Competition Along Elevational Gradients: A Resource Battle Between Rodents and Ants

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ABSTRACT

Understanding competitive interactions for resources within an ecological community is fundamental for understanding the life histories of organisms in that community. Interspecific competition (competition between members of different species over a limiting resource) is often studied between species of similar size or close evolutionary relationship. Competitive interactions between species of distant taxonomic relationship or very different sizes have been rarely studied. For 22 sites along three transects in the Colorado Front Range and San Juan Mountains, signs of potential competitive interactions between small mammals and ants along elevational gradients were examined. Abundances of ants and small mammals were determined through pitfall (trap sunk into the ground) and mark-and-recapture (trapping, tagging and releasing of animals for recapture to estimate population size) trapping techniques. Proportions of pitfall traps containing ants were determined and compared to the minimum number of mammals known alive (MNKA, number of individuals marked in a trapping effort) using Spearman's rank-order correlation tests to determine correlations between variables. No direct evidence was found for competition between ants and small mammals (Spearman's Rank Correlation Coefficient was 0), indicating little to no competition between ants and small mammals in these areas whether food or space resources are readily available. This study is the first of its kind conducted outside of desert ecosystems. Understanding the ecological community as a whole, including any and all possible competitive interactions, is fundamental in conservation efforts, especially as organisms expand into higher elevations historically located outside of their ranges.

INTRODUCTION

Many types of direct and indirect competition can occur between organisms. Mechanisms of this competition can be separated into three broad categories: i.e. (i) interference competition, where individuals aggressively compete to forage, reproduce or establish a territory (home range), (ii) exploitation competition, where use of a shared limiting resource (resource available in limited quantities), such as food or space, depletes the amount available to others, and (iii) apparent competition, where two or more species are preyed upon by the same predator (Branch, 1984). These mechanisms of competition apply equally to intraspecific and interspecific competition (Branch, 1984). Intraspecific competition occurs when members of the same species compete for the same resources in an ecosystem. Interspecific competition occurs when individuals of two or more different species compete for the same resources in an ecosystem.

Many ecological studies have examined interspecific competition for food resources and the resulting effects of this competition on the population sizes and distributions of the participating species (Abrahams, 1986; Brown and Davidson, 1977; Brown et al., 1979a; Brown et al., 1979b; Dobson and Jones, 1985; Fretwell and Lucas, 1969; Kozár, 1987; Lomolino, 2001; Mountainspring and Scott, 1985; Nathan et al., 2008; Rickart, 2001; Rowe, 2009). Most of the later research has examined taxonomically closely related species, for example two birds from the same genus, or species that are similar in size (Aguiar et al, 2001; Kozár, 1987; Mountainspring and Scott, 1985). However, considering the extremely complex organization of an ecological community, even small overlaps in resource use could have major implications on the abundances and distribution patterns of every species in that community (Mac Nally, 1983). This idea extends even to organisms that are taxonomically distantly related but exploit similar food resources, for example owls and skunks or ants and rodents (Brown and Davidson, 1977; Brown et al., 1979a; Brown et al., 1979b).

For ants and small mammals (rodents, shrews, etc.), various hypotheses exist for potential competitive interactions (Abrahams, 1986; Brown and Davidson, 1977; Brown et al., 1979a; Brown et al., 1979b; Dobson and Jones, 1985; Fretwell and Lucas, 1969; Heaney, 2001; Nathan et al., 2008; Ostfeld et al., 1985). Ants and even the smallest of rodents live in different levels of an ecological community due to their range in body sizes from 0.75 to 52 mm in ants and 50 to 1400 mm in rodents (Hölldobler & Wilson, 1990; Wilson and Reeder, 2005). The resources exploited by differently sized animals should vary in absolute size (e.g., weight of a single seed) to overall quanitity consumed per day (e.g., sum of seeds consumed in 24 hours) (Armstrong, 1994; Brown and Davidson, 1977; Brown et al., 1979a; Brown et al. 1979b; Heaney, 2001; Kaspari et al., 2000b; Sanders, 2002). Despite their differences in body sizes, both ants and rodents fill similar niches in the ecological community and do so in strikingly similar ways (Brown and Davidson, 1977; Brown et al., 1979a; Brown et al. 1979b; Heaney, 2001), predominately because they live in the similar environments, and consume, cache, and disperse seeds and other food resources.

