been reflected in studies of an animal’s response to cache loss. However, the results of these studies have been mixed (Huang *et al.* 2011, Luo *et al.* 2014), showing both increases and decreases in hoarding behavior, even within the same species. One reason for the mixed results could be due to misrepresentation of cache loss in studies. Seed caches are dynamic, with caches being recovered or pilfered and then re-cached repeatedly until consumption (Vander Wall and Joyner 1998, Jansen *et al.* 2004, 2012, Perea *et al.* 2011). In one of the most recent and extensive studies of cache pilfering (Jansen *et al.* 2012), 57% of caches were recovered or pilfered by an animal within one week, with 99% of the caches being recovered or pilfered within the study time of one year. Seeds within caches were frequently pilfered from caches multiple times, up to 36 times, sometimes being moved multiple times in a single day. Most removals (84%) were pilferage events and despite being constantly handled most seeds were recached rather than eaten (Jansen *et al.* 2012).

Pilfering has been hypothesized to allow the coexistence of ecologically similar rodents (Price and Mittler 2003, 2006, Vander Wall and Jenkins 2003, Dittel 2016, Chapter 1). Specifically, the reciprocation of cache pilfering can negate harvesting
advantages one species may have over others by allowing pilferers access to seeds they could not acquire from the source. Recent work has supported the theory of reciprocal pilfering both intraspecifically (Jansen et al. 2012) and interspecifically (Vander Wall 2000, Dittel 2016, Chapter 1). Pilfering, or the lack there of, can help explain why some species larder-hoard instead of scatter-hoard (Thayer and Vander Wall 2005, Vander Wall et al. 2009, Dittel 2016, Chapter 1). It is also known that ungulates can have negative effects on rodent abundance, diversity and caching behavior (Guimaraes et al. 2005, Muñoz and Bonal 2007, Suselbeek et al. 2014) by pilfering from their caches. Rodents cannot reciprocate pilferage from seed predators like ungulates, so food loss from ungulates cannot be easily replaced. However, the presence of a non-caching consumer may also promote and sustain rodent coexistence (Price and Mittler 2003, 2006).

Lastly, cache pilferage has consequences for the mutualism between seed-caching animals and the plants they disperse. Many of the consequences of pilfering listed above have positive effects on plant recruitment. Rodent microhabitat preferences to avoid pilferage, often coincide with ideal germination locations for plants (Vander Wall and Joyner 1998, Longland et al. 2001, Pearson and Theimer 2004, Jansen et al. 2012). Recaching of pilfered seeds and caching patterns to prevent pilferage can decrease Janzen-Connel effects. By decreasing the cache size or increasing the space between seeds, rodents can decrease density dependant predator effects (Vander Wall and Joyner 1998, Hirsch et al. 2012). Cache pilfering has also caused some plants to evolve rapid germination to prevent animals from recovering the seeds before the plant has a chance to germinate (Jansen et al. 2006, Yang et al. 2012).
Despite the effects of pilfering being well studied, we lack a good understanding of how a population or community of competitors affects pilferage rates. In the arid and semi-arid western United States moisture is one driving factor of pilferage (Vander Wall 2000). However, in the eastern United States and other places with relatively high rainfall such as the tropics it we cannot observe the effect of moisture has on pilferage because of consistently high soil moisture. Most work has focused on the behavior of individuals, and by not fully examining caching and pilfering at the population and community scale, we are likely missing important information on the mechanisms described above. Two potentially important factor influencing cache pilferage that have been largely ignored are rodent abundance and richness. Richness and abundance are likely proxy variables for competition among seed-caching animals. An increase in either likely results in an increase in competition; high abundance could suggest high intra- and/or interspecific competition while high richness could suggest high interspecific competition. Abundance and richness could have large effects on seed-caching animals as they are unlikely able to escape the increased competition and would have to adjust their caching behavior accordingly.

Abundance is likely to increase cache pilferage. With more animals, the demand for a limited resource increases as well as the number of individuals attempting to pilfer. As a response to higher abundances, animals likely change their caching behavior in the above described ways. Increased richness offers a different challenge for scatter-caching rodents than abundance. Different species vary in behavior, size, physiologically, in phenotypic adaptations, and habit more so than individuals of a single species. Some species may excel at sequestering seeds, may be larger and therefore able to outcompete
competitors. Additionally differences in when species are active (diurna/nocturnal) might allow species to avoid competition. In this paper I investigate the affect of rodent abundance and richness on pilfering rates. I predict that when soil moisture is high, as rodent abundance and richness increase so will pilfering rates. This is because as abundance and richness goes up, competition for a limited food source (cached seeds) increases.

**Methods**

*Study Location*

This study was conducted across seven different habitat types in western Nevada: sand dune, low desert shrub, piñon forest, juniper forest, montane shrub, Jeffrey pine forest, and an alpine shrub site. Different habitats were necessary in order to have large enough differences in rodent abundance and richness among trails to test for differences. The sand dune community site was located in the Hot Springs Mountains, located 14 km east of Fernley in western Nevada (39° 42’ 2” N, 119° 3’ 34” W; Elevation ~1270 m). The Hot Springs Mountains are an arid environment with a loose, course sandy substrate (Murray *et al.* 2006). The plant community consists mainly of Indian ricegrass (*Achnatherum hymenoides*), but also consists of some shrub species such as greasewood (*Sarcobatus vermiculatus*), shadscale (*Atriplex confertifolia*), and fourwing saltbush (*Atriplex canescens*) (Longland *et al.* 2001).

The low desert shrub community was located in Nightingale Flats, approximately 30 km northeast of Fernley, Nevada (39° 42’ 5” N, 119° 1’ 58” W; Elevation ~1261m). The substrate here is different from the Hot Springs Mountains as it is more course and
stable substrate. The shrub community at Nightingale Flats is dominated by shadscale, greasewood, and winter fat (*Krascheninnikovia lanata*) (Jones and Longland 1999).

Both trials conducted in piñon and juniper forest were conducted in the Pine Nut Range, located 12 km south east of Carson City, Nevada (39° 5’ 10” N, 119° 39’ 0” W; Elevation ~1920 m). Both sites are semi-arid and consisted of sandy loose soils. The vegetation consists primarily of single-leaf piñon pine (*Pinus monophylla*) and Utah Juniper (*Juniperus osteosperma*). The piñon forest site was at a location dominated by piñon, while the juniper forest site was at a location dominated by juniper. The shrub understory is dominated by sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Chrysohamnus nauseosus*), gooseberry (*Ribes velutinum*), and Mormon tea (*Ephedra virdis*) (Hollander and Vander Wall 2004).

The montane shrub and Jeffrey pine forest sites were located in Whittell Forest and Wildlife Area (henceforth Whittell Forest), located 30 km south of Reno in the Carson Range of western Nevada (39° 15’ 10” N, 119° 52’ 35” W; elevation ~1975 m). Whittell Forest is a semi-arid environment with decomposed granite soils. The forest community consists mainly of Jeffrey pine (*Pinus jeffreyi*) and lodgepole pine (*Pinus contorta*) with a shrub understory primarily comprised of greenleaf manzanita (*Arctostaphylos patula*), tobacco brush (*Ceanothus velutinus*), Sierra bush chinquapin (*Castanopsis sempervirens*) and antelope bitterbrush (*Purshia tridentata*). The montane shrub site was located on the eastern slope of the Carson range within Whittell forest and was dominated by greenleaf manzanita and tobacco brush with sparse Jeffrey pine saplings no higher than 1.5 m. The Jeffrey pine forest site was located between the Carson Range and the Sierra Nevada at a site within Whittell Forest called Little Valley.
The Little Valley study site is secondary Jeffrey pine forest with a greenleaf manzanita and antelope bitterbrush understory.