Both ants and rodents are food resource generalists, consuming resources ranging from vegetation and seeds to insects and carrion (Abrahams, 1986; Armstrong, 1994; Brown and Davidson, 1977; Brown et al., 1979a; Brown et al. 1979b; Fretwell and Lucas, 1969; Heaney, 2001). Each group contains specialized granivorous (seed-eating) species that flourish in desert areas where seeds are the most abundant resource (Brown and

Davidson, 1977; Brown et al., 1979a; Brown et al. 1979b). Several previous studies in desert environments show competitive interactions between ants and rodents foraging on seed resources to have a major impact on the relative population abundances and number of species in each taxon within the study area (Brown and Davidson, 1977, and Brown et al., 1979a and 1979b). In wetter temperate and tropical regions with a greater variability and availability of food resources, fewer species specialize on a single food source and therefore generalist ant and rodent species exist (Armstrong, 1994; Heaney et al., 2001; Nadkarni and Wheelwright, 2000).

Utilization of elevational gradients is a strong methods for testing mechanisms that drive species diversity and population abundance patterns (Bateman et al., 2010; Brown, 2001; Lomolino, 2001; McCain 2005). Elevational gradients demonstrate similar patterns as latitudinal gradients but exist on a much smaller spatial scale, thus making thorough trapping efforts both economically and temporally feasible (Ferro and Barquez, 2009; Heaney, 2001; Li et al., 2003; McCain, 2007). There are also many mountains globally, on which these tests and patterns of species abundance and diversity could be replicated and compared (Ricket, 2001; Rowe, 2009). Along these elevational gradients, climatic factors, such as temperature and precipitation, have indirect effects on species richness (the number of different species represented in an ecological community) of both small mammals and ants (Andrews and O'Brien, 2000; Brown, 2001; Heaney, 2001; Kaspari et al., 2000a; Kaspari et al., 2000b Lomolino, 2001; McCain, 2005). These climatic factors influence high-energy areas (areas with high productivity) capable of supporting the relatively highest population densities and species richness (Currie, 1991; Currie et al., 2004; Evans et al., 2005; Kaspari et al., 2000a; Kaspari et al., 2000b;

Kaspari et al., 2003; Kerr and Packer, 1997; McGlynn et al., 2010; Mittelbach et al., 2001; Waide et al., 1999). Highly productive areas have high food availability, and this abundance of food resources has led to increased population sizes and species richness (Andrewarth and Birch, 1954; Forsman and Monkkonen, 2003; Hutchinson, 1959; Kaspari et al., 2000a; Kaspari et al., 2000b; Li et al., 2003; McGlynn et al., 2010; Sanchez-Cordero, 2001). Competition has been placed into the context of the Ideal Free Distribution (IFD) theory, which states that animals distribute themselves according to the quality of food patches available to them (Abrahams, 1986; Fretwell and Lucas, 1969). As population abundances increase, animals begin competing for resources and inhabiting smaller home ranges, thus spacing themselves further apart (Abrahams, 1986; Fretwell and Lucas, 1969), which would ultimately lead to areas where ants and rodents competing for the same resources will competitively exclude each other.

The work done by Heaney in the Philippines (2001) where ants and rodents were observed as potential competitors for resources, led to the present project. In tropical regions, ants and rodents occur in large numbers and, according to the IFD theory, should compete more readily due to limitations on space and resource availability. This idea was expanded on in the temperate regions assessed in this study. As I compared the abundances of both ants and small mammals for 22 sites in the Colorado Front Range and San Juan Mountains, the question of whether there was a competitive interaction between these two populations was posed. It was predicted that as the abundance of one group increased, the other would decrease in abundance. For example, in areas where ants occurred in large numbers, there would be fewer small mammals. If no signs of

competitive interactions between these groups were found, other climatic factors would be investigated to understand other potential drivers of abundance patterns.