The final study site, high alpine shrub, was approximately 4 km south by southwest of Mount Rose (39° 18’ 31” N, 119° 55’ 17” W; elevation ~2800 m). I chose this site as a study site by following Clark’s Nutcrackers (*Nucifraga columbiana*) collecting seeds from the general area around Whittell Forest to the area where they cached seeds. While the area Clark’s nutcrackers cached seeds was larger than the study site, it was well within the range I observed Clark’s nutcracker’s caching. The soil here is also decomposed granite and the woody-plant community is dominated by the prostrate shrub, pine-mat manzanita (*Arctostaphylos nevadensis*). White bark pine (*Pinus albicaulis*) was present within the study site but not abundant.

**Data Collection**

Rodent abundance and richness was estimated through live-trapping. I placed fifty Sherman live animal traps (H. B. Sherman Inc.) in a 5 × 10 trapping grid with 15 m spacing between each trap at each site. Traps were left open for 5 days and 5 nights for a total of 250 trapping nights, and checked twice daily (morning and evening). I placed a single Sherman live animal traps at each point on the grid and baited the trap with bird seed mix (sunflower and millet) or only sunflower seeds depending on the location. Heteromyid rodents prefer the bird seed mix, so I used the mix at locations where their presence was likely. Millet was not required at sites with out heteromyids as sciurids prefer sunflower seeds. I identified captured rodents to species and marked each individual with a serially numbered ear tag to prevent recounting. Capture data were used to enumerate abundance and richness.
Concurrent with rodent trapping, I established three wandering transects of seed caches spaced approximately 5 m apart. The seed cache transects started at least 15 m along one side of the trapping grid and “wandered” around the trapping grid, never entering it. Each seed cache transect consisted of 50 caches. Half of the caches were made with seeds native to the study site, and the other half were made with sunflower seeds (*Helianthus annuus*) to act as a standard treatment across study locations. A non-native seed type was necessary as there is not a native seed found across all habitat types. Native seeds used were Indian rice grass (low desert shrub and sand dune sites), piñon pine (piñon and juniper forest sites), antelope bitterbrush (montane shrub and Jeffrey pine forest sites), and Jeffrey pine (alpine shrub). Jeffrey pine seeds were used at the alpine shrub site to mimic Clark’s nutcracker caches. Indian rice grass caches contained 50 seeds (McMurray *et al.* 1997), piñon caches contained 3 seeds (Vander Wall 1997), antelope bitterbrush caches contained 10 seeds (Vander Wall 1994), and Jeffrey pine caches contained 5 seeds (Tomback 1982). Sunflower seed caches were constant at 5 seeds per cache across all sites, this made the sunflower seed caches approximately equal in value (cache size) to each native cache as well as across the sites. I kept cache depth constant across sites at 10 mm deep, this fell within the mean of most caches made by rodents and Clark’s nutcrackers (Tomback 1982, Vander Wall and Joyner 1998, Vander Wall 2000, Longland *et al.* 2001). I made caches using a metal spoon to minimize contaminating seeds with human scent, and I inconspicuously groomed the soil after cache placement to conceal signs of digging. I marked caches with natural objects (e.g. sticks and rocks) to avoid rodents learning visual cues of cache locations. In order to
prevent learning, I made an attempt to make no two cache markings within a transect the same.

I checked the wandering seed cache transects daily for 5 days staring the day after establishment. The transects were checked by walking the transect looking for disturbance at the cache site. If dig marks were apparent at the cache site, I would excavate the cache to verify seeds were removed. If seeds were removed from the caches, I would record the date and cache type removed. If seeds were not removed I would rebury them hiding my disturbance as described above. It has been shown rodents have difficulties detecting caches under dry conditions (Vander Wall 2000) so all trials followed significant rain events. To ensure soil moisture conditions were conducive to cache detection, I collected 5 soil samples at day 0 and day 5 in Whirl-pack®, plastic bags. Plastic bags were sealed and kept in a cool location until returned to the lab. In the lab, I weighed the soil samples, dried them in an oven at 100° C for 48 hours, and then reweighed. In order to be used in data analysis a study site had to have an initial soil moisture of ≥3.5% and not go below 1.5% on day 5.

Data Analysis

I analyzed all data using program R (R Core Team 2015). Rodent capture data (number of unique individuals) were used to calculate abundance and richness. I analyzed the differences in cache removal using survival analysis (package survival, Therneau and Grambsch 2000, Therneau 2013) and models with censoring and Weibull distributions. I analyzed each site independently comparing each transect and seed type (native vs non-
native). Additionally, I analyzed native and non-native caches (sunflower seeds) to
determine if there were differences in removal across sites. I regressed rodent abundance
and richness with mean removal rate to determine if there were any effects of abundance
or richness on removal rates. I calculated mean removal rate as the mean daily removal
rate across transects at each site. I then used linear models to compare mean removal rate
to rodent abundance and richness. When making linear models I assumed there could not
be any removal without rodents so I forced the y-intercept at zero for all models.

Results

There was a total of 250 trap nights at each site. Abundance and richness differed
across sites, but richness varied less than the numbers of individuals captured (Table 1).
Low desert shrub and the Jeffrey pine forest site had the highest total abundance (n=38
individuals), while the alpine shrub site had the lowest abundance (n=3). Richness
averaged ~4 species per site, with a maximum of 5 species (3 sites, table1) and a
minimum of 2 (Alpine shrub site).

All seven sites were initially above 4% soil moisture when seed cache transects
were established and did not drop below 1.5% after 5 days. Sunflower seed cache
removal differed from native seed cache removal at three of the seven sites: juniper forest
($\chi^2=25.6$, df=1, p<0.001), piñon forest ($\chi^2=15.36$, df=1, p<0.001), and low desert shrub
($\chi^2=11.85$, df=1, p<0.001, Fig. 1). In the juniper and piñon forest sites piñon seeds had a
lower survivorship than sunflower seeds and were removed more quickly than sunflower
seeds. At the low desert shrub site sunflower seeds had higher initial removal rates and
lower survivorship than Indian ricegrass.
There were significant differences across sites when comparing sunflower seed removal ($\chi^2=372.84$, df=6, $p<0.001$, Fig. 2). Low desert shrub site experienced the highest rate of removal (mean = 56% ± 14 per day) while the alpine shrub site experienced the lowest removal rate (mean = 2% ± 1 per day). The sand dune (30% ± 16 per day) and Jeffrey pine forest site (24% ± 7 per day) experienced the second highest mean removal rates followed by montane shrub (12% ± 3 per day) and piñon forest (7% ± 2 per day), and finally juniper forest (3% ± 1.4 per day). Seed removal rate was positively correlated with rodent abundance for sunflower seed removal ($F_{1,6}=8.053$, $p=0.036$, $R^2 = 0.80$, Fig. 3) and native seeds ($F_{1,6}=24.39$, $p<0.001$, $R^2 = 0.91$, Fig. 3). The increase in mean removal rate for each model is 1% per day per individual (Sunflower) and 1.6% per day per individual (native seeds). Mean removal was not associated with rodent species richness for sunflower seeds ($F_{1,6}=0.66$, $p=0.46$) nor native seeds ($F_{1,6}=0.49$, $p=0.08$). One family of rodents (Sciuridae) was found in every study site; neither the abundance ($F_{1,6}=0.018$, $p=0.898$) nor species richness ($F_{1,6}=0.014$, $p=0.911$) of sciurids was associated with mean removal rate.

Discussion

Natural rainfall events were sufficient to promote seed cache removal during this study, as all sites experienced removal. However, the use of natural rain events prevented the control of soil moisture across sites. Not all rain events were equal so some sites experienced higher soil moisture during the study period than others. Despite differences in rainfall, the minimum soil moisture required was met for all trials, but maximum soil moisture varied. The relationship between soil moisture and detections is a step function
with approximately a 0.5% threshold (Vander Wall 2000, 2003). Once soil moisture levels reach the threshold seeds become detectable to rodents. Additionally, it is unlikely that trapping concurrently with seed cache trials at all sites affected removal rates. Seed cache transects were set far enough away from the trapping grid and moved away from the trapping grid to limit the number of animals being trapped that would be potential pilferers.

Seed type seemed to have a small effect on removal except at three sites (Fig. 1). At the low desert shrub site where Indian Rice grass was used, rodents initially removed sunflower seeds at a faster rate than native seeds. A previous study by Hollander et al. (2012), conducted in similar environments found that rodents removed cultivated non-native seeds more quickly than natives. One hypothesis why non-natives are removed more rapidly than natives is the crypsis hypothesis (Paulsen et al. 2013, 2014). Paulsen et al. (2014) hypothesize that seeds have evolved water impermeable seed coats to reduce the release of volatiles and therefore reduce rodents’ ability to detect seeds through olfaction. Cultivated sunflower seeds have been selected for increased nutrition and palatability primarily for use as oil and bird feed. It is possible that the seed coats’ ability to keep volatiles in has diminished, in addition with being placed in non-native habitat, making them more detectable than native Indian ricegrass. Rodents at the juniper and piñon sites removed the native seed (piñon pine) faster than sunflower. Additionally, at the remaining sites sunflower seed removal was statistically equal to native seed removal. This does not follow the crypsis hypothesis, and one explanation is that Indian ricegrass seeds are the only seeds with an indurate seed coat. These seed coats potentially block odors from leaving the seed when moist. Additionally, soil water moisture was
sufficiently high enough that all seeds lacking an indurate seed coat were equally detectable. Higher piñon pine removal therefore may be a result of preference and familiarity. Piñon pine preference has been reported in deermice populations (Everett et al. 1978) and is likely to hold true for all granivorous rodent species within *P. monophylla* distribution as it is a large nutritious seed.

Rodent abundance was the only tested variable correlated with pilfering rates; as rodent community size increases so do pilferage rates. The model using rodent abundance accounts for most of the variation in the data for sunflower removal ($R^2 = 0.80$) and native seed removal ($R^2 = 0.91$). This study shows that a relatively small changes in population sizes could have significant effects on pilferage rates. Cache pilferage is an important phenomenon in seed-caching rodent communities, and it is not surprising that abundance of rodents influences the rate at which it happens.

Since all caches were created by me, all seed removal during this study is the result of pilfering and not cache recovery. Cache pilferage is experienced by all scatter-hoarding animals and they have to be able to tolerate or counteract pilferage or risk extirpation. One method to tolerate cache pilferage is reciprocal pilferage. Under this hypothesis animals should be able to reciprocate pilferage at near equal rates as their competitors allowing individuals to mitigate the effects of pilferage (Vander Wall and Jenkins 2003). Previous work at the study sites supports reciprocal pilfering for rodents species (Vander Wall 2000, Dittel 2016, Chapt. 1), but scatter-caching birds (corvids) are seemingly unable to reciprocate pilferage (Thayer and Vander Wall 2005). Many jays and other corvids attempt to protect stored food by making sham caches, increasing the amount of food they eat, or re-caching seeds frequently when they suspect they are being
watched (Dally et al. 2005a, 2006). However, these tactics do not defend against rodents detecting caches via olfaction. Another strategy to avoid cache pilferage may be to make caches away from conspecific competitors.

One potential example of an animal making caches away from conspecifics are Clark’s Nutcrackers (*Nucifraga columbiana*), which cache seeds on steep slopes at higher elevations than where seeds are collected (Vander Wall and Balda 1977, Hutchins and Lanner 1982, Tomback 1982, Tomback and Linhart 1990). Clark’s Nutcrackers invest a lot of energy to transport seeds to these high elevation sites and may be selecting these cache sites based on pilferage rates. Pilferage rates were much lower at the alpine shrub site (2\% \pm 1 per day) where Clark’s nutcrackers cache seeds. With high pilferage rates of approximately 24\% \pm 7 caches being removed daily at lower elevations (i.e. Jeffrey pine site), and similar rates in other studies (Vander Wall and Jenkins 2003), there would be strong selective pressure to cache at high elevation sites that experience less daily pilferage despite the energy costs of transportation. Two species of rodents were captured at the alpine shrub site; *Tamias amoenus* and *Peromyscus maniculatus* (total abundance of n=3). The sites chosen by nutcrackers, high elevation and steep slopes, are not preferred habitats for chipmunks (Chappell 1978) and is near the elevation maximum for *T. amoenus* (2900 m, Reid 2006). *Peromyscus maniculatus* are habitat generalist and are found regularly at this elevation and higher (up to 3,500 m, Reid 2006). Their population sizes are likely lower at these sites as population densities of *Peromyscus* are highest around 2150 m and decrease as one approaches higher elevations (Dunmire 1960). Clark’s nutcracker cache sites would have to have approximately an order of magnitude larger rodent populations to match pilferage rates near seed sources. This seems unlikely
in mostly open and steep sloped alpine habitats. Snow also covers caches for much longer (1-2 months) at higher elevations sites, during periods of snow cover pilferage rates are at approximate 0% per day. Therefore, caches at higher elevations would be available to pilferers for shorter time periods than at lower elevation sites where the seeds are harvested from. Lastly, an additional species, not caught at the field site but may be present, is *Callospermophilus lateralis*. It is unlikely that *C. spermophilus* would influence the pilferage rate if present at the site because it is unable to locate caches (Vander Wall *et al.*2009, Dittel 2016, Chap. 1) at rates greater than random.

Finally, these results should be viewed in context. All removal trials were performed during moist soil conditions and rodents in the semi-arid and arid environments, where this study was conducted, are likely only able to detect seeds under moist soil conditions (Johnson and Jorgensen 1981, Vander Wall 2000). If there is not sufficient moisture for detection, the effect of rodent population size on pilferage rates may be greatly reduced. Therefore, these results do not indicate a continuous daily pilferage rate. However, the results are likely representative for sites that are not semi-arid or arid though, as moisture is not a limiting factor.

These results have broader implications for understanding competitor coexistence and seed dispersal mutualisms. Seed-caching rodent populations fluctuate frequently (Whitford 1976, Crawley 2000, Schnurr *et al.*2002) and rodents likely have behavioral responses to these changes in abundance and potentially alter their caching strategy in where and how they make caches (Preston and Jacobs 2001, 2005, Swartz *et al.*2010) that support coexistence. These changes in behavior can also benefit plants. Seed-eating rodents have long been considered detrimental to plants (Kollmann *et al.*1998, Moles *et
al. 2003, Paine and Beck 2007), but studies have shown pilfering does not equate to predation (Vander Wall and Joyner 1998, Jansen et al. 2012, Dittel et al. 2015). Cache pilferage may in fact increase seed survival by reducing Janzen-Connell effects and placing seeds in favorable germinating conditions. While this study is an attempt to further understand the underlying mechanisms of cache pilferage further work is needed. The effects of pilferage have been well studied, but without a strong understanding of the mechanisms, we are unable to predict the conditions that affect not only seed-caching rodent communities but the mutualism they have with animal dispersed plants. Similar studies to this one need to be conducted in non-arid habitats to determine if the relationship with abundance holds true and what other factors may affect pilferage rates when moisture is not a limiting factor.
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**Figure 1:** Survivorship curves of native and non-native (sunflower) seeds at each site over the five-day trial period. X-axis represents time (days) and the y-axis represents the proportion of caches remaining. Dashed lines represent native seeds while solid lines represent sunflower seeds. There is no difference in survivorship in four of the seven sites. At the juniper and piñon forest sites native seeds (piñon pine) had a lower survivorship than sunflower seeds ($\chi^2=25.6$, df=1, p<0.001 and $\chi^2=15.36$, df=1, p<0.001 respectively). At the Low desert shrub site sunflower seeds had a lower survivorship ($\chi^2=11.85$, df=1, p<0.001) than the native seed (Indian ricegrass).