To my knowledge, a study comparing the abundances of ants and small mammals as a signal of competition has never been done in the temperate zone. Finding signs for competitive interactions could have widespread implications in conservation efforts for these and many other species. This study focused on the abundances of small mammals and ants along elevational gradients in the Colorado Front Range and San Juan Mountains and addressed the following questions:

- 1. Is there a signal in the abundances of ants and small mammals of a competitive interaction?
- 2. Does elevation affect the abundances of ants and small mammals?
- 3. Are climatic factors, temperature and precipitation, affecting the abundances of ants and small mammals?

METHODS

Study Site Selection

Data were collected during a larger study conduced along four transects in the San Juan Mountains and the Front Range in Boulder during 2010-2013. Eight sites were chosen along each transect about every 200-300m in elevation between the lowest and highest elevations on the mountains (e.g., 1500-3700 m). Some elevations were not viable site options because they were unreachable by the crew, located on a steep slope considered dangerous for trapping, or heavily travelled by people along hiking trails. The three transects utilized for this study were the Boulder, Big Thompson, and Lizardhead

transects, as seen in Figure 1. The Boulder and Big Thompson transects were located in the Front Range Mountains and the Lizardhead transect was located in the San Juan Mountains.

The Boulder transect extended almost directly west from Boulder, CO (Fig. 1). The 8 sites along this transect were: Sunshine Canyon at 1800 m, Betasso Reserve at 1900 m, A1 at 2200 m, B1 at 2800 m, The Mountain Research Station (MRS) at 2900 m, C1 at 3100 m, Saddle at 3500 m, and Green Lakes Valley (GLV) at 3700 m. The Big Thompson transect extended west from Loveland, CO (Fig. 1). The 8 sites along this transect were: Sylvandale at 1700 m, Cow Camp at 1900 m, Cedar Park at 2100 m, McGraw at 2400 m, Beaver Ponds at 2800 m, Hidden Valley at 3000 m, Tombstone at 3400 m, and Sundance at 3600 m. The Lizardhead transect was located west and north of Cortez, CO (Fig. 1). The 8 sites along this transect were: Yellowjacket at 1500 m, Hovenweep at 1700 m, McPhee at 2200 m, Mavreeso at 2500 m, Willow Creek at 3000 m, Road 616 at 3200 m, Navajo at 3400 m, and El Diente at 3600 m.

The sites along each transect were representative of the habitat of the region and were separated into five broad categories for ease of identification in this study. Meadow areas were open spaces with grasses and sparse tree cover. Forest areas were dominated by trees and possessed little underbrush flora or plant-life. Rocky areas were sparse in flora and exhibited very loose, rocky dirt. Riparian areas had a body of water, a stream or pond, running through the site or evidence of water running through the site at certain times of the year. Tundra areas were open habitats with no trees at higher elevations. The trapping transects, consisting of 150 flags with each flag 10 m apart, were placed in

each site to contain a representative proportion of each broad type of habitat present at the site.



Figure 1: Four site transects in the Colorado Front Range Mountains and San Juan Mountains. The three used for this study were the two transects in the Front Range Mountains and the northern transect in the San Juan Mountains.

Vegetation Plots and Insect Pitfall Traps

Twenty vegetation and insect survey plots were placed in each site located approximately every seventh flag along the trapping transect. An area of 5 m circumference from the transect flag center was selected to either the right or left of the transect (Fig. 2). Elevation and GPS coordinates of the vegetation plot were recorded from the center flag. Using a rope with marks at the 1-, 3-, and 5-meter marks and a compass, flags labeled with the distance and direction from the center flag (e.g., 3 m N) were placed in the 4 cardinal directions at 1-, 3-, and 5-meters from the center flag.



Figure 2: Vegetation plot diagram. The T was a Sherman trap placed at the center of the plot. Black circles were four points of measurement for understory vegetation height (<1 m) and canopy coverage with a densitometer taken facing plot center. White circles were the locations of two insect pitfall traps. The dark grey 1 meter-radius was estimated for coverage class. The light grey 5 meter-radius was estimated for the number and species of trees, and the diameter at breast height (dbh) of trees with a dbh of 3 cm or greater.