**Figure 2:** Survivorship curves of sunflower seeds across sites. There were significant differences across sites ($\chi^2=372.84$, df=6, p<0.001). X-axis represents time (days) and the y-axis represents the proportion of caches remaining. Daily mean removal rates for each site are: Low desert shrub 56% ± 14, Sand dune 30% ± 16, Jeffrey pine forest site 24% ± 7, montane shrub 12 ± 3, piñon forest 7% ± 2, juniper forest 3% ± 1.4, and alpine shrub site 2% ± 1.

**Figure 3:** Linear regression of mean daily removal rate and rodent abundance. Circles represent sunflower removal and the model is represented with the solid line. Triangles represent native seed removal and the model is represented with the dashed line. Daily mean removal rate is positively correlated with rodent abundance for both seed types (Sunflower: $F_{1,6}=8.053$, p=0.036, $R^2 = 0.8$ Native: $F_{1,6}=24.39$, p<0.001, $R^2 = 0.54$). Sunflower model equation: $y=0.01x$. Native model equation: $y=0.016x$. 
Table 1: Abundance (number of individuals) and richness (number of species) at each study site.

<table>
<thead>
<tr>
<th></th>
<th>Low desert shrub</th>
<th>Sand dune</th>
<th>Juniper forest</th>
<th>Piñon forest</th>
<th>Montane shrub</th>
<th>Jeffrey pine forest</th>
<th>Alpine shrub</th>
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<td>Total abundance</td>
<td>38</td>
<td>17</td>
<td>9</td>
<td>16</td>
<td>21</td>
<td>38</td>
<td>3</td>
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<tr>
<td>Richness</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td>3</td>
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</table>
Figure 1:
Figure 2:

[Graph showing the rate of caches remaining over time for different habitats such as Low desert shrub, sand dune, Juniper forest, Pinon forest, Montane shrub, Jeffrey pine forest, and Alpine shrub.]
Figure 3:
Chapter 3: The mismatch of species richness of vertebrates and the plants that they disperse

Jacob W. Dittel\textsuperscript{1,2}, and Stephen B. Vander Wall\textsuperscript{1,2}

\textsuperscript{1}Program in Ecology, Evolution and Conservation Biology, University of Nevada, Reno, NV, 89557; \textsuperscript{2}Department of Biology, University of Nevada, Reno, NV, 89557;

Keywords: Seed dispersers, scatter-hoarders, frugivores, species richness, seed dispersal
INTRODUCTION

Richness distributions are one of the most discernable patterns in ecology (Francis et al., 2003) and yet are one of the most debated patterns in ecology (Kissling et al., 2009). Climate is often one of the important explanatory variables in ecology for variation in taxonomic richness (Currie et al., 2004), and there has been considerable effort in studying species’ distributions using environmental factors (Belmaker & Jetz, 2011). Yet it is known that biotic interactions such as competition (Brown, 1971; Patterson, 1980; Patterson & Brown, 1991), predation (Hecnar & M’Closkey, 1997; Shurin & Allen, 2001), and/or mutualisms (Stachowicz, 2001; Bronstein, 2009) influence species’ distribution. In this study, I attempt to further understand the relationship between mutualistic species’ distribution with each other and their environment. One particular type of mutualism, seed-dispersal, is interesting because species distribution may not only be correlated with environmental variables (Kissling et al., 2009; Vander Wall & Jenkins, 2011), but may also be correlated with the presence of their mutualist plant partners.

Seed dispersal is a critical stage in the life history of plants (Howe & Smallwood, 1982; Herrera, 1985; Terborgh, 1990), and plants have evolved multiple abiotic and biotic methods to disperse their seeds. Of the many seed dispersal syndromes, dispersal mutualisms are arguably the most important as they potentially disproportionately move seeds into favorable germination sites rather than random movement (Howe & Smallwood, 1982; Jordano et al., 2011). Despite the importance and commonality of this mutualism, the distribution and prevalence of seed dispersal mutualisms are still poorly known globally (Vander Wall et al., submitted; Willson et al., 1990; Almeida-Neto et al.,...
Recently, Vander Wall et al. (submitted) described the distribution of plants dispersed by animal mutualists in North America. Vander Wall et al. (submitted) found that a significant proportion of plants (16.2%) are dispersed by animals, and determined that seed dispersal mutualisms decrease with increasing latitude and elevation, and increase with increasing precipitation. Although these patterns of distribution are consistent with patterns observed in other plant communities (Lobo et al., 2001; Vetaas & Grytnes, 2002; Francis et al., 2003), it is not known whether these patterns are influenced by the animal mutualist or by the abiotic environment. Plants with seed-dispersal mutualists appear to be more sensitive to environmental variables but it is unknown whether their animal dispersers contribute to this pattern (Vander Wall & Moore, submitted).

Other work has focused on the distribution of frugivorous birds (Jetz & Rahbek, 2002; Kissling et al., 2007, 2009) and thus tangentially looked at seed dispersing birds. Many of these studies have found that climatic factors, primarily those measuring productivity and seasonality, best describe species diversity patterns (Karr, 1976; Hawkins et al., 2003; Kissling et al., 2009). The results are consistent with many groups of animal species and seems to be a common phenomenon for species richness (Currie et al., 2004). Additionally, factors such as food diversity (i.e. plant diversity) (Fleming, 2005; Kissling et al., 2007) and biogeographical history (Kissling et al., 2009) have been found to be significant predictors of frugivorous bird richness. Many frugivorous birds though are not seed dispersers and therefore the distribution of frugivorous birds and the climatic factors that predict the distribution of the birds do not give us much insight into the distribution of the mutualism with plants.
Despite the amount of work in describing the richness of species at continental and global scales, there has not been a study that specifically investigates the patterns of species distribution in seed dispersing animals relative to the plants that they disperse. Determining the distribution of species richness of seed dispersing animals would allow researchers to focus future studies in locations that are seed disperser “hotspots” or “cold spots.” Work in these areas may help ecologists further elucidate the underlying ecological and evolutionary mechanisms of seed dispersal mutualisms advancing theory on the strength of coevolution in these ecosystems. Additionally, the distribution of seed dispersing animals may give insight into which climatic variables promote seed dispersing interactions.

In this study, I investigated the distribution of terrestrial bird and mammal seed dispersers in temperate North America. The primary goal of this study was to determine the distribution of seed dispersing animals and the richness of these seed dispersing bird and mammal guilds across North America. Secondarily, I looked for broad ecological and environmental correlations with the distribution of seed dispersing animals. I hypothesized that if the mutualisms are specialized between plants and seed dispersers, then the richness distribution of the seed dispersers would be correlated with the distribution of plants. In other words, as the richness of plants dispersed by animals increased so would the richness of the animals dispersing their seeds. Alternatively, if the mutualisms between plants and seed dispersing animals are diffuse or weak, then I expect them to not be correlated. In this scenario, other factors (e.g. climate) would better explain the distribution of seed disperser richness. Because previous studies have found strong correlations between animal richness and climatic factors (Vander Wall et al.,
submitted; Vander Wall & Moore, submitted; Lobo et al., 2001; Kissling et al., 2007, 2009), I predict that climatic variables related to evapotranspiration (used as a proxy for ecosystem productivity), precipitation, elevation, and latitude will be strong predictors of animal species distributions.

MATERIALS AND METHODS

Guild Determination and Mutualist Identification

To examine the potential relationship between terrestrial bird and mammal seed dispersers have with the plants that they disperse, I first assigned both the birds and mammals of North America (United States and Canada) to two seed dispersing guilds; frugivorous and scatter-hoarding seed dispersers. Animals were considered frugivorous seed dispersers if they habitually consume fruits containing seeds, and the seeds remain viable after being either regurgitated or passed through the digestive tract. Animals that are frugivorous (i.e. diet composed largely of fleshy fruit) but not a seed disperser, because seeds are not viable after consumption, were not included in this study. For example, birds such as northern cardinals (Cardinalis cardinalis) frequently eat fruit, but possess gizzards that destroy seeds by grinding them up. Additionally, animals that seldom eat fruit and pass seeds intact were also not included in my analysis, as they are unlikely to influence plant-disperser relationships in a significant way. Scatter-hoarding, which frequently results in a mutualism with plants, is limited to the bird family Corvidae and the mammal order Rodentia in North America (Vander Wall, 1990) and therefore I limited the data to these two taxa. A species was considered a scatter-hoarder if seeds are a significant portion of its diet, it scatter-hoards in the soil, and there is a reasonable
expectation that some of those seeds germinate. Some scatter-hoarding animals are also frugivorous and were included in the frugivorous list. All animals were initially identified to be frugivorous or scatter-hoarders through personal knowledge and verified with primary literature when available. The primary source for birds was Bent’s Life History of Birds series (Bent, 1919-1968), and for mammals a search of the primary literature was performed on a species basis. If no source provided evidence for either behavior I excluded the species from the list. The taxonomy of all species is based on current species lists published for mammals and birds of North America (American Ornithologists’ Union, 1998; Wilson & Reeder, 2005). I recognize that this list is unlikely to be exhaustive and the inclusion or exclusion of certain species could be debatable. Hereafter, I use the terms frugivorous and scatter-hoarding to mean species that are seed dispersers.

Data Acquisition

Bird distribution data were obtained from BirdLife International and NatureServe (Ridgley et al., 2007; BirdLife International and NaturServe, 2014) and mammal distribution data were obtained from the International Union for Conservation of Nature Red List (IUCN, 2012). Data were downloaded as shape files, rasterized, overlaid, and projected using Program R (R Core Team, 2014) using packages maptools (Lewin-Koh et al., 2011), raster (Hijmans, 2014), sp (Pebesma & Bivand, 2005; Bivand et al., 2008), and rgdal (Keitt et al., 2014). Each individual distribution map was rasterized to 3,996 × 3,996 matrix of cells across North America (lat + long ranges). Then each cell of the individual species distribution maps was given a value of 1 for presence or 0 for absence.
Composite distribution maps were made for all frugivorous animals, frugivorous birds, frugivorous mammals, all scatter-hoarding animals, scatter-hoarding birds, and scatter-hoarding mammals by overlaying each individual raster distribution map and adding the cells together for a total number of species present (i.e., species richness) per cell. I reviewed the species list for both frugivorous and scatter-hoarding animals at each site to eliminate species that were supposedly present according to their range maps but were unlikely actually present due to elevational or ecological limitations.

Plant data were obtained from the North American Seed dispersal Project (NASD), Vander Wall et al., submitted; Vander Wall & Moore, submitted). In their study, Vander Wall et al. enumerated the number of plants dispersed by animals and described their dispersal mode at 197 sites across North America. For this study, I selected the plant species at each site that had a dispersal mode that included either “frugivory” or “scatter-hoarded” to use in analysis. See Vander Wall et al. (submitted) for details on their methods and dispersal mode determination. Distribution maps of plant richness were created using the kriging function from the kriging package (Olmedo, 2014) in program R to extrapolate the point estimates from the NASD project across North America. The default settings were used with the kriging function with pixels set to 1000. These maps were only used to approximately visualize the data and were not used in any data analysis.

To obtain the species richness of animals with a mutualistic relationship with plants, I used the extract function from the raster package. This function works by extracting specified data from a raster at given points. The latitude and longitude of the center (mean latitude and longitude) of each site was used as x, y coordinates for data
extraction. The center of each site was deemed acceptable because the range maps of the included animals are not detailed enough to show significant differences within a study site.

Precipitation data were obtained from Bioclim (Hijmans et al., 2005), and annual actual evapotranspiration (AET) data were obtained from the Global-AET Database (Trabucco & Zomer, 2010). AET was used as a proxy variable for productivity. All data were downloaded in 10-arc minute spatial resolutions except for AET which were only available in 30-arc second resolution. Elevation data were obtained from the NASD project. Climate data were extracted from the rasters for each variable using the same methods as stated above for extracting species richness.

Data Analysis

Species richness of frugivorous animals, scatter-hoarding animals, and the plants they disperse were z-transformed so that a visual comparison of richness could be made. The z-scores of animals were subtracted from the plants they dispersed and the resulting number was used to determine if relative animal or plant richness differed at a site. These points were plotted and kriged as explained above to extrapolate across North America and create a visual distinction between animal and plant richness. These data were not used in any further analyses.

Data analysis was broken into three major categories; all seed dispersers, frugivorous animals, and scatter-hoarding animals. Each guild was further broken down between birds and mammals and analyzed separately. Generalized linear models were built comparing each independent variable (plant richness and climate variables) to
animal species richness for each category. Despite being count data (species richness) a Gaussian distribution was used because the data did not deviate from a normal distribution. Plant richness for each site was area adjusted (Vander Wall et al., submitted) by using a $n/\log_{10}(\text{area})$ transformation, where $n$ equals the number of plant species at a given site. This adjustment was not necessary for animal species richness as it was a point estimate. Sites that did not include frugivorous animals, scatter-hoarding animals, or that lacked plants that were dispersed by these two guilds (i.e. had a value of zero) were discarded from analysis. Spatial autocorrelation is a common occurrence in range map and atlas survey data (Dormann et al., 2007) and was an issue in this study with abiotic variables but not richness of either plants nor animals. To correct for spatial autocorrelation generalized least squares models (GLS) were built following (Crawley, 2007) for all analyses with abiotic variables. Data were log$_{10}$-transformed when necessary. All analysis was performed in program R (R Core Team, 2014).

RESULTS

Scatter-hoarding mutualists

There are a total of 183 animals involved in seed-dispersal mutualisms based on my criteria, 68 species are birds while 115 are mammals (Appendix 1 & 2). A total of 7 corvid species are considered to be both scatter-hoarders and frugivores. Seed disperser richness decreases with an increase in latitude ($F_{1,195}=188$, $p<0.001$, Fig. 1A). The richness of seed dispersers is highest in southeastern Arizona and southwestern New Mexico, central New Mexico and south-central Colorado (Fig. 2B). The Southwest United States is the most species rich region in general but most of southern North
America has moderately high seed disperser richness. Areas of low richness include some parts of the Sonoran and Mojave deserts, central valley of California, and most of Canada, and Alaska.