At the four cardinal directions at the three m flags as denoted by the black circles in Figure 2, the height of the tallest plant under one m in height was recorded and canopy coverage, the amount of the sky above an area that is covered by the crown of a plant species (e.g., tree cover), was taken with a densitometer, an instrument used for taking measurements of canopy cover, while facing the plot center. Within the one meter-radius, the dark grey shaded area in Figure 2, the coverage classes were estimated according to the Braun-Blauquet system separating foliage coverage into five categories of grass, herbs, shrubs, cacti, and bare ground. Within the five meter-radius, estimations were made for the number and species of living trees, and the diameter at breast height (dbh) was taken for trees with a dbh of three cm or greater. Two insect pitfall traps were placed at the East and West three m markers as denoted by white circles in Figure 2.

Insect pitfall traps (Fig. 3) were constructed using a trowel, two plastic cups, three wooden shims, small sticks or rocks, a large rock or log, a plastic plate, and low-toxicity

ethylene glycol (antifreeze). A hole large enough to hold the plastic cups was dug next to the three m flags at east and west. If there was no viable spot for the pitfall traps at east and/or west then the pitfalls were placed at the north and south markers. The cups were placed into the hole with one inside of the other so that the inside cup could be easily removed and replaced into the second cup for ease of repeated sample collection. Dirt was packed around the cups so that the lips of the cups rested flush with the ground. The three shims were placed, as though they were spokes extending from a bicycle wheel, around the cups to act as small drift fences guiding insects and shrews into the cups, and were held in place with small rocks or sticks. Any loose dirt and debris was removed from the top cup and the cup was filled to $1/3^{rd}$ with ethylene glycol. A plastic plate was held over the cups by smaller sticks and/or rocks to prevent rain and excess debris from getting into the cups. A large rock or log was used as a weight to keep the plate in place over the pitfall trap.



Figure 3: Completed insect pitfall trap.

Trapping

Closed traps were placed along the trap line with two traps at each flag during the first trapping day. Small perforated $(2 \times 2.5 \times 6.5 \text{ in})$, small solid $(2 \times 2.5 \times 6.5 \text{ in})$, and large solid $(3 \times 3.5 \times 9 \text{ in})$ Sherman traps were used for trapping. At approximately four or five pm on the first night of trapping, the crew set the traps at five m on either side of the trapping flag. These traps were placed in areas where it would be more likely to catch small mammals such as along fallen logs and next to visible burrows. If there was a vegetation plot, the trap on the side with the plot was placed at the plot's center flag, as seen in Figure 2. Traps to the right of the trap line were baited with a seed mixture scented with vanilla and traps to the left of the line were baited with a peanut butter and oat mixture. At cold sites, every trap had a small amount of cotton fluff placed inside so that any trapped animals could build a nest and not freeze overnight.

At approximately seven am, the crew checked the traps. Disturbances to the traps, closed traps with no animals inside as well as moved traps were recorded. Open traps were closed to prevent animals from entering during the day. Any traps containing an animal were carefully handled using a trapping bag while the crew prepared the equipment to handle and measure the animal. The sex and reproductive status of the animal was recorded as well as the weight of the animal using a scale clipped to the base of the tail. If the species could be determined, the animal was tagged with either an ear tag or toe clipping (voles only) and released. If species could not be determined, the animal was placed into a plastic container with Isoflurane gas for collection and later species identification using teeth and skull characteristics. Any animals found dead in the

Sherman traps were also collected. All collected specimens were deposited in the CU Museum of Natural History collections.

This process was repeated for five days of trapping at each site. After the first day of set up, the traps were reopened at approximately six pm and re-baited if necessary. Any animals caught on the second through fifth day were checked for tags and labeled as a recapture if they had been tagged. If the animal was a new capture, measurements were taken and the animal was released after tagging. On the final day of trapping, any new animals were not tagged but labeled as new in the data and released after all measurements were taken. For each site, the total number of small mammal species and abundances of each species were compiled.