There is a positive correlation between seed disperser richness and the richness of the plants they disperse \((F_{1,195}=5.88, p=0.02, \text{Fig. 3A})\). However, if the latitude of data points is considered there is a natural split of the data at approximately 50° latitude (Fig. 3B). When analysis is divided between high \((\geq 50°)\) and low \((< 50°)\) latitude sites, there is no correlation between seed disperser richness and the plants they disperse at low latitudes \((F_{1,178}=4.9, p=0.16, \text{Fig. 3C})\) but there is positive correlation at high latitudes \((F_{1,15}=27.49, p<0.001, \text{Fig. 3D})\). There was no correlation of total seed disperser richness with precipitation \((t=1.57, df=195, p=0.12)\), but there is a positive correlation with median elevation \((t=4.22, df=195, p<0.001)\) and with AET \((t=2.31, df=195, p=0.02)\) (Fig. 1B - D).

*Frugivorous Animals*

A total of 88 animals were determined to participate in frugivorous seed-dispersal mutualisms, 65 species were birds while 23 were mammals (Table 1). Richness of frugivorous animals decreases with an increase in latitude \((F_{1,195}=262.6, p<0.001, \text{Fig 4A})\), with richness highest in the southern portions of North America (Fig. 5B). The highest richness areas are primarily in southeastern Arizona, southwestern New Mexico and central Texas. Richness is relatively low in the Great Basin Desert and Mojave deserts, with the lowest regions being northern Canada and Alaska.
There is a positive correlation between the richness of frugivorous animals and the richness of plants that they disperse \( (F_{1,195}=25.4, \ p<0.001, \ \text{Fig. 6A}) \). Similar to all seed dispersers, frugivore richness is only correlated with the richness of the plants they disperse above 50° latitude. There is no correlation between frugivorous animal richness and the plants they disperse at low latitudes \( (F_{1,180}=1.7, \ p=0.19, \ \text{Fig. 6C}) \) but there is positive correlation at high latitudes \( (F_{1,15}=18.88, \ p<0.001, \ \text{Fig. 6D}) \). There was no correlation with precipitation \( (t=1.43, \ df=195, \ p=0.15) \), nor median elevation \( (t=1.9, \ df=195, \ p=0.06) \) but there is a positive correlation with AET \( (t=2.0, \ df=195, \ p=0.04) \) (Fig. 4A-D).

Frugivorous bird richness follows a similar pattern as the whole frugivory guild. Frugivorous bird richness was also negatively correlated with latitude \( (F_{1,194}=380, \ p<0.001) \) and positively correlated plant richness \( (F_{1,194}=8.43, \ P=0.004) \). Again, there is a demarcation at 50° latitude with no correlation at latitudes lower than 50° \( (F_{1,178}=2.38, \ p=0.13) \) and a positive correlation at latitudes above 50° \( (F_{1,14}=65.57, \ P<0.001) \). There is no significant correlation with precipitation \( (t=0.48, \ df=194, \ p=0.64) \), median elevation \( (t=1.71, \ df=194, \ p=0.09) \) nor with AET \( (t=1.26, \ df=194, \ p=0.22) \).

Frugivorous mammal richness also follows a similar pattern as the whole frugivory guild; mammal richness is negatively correlated with latitude \( (F_{1,186}=37.33, \ p<0.001) \). The richness of frugivorous mammals is positively correlated with the plants they disperse \( (F_{1,186}=9.11, \ p=0.002) \), however this correlation also disappears at latitudes below 50° \( (F_{1,173}=1.91, \ p=1.69) \) but remains significant at latitudes above 50° \( (F_{1,13}=8.08, \ p=0.01) \). Frugivorous mammal richness has no significant correlation with precipitation.
(t=2.21, df=186, p=0.39), median elevation (t=1.94, df=186, p=0.47), but are positively correlated with AET (t=1.67, df=186, p=0.01).

Scatter-hoarding animals

A total of 102 animals were determined to be scatter-hoarders involved in a seed dispersal mutualism, 10 species were birds and 92 were rodents (appendix 2). As with frugivorous animals, scatter-hoarder richness decreases with latitude (F$_{1,185}$=14.88, p<0.001, Fig 4A) and is concentrated in the southwestern United States. Scatter-hoarder richness is highest in New Mexico, and western Texas, with small richness hotspots in the Great Basin and Mojave Desert. The Sonoran Desert has a surprisingly low scatter-hoarder richness (Fig 5B). Richness is also lower in the eastern United States with the lowest regions being along the eastern coast and northern Canada.

Unlike all seed dispersers and frugivorous animals there is no correlation between scatter-hoarders and the plants they disperse (F$_{1,185}$=3.20 p=0.08) even when taking the 50° latitude break into account (Fig. 9). Scatter-hoarder richness is not correlated with precipitation (t=1.29, df=185, p=0.24, Fig 4B) nor AET (t=1.66, df=185, p=0.07, Fig. 7D). Richness is positively correlated with median elevation (t=17.14, F$_{1,185}$=300.5, p<0.001, Fig. 7C).

Scatter-hoarding bird richness is not correlated with the richness of plants they disperse (F$_{1,164}$=1.46, p=0.14), with latitude (F$_{1,164}$=3.189, p=0.08), precipitation (t=1.96, df=164, p=0.50) nor AET (t=2.87, df=164, p=0.19). Scatter-hoarding bird richness is positively correlated with median elevation (t=4.93, df=164, p<0.001). Scatter-hoarding rodent richness is not correlated with the richness of plants they disperse (F$_{1,180}$=2.89,
p=0.09). Scatter-hoarding rodent richness is negatively correlated with latitude 
\((F_{1,180}=12.39, p<0.001)\), but is not correlated with precipitation 
\((t=0.47, df=180, p=0.63)\), and AET \((t=0.64, df=180, p=0.47)\). Scatter-hoarding rodent richness is positively 
correlated with median elevation \((t=5.41, df=180, p<0.001)\).

**DISCUSSION**

An assumption of studies using species range data is that the abundance of a 
species is equal across its range and at least high enough throughout the range to be an 
effective part of the community. However, it is known species do not not occur at all 
locations throughout their range (Hurlbert & Jetz, 2007), so range maps are likely 
overestimates of richness, but not necessarily biased estimates. This is partially because 
occurrence maps are typically the only data available at large spatial scales. The lack of 
abundance data may obfuscate coevolutionary patterns that are density dependent and by 
assuming species are effective mutualists across their range it prevents us from observing 
the prevalence of interactions between species. Despite the short-comings of species 
range maps, they reasonably represent richness over a larger region and allow us to infer 
broad patterns across large geographic scales.

Hurlbert & Jetz (2007) also suggest a mismatch of scale between occurrence data 
and climatic factors can lead to erroneous results. Instances of mismatch often occur 
when species occurrence data (generally course resolution) is overlaid onto climatic 
variables (generally finer resolution). I believe the concerns of mismatch are minimal for 
this study as the overarching aim was to identify the distribution of animals in 
comparison to the plants that they disperse. Analyses with climatic variables were chosen
based on previous findings and hypotheses and the data were taken at the coarsest scale available to match occurrence data as best as possible. As with similar studies, the purpose of these analyses is to identify broad patterns of distribution with the goal of providing focal points for finer scale studies and not to suggest detailed patterns.

Overall species richness of seed dispersing animals, frugivores, and scatter-hoarders decrease with an increase in latitude (Fig 1). This pattern matches the pattern observed for the plants that they disperse (Vander Wall et al., submitted; Vander Wall & Moore, submitted). The decrease of species richness with increasing latitude is not a surprising result as the generality of the latitudinal diversity gradient has been found to be robust (Hillebrand & Thomas, 2004). The only guild of animals that did not show a significant latitudinal gradient were scatter-hoarding birds ($F_{1,194}=3.08$, $p=0.08$). This is likely a result of the scatter-hoarding behavior being limited to one generalist family of birds (Corvidae) that have a large latitudinal range across North America. Seed dispersers exhibit a richness hotspot along the Arizona and New Mexico (Fig 2B) border with the highest species richness (45 frugivorous spp. and 24 scatter-hoarding spp.) occurring at that region. Frugivorous animals have additional hot spots in western and central Texas, and Colorado (Fig. 5B) with 42-48 species co-occurring, but are generally species rich (>35 spp.) in the southeastern portions of North America. Scatter-hoarder richness is much more restricted with the most species occurring from the Arizona/New Mexico border northeast into Colorado (Fig. 8B). The Great Basin and Mojave deserts are also fairly species rich with 16-19 species co-occurring throughout these regions.

The distribution of animal richness is in contrast of the richness distribution of the plants being dispersed by those animals (Figs. 2A, 5A, 8A). Plants dispersed by frugivory
and scatter-hoarding have the highest richness around the Great Lake regions of North America and eastern parts of the United States in general (Fig. 2A). This mismatch of species richness between plants and the animals that disperse them is clearly seen in Figures 2C, 5C, and 8C with animal richness being greater in southwestern North America and plant richness being greater in eastern North America.

The strength of coevolution between individual plant and vertebrate disperser species has been suggested to be diffuse (Thompson, 1982; Wheelwright & Orians, 1982; Herrera, 1985). In particular seed dispersal networks between plant and animal species have found that species interactions are often asymmetrical, variable in time and space, and non-obligate (Janzen, 1980; Wheelwright, 1988; Bascompte & Jordano, 2007). This is particularly driven by generalists which are species that depend on multiple species causing high complementarity and trait convergence (Guimaraes Jr. et al., 2011). Most, if not all, of the species in North America that I considered seed disperser mutualists would fall under this definition of generalists as they have wide diet breadths. The plants dispersed by animals in North America are also generalists as fruits and seeds have evolved to attract a variety of dispersers and not any one species in particular. Generalists’ diffuse interactions inhibit strong direct specific coevolution that is often witnessed in antagonistic interactions and some mutualisms and lead to the diffuse patterns we witness.

The current distribution of plants and animals in North America has changed over the last 18,000 years (Ray & Adams, 2001). The last glacial maximum dramatically altered species distributions across North America, and it may be that there has not been enough time since the last glacial maximum for coevolutionary selection pressures to
form or be strong enough to be detected at coarse spatial scales. It is also probable that animals have migrated faster than the plants they disperse because of the diffuse relationship between animals and plants, in addition to the short time period since the last glacial maximum. It has been shown that some animal-dispersed plants have not reached their potential distributions since the last glacial maximum, despite their dispersers being present across the plant’s potential distribution (Davis et al., 1986; Woods & Davis, 1989).

As with previous studies (Karr, 1976; Hawkins et al., 2003; Kissling et al., 2009), climatic factors are strongly correlated with animal species richness distribution. Seed dispersers as a whole and frugivorous animals were positively correlated with AET (Fig. 7). AET is a proxy for terrestrial productivity (Mackey & Currie, 2001), so seed dispersers likely do better in more productive environments, where there is more food as many of them are not strict frugivores or granivores and have generalist diets. Seed dispersers and a scatter-hoarders were positively correlated with median elevation. The positive correlation does not follow the global pattern; a decrease in richness with an increase in elevation (Rahbek, 1995). Richness is believed to decrease at higher elevations partially due to a decrease in productivity, smaller land area, and harsher climates leading to higher extinction and lower dispersal due to greater distances between suitable habitat (Rahbek, 1995; Rowe, 2009; Wu et al., 2013). In southwestern North America, where the majority of seed disperser richness is found, net productivity actually increases with elevation into the montane forests before decreasing again above tree line (Whittaker & Niering, 1975). Since seed dispersers are positively correlated with AET, this may influence the correlation with elevation. The increase in habitat heterogeneity in
the western United States along with the isolation at higher elevations may cause an increase in speciation among small mammals increasing richness for the region. The increase in habitat heterogeneity could also lead to the increased inclusion of more species regionally and be a scale effect mentioned above. Again, I do not believe the scale effect is large enough to affect the results of this study because each site’s species list was reviewed and I attempted to limit the number of misplaced species.

This study is the first to identify the collective distribution of animals involved in seed dispersal mutualisms in North American and to compare them to the distribution of the plants they disperse. There is an apparent mismatch in animal and plant richness with seed disperser richness being highest in southwestern North American and plant species richness being highest in southeastern North America. The mutualism between dispersers and plants does not describe the distribution of either group. While this study identified some climatic variables that help explain animal richness (AET for frugivores and precipitation, AET, and median elevation for scatter-hoarders) further work is need to better understand the effect of climate on species distributions of seed dispersing animals. With the distribution data of seed dispersing animals, we can now identify locations that warrant further study either to better understand seed-dispersal mutualisms or the factors that influence the distribution of the plants and animals involved in the mutualism.
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Figure 1: Richness of seed dispersing animals and latitude (A), precipitation (B), median elevation (C), and actual evapotranspiration (D). Regression line denotes significant linear model. Latitude ($F_{1,195}=188$, $p<0.001$), precipitation ($t=1.57$, $df=195$, $p=0.12$), median elevation ($t=4.22$, $df=195$, $p<0.001$), and AET ($t=2.31$, $df=195.13$, $p=0.02$).

Figure 2: Distribution of seed disperser richness. (A) is the distribution of plants involved in seed dispersal mutualisms, the map is an extrapolation of plant richness data collected by (Vander Wall et al., submitted). (B) is the richness distribution of animals involved in seed dispersal mutualisms, and (C) is the difference between plant and animal richness involved in seed-dispersal mutualisms based on z-scores. In (A) and (B) shades of blue indicate fewer species and shades of red indicate more species. In (C) shades of green indicate plant richness is higher, shades of brown indicate animal richness is higher, and white indicates richness is nearly equal.

Figure 3: Seed disperser richness and plant richness. (A) is the regression of all 197 sites ($F_{1,195}=5.88$, $p=0.02$). In (B) – (D), blue shows the distribution of data when divided into low (< 50°) latitudes and red shows high (≥ 50°) latitudes. In (C) there is no relationship between frugivore richness and the richness of plants they disperse ($F_{1,178}=4.9$, $p=0.16$) at low latitudes. Finally, (D) the positive relationship between frugivore richness and the richness of plants they disperse at high latitudes ($F_{1,15}=27.49$, $p<0.001$).

Figure 4: Richness of frugivorous animal and latitude (A), precipitation (B), median elevation (C), and AET (D). Regression line denotes significant linear model. Latitude
(F_{1,195}=262.6, p<0.001), precipitation (t=1.43, df=195, p=0.15), median elevation (t=1.9, df=195, p=0.06), and AET (t=2.0, df=195, p=0.04).

**Figure 5:** Distribution of frugivorous mutualism richness. (A) is the distribution of plants involved in frugivorous seed dispersal mutualisms after Vander Wall *et al.* (submitted). (B) is the richness distribution of animals involved in frugivorous seed dispersal mutualisms, and (C) is the difference between plant and animal richness involved in frugivorous mutualisms based on z-scores.

**Figure 6:** Frugivore richness and plant richness. (A) is the regression of all 195 sites (F_{1,195}=25.4, p<0.001). In (B) – (D), blue shows the distribution of data when divided into low (< 50°) latitudes and red shows high (≥ 50°) latitudes. In (C) there is no relationship between frugivore richness and the richness of plants they disperse (F_{1,180}=1.7, p=0.193) at low latitudes. Finally, (D) is the positive relationship between frugivore richness and the richness of plants they disperse at high latitudes (F_{1,15}=18.88, p<0.001).
**Figure 7:** Richness of scatter-hoarding animal as a function of latitude (A), precipitation (B), median elevation (C), and AET (D). Regression line denotes significant linear model. Latitude ($F_{1,185}=14.88$, $p<0.001$), precipitation ($t=1.29$, $df=185$, $p=0.24$), median elevation ($t=17.14$, $F_{1,185}=300.5$, $p<0.001$), and AET ($t=1.66$, $df=185$, $p=0.07$).

**Figure 8:** Distribution maps of frugivorous mutualism richness. (A) is the distribution of plants dispersed by scatter-hoarders after Vander Wall et al. (submitted). (B) is the richness distribution of scatter-hoarders, and (C) is the difference between plant and animal richness involved in scatter-hoarding based on z-scores.

**Figure 9:** Scatter-hoarder richness and plant richness adjusted for area. A shows the regression of 185 sites where scatter-hoarded plants and animals occur ($F_{1,185}=3.20$, $p=0.08$), blue shows the distribution of data when divided into low ($<50^\circ$, blue) latitudes and high ($\geq 50^\circ$, red) latitudes. There was no significant correlation with scatter-hoarder richness and plant richness.
Figure 1:

(A) Relationship between animal richness and latitude.

(B) Relationship between animal richness and log precipitation (mm).

(C) Relationship between animal richness and median elevation (m) (partial residuals).

(D) Relationship between animal richness and AET (mm/yr) (partial residuals).
Figure 2:

(A) All plants dispersed
- < 7
- < 14
- < 21
- < 28
- < 35
- < 42
- < 49

(B) All animal dispersers
- < 9
- < 18
- < 27
- < 36
- < 45
- < 54
- < 63

(C) Difference
- > animals
- animals ≈ plants
- > plants
Figure 3:

(A) Animal richness vs. Plant richness (n/area)

(B) Animal richness vs. Plant richness (n/area)

(C) Animal richness vs. Plant richness (n/area)

(D) Animal richness vs. Plant richness (n/area)
Figure 4:
Figure 5:
Figure 6:

(A) Frugivore richness vs. Plant richness (n/area)

(B) Frugivore richness vs. Plant richness (n/area)

(C) Plant richness (n/area) vs. Frugivore richness

(D) Plant richness (n/area) vs. Frugivore richness
Figure 7:

(A) Scatter plot of scatter hoarder richness against Latitude.
(B) Scatter plot of scatter hoarder richness against Log precipitation (mm).
(C) Scatter plot of scatter hoarder richness against Median elevation (m).
(D) Scatter plot of scatter hoarder richness against AET (mm/yr).
Figure 8:

(A) Plants: scatter-hoarded
- < 2
- < 4
- < 6
- < 8
- < 10
- < 12
- < 14

(B) Animals: scatter-hoarders
- < 4
- < 8
- < 12
- < 16
- < 20
- < 24

(C) Difference
- > animals
- animals = plants
- < plants
Figure 9: Scatter plots showing the relationship between plant richness (n/area) and scatter-hoarding richness.

(A) Scatter plot with plant richness on the x-axis and scatter-hoarding richness on the y-axis.

(B) Scatter plot with plant richness on the x-axis and scatter-hoarding richness on the y-axis.
Table 1: List of frugivorous animals broken up into frugivorous birds (top) and frugivorous mammals (bottom). Species are listed alphabetically by family then genus, order of species does not insinuate a species ability to disperse seeds via frugivory.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Species</th>
<th>Family</th>
<th>Common Name</th>
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<td>Bombycilla cedrorum</td>
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<td>Bombycillidae</td>
<td>Cedar Waxwing</td>
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<td>Bombycilla garrulus</td>
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<td>Bombycillidae</td>
<td>Bohemian Waxwing</td>
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<td>Band-tailed Pigeon</td>
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<td>Columbidae</td>
<td>White-crowned Pigeon</td>
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<td>Columbidae</td>
<td>White-winged Dove</td>
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<td>Scrub Jay</td>
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### Fruigivorous Mammals of North America

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Table 2: List of scatter-hoarding animals broken up into scatter-hoarding birds (top) and scatter-hoarding rodents (bottom). For both scatter-hoarding birds and mammals only one family possesses scatter-hoarding behavior (Corvidae and Rodentia respectively), therefore species are listed alphabetically by genus. Order of species does not insinuate a species ability to disperse seeds via scatter-hoarding.

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<td>Tamias sonomae</td>
<td>Sonoma Chipmunk</td>
</tr>
<tr>
<td>Tamias speciousus</td>
<td>Lodgepole Chipmunk</td>
</tr>
<tr>
<td>Tamias townsendii</td>
<td>Townsend's Chipmunk</td>
</tr>
<tr>
<td>Tamias umbrinus</td>
<td>Uinta Chipmunk</td>
</tr>
</tbody>
</table>
SUMMARY

This dissertation set out to investigate patterns of seed disperser distribution and coexistence. The first chapter set out to determine if one behavior, cache pilfering, may support high levels of diversity observed in scatter-caching rodent communities. I used a series of trials to determine if cache-pilfering was reciprocal or asymmetrical among a community of scatter-hoarding rodents. Through these trials I determined pilfering is reciprocal among scatter-caching rodents; the only rodents unable to pilfer primarily used an alternative seed-hoarding behavior, larder-hoarding. Because this species is defending a single large larder of food, it is less likely to have the opportunities to pilfer caches and therefore never adapted the olfactory and behavioral tendencies to do so. The ability of scatter-hoarding species to be able to reciprocate pilfering is important because current theories of niche- and resource-partitioning have been unable to fully explain the high levels of coexistence observed in scatter-hoarding rodent communities. Reciprocal cache pilfering could negate any long-term advantages one species may have over others, allowing for the coexistence and maintenance of species diversity.

The second chapter investigated how seed-caching rodent communities may influence seed pilfering. In order to investigate this, I conducted seed removal trials across an environmental gradient in western Nevada. The gradient was necessary in order to obtain community differences in both species composition and abundance. I observed a difference in pilfering rates across sites, and found that seed pilfering was positively correlated with rodent abundance but not with rodent species richness. Secondarily, I discovered that across my studies sites individual rodents pilfered at near equal rates.
despite being different species, and the addition of a single individual increased pilfering rates by approximately 1.3% per day.

Lastly, in chapter 3 I determined the distribution of all vertebrate North American seed dispersers and studied if either the plants they dispersed or climatic variables influenced the distribution of seed-dispersers. This study was the first to identify the distribution of seed-dispersers and compare it to the distribution of the plants they disperse. There is an apparent mismatch in richness between seed-dispersers and the plants they disperse. Seed-disperser richness is highest in the southwest regions of North America while plant richness is highest in the eastern and southeastern portions of North America. Climatic variables were much better at predicting seed-disperser richness than plants. Animal richness decreased with an increase in latitude for all seed-dispersers. However, there were differences between the guilds, additionally scatter-hoarder richness increased with elevation while frugivore richness increased with actual evapotranspiration.

This dissertation was the first step in answering many of the questions proposed within. Further study needs to be conducted to determine the context dependency of the reciprocal pilfering results to determine if they are limited to the arid and semi-arid regions of western Nevada or if the pattern is a common result of seed-dispersing rodent communities world-wide. With the results from my third chapter, I have been able to identify hot- and cold-spots of seed dispersing animal diversity that may be ideal areas to further study reciprocal pilfering and other mechanisms of coexistence. Lastly, further study is needed across North America to determine if the large-scale predictor variables found correlated with seed dispersal can be scaled down to smaller levels of study, or if
there are other, potentially more important, variables at local levels that better predict seed-disperser diversity.