Pitfall Collection

Pitfall traps were collected approximately every few weeks if possible or, for the harder to reach sites, each month. Any disturbed vegetation plots and pitfall traps were initially replaced, however as further disturbance occurred (e.g. from bears or other animals) the traps were removed from some vegetation plots. At each site, the crew went along the transect to each vegetation plot and checked that pitfalls were still in place. If there was disturbance, the disturbance was noted and salvageable data saved. If there was no disturbance, the plate covering the pitfalls was removed and the top cup was pulled from the trap. The ethylene glycol was checked for any small mammals or lizards that may have fallen in and those specimens were stored separately from the remainder of the sample. The rest of the ethylene glycol was poured out of the cup and into a whirl-pack labeled with the site, trap number and direction, and the date the sample was

collected (e.g., Navajo, F10E, July 24 2012). In addition to labeling the whirl-pack, a small piece of write-in-rain paper with the same information was placed inside the whirl-pack. The cup was refilled to $1/3^{rd}$ with ethylene glycol and replaced into the trap with the plate back on top.

Once in the lab, insect samples were cleaned and stored in plastic jars filled with ethyl alcohol. Samples were poured out of whirl-packs into glass jars and ethylene glycol was strained using mesh netting into a separate container for disposal or reuse. Insects were then rinsed with water and strained until no trace of ethylene glycol remained. Large debris was removed from the sample as well as any dirt or ash that could be removed. Once clean, insects were poured into plastic jars labeled with site name, trap number and direction, and date collected. Jars were filled with enough ethyl alcohol to cover insects completely for long-term preservation.

Insect samples were sorted into five categories: Formicidae (ants), Orthoptera (grasshoppers and crickets), Lepidoptera (moths and butterflies), carrion beetles, and the remaining stored as a mixed sample of arthropods. Insects were removed from the alcohol and left to dry on a metal tray. A total count was taken for each category except the remaining mixed sample of arthropods and unless there were greater than 50 specimens present in any one category. Dry weights of each category were taken using a small scale and recorded. Once weighed, each insect category was placed into separate glass or plastic jars with write-in-rain paper indicating site, trap, collection date, and category.

Data Analysis

Ant abundance was quantified as a proportion of pitfall traps containing ants. Total pitfall traps collected over the course of the three-month trapping season were counted in terms of individual collected samples, with each sample considered a separate trap in the total count. This total trap count was separated into traps containing ants and traps with no ants. The total trap count divided by the traps containing ants was the proportion of traps containing ants at each site. This proportion was used as the measure of ant abundance at each site.

Proportion of traps containing ants was used as a measure of abundance because it is the best method for looking at the densities of total ants at each site. While lack of an accurate count of individual ants present (due to stopping at a count of fifty ants) prevented total numbers from being used, a count of individuals was not considered an accurate representation of potential competition with mammals. Individual ants are not competitors on their own, but ant colonies taken as a whole are potential competitors with small mammals for resources. Dry weights taken for each trap were also not used due to a wide range of size and weight for ant species. Large numbers of very small ants often times were not heavy enough to register a weight on the scale used in lab (measuring weight to 0.01 g) while one or two large ants were heavy enough to register a weight on the scale. An ant colony small in physical size can be made up of many individuals with each individual capable of bringing in resources. These small ants, occurring in large numbers that may not register a weight on the scale used, are thus capable of taking in more resources than a single large ant that does register a weight on the scale. Ants as a

group were used in this analysis as opposed to number of species present because specific identifications of ants present at the sites was not available.

Mammal abundance was quantified as the minimum number of mammals known alive at each site. Utilizing the minimum number known alive at each site provides a minimum measure of potential competition. All species of mammals caught were included in this count as many of the species are generalist feeders utilizing many resources available in the environment. Estimates of abundance were not used in this analysis as some species were still being identified as part of the larger project and accurate estimates were not available.

Elevation of each vegetation plot was recorded using a handheld GPS unit in the field. The twenty elevations recorded at each site were taken together and averaged into a single measurement for data analysis. Temperature and precipitation data were taken from the BIOclim database based on the elevations of the sites in Colorado.

Spearman's rank-order correlation was used to analyze data. This test was a nonparametric test that measured the strength of association between two ranked variables. A nonparametric test was chosen because it was one where the data were not required to fit a normal distribution and the data obtained in this study was ordinal and relied on a ranking or ordering of the values as opposed to the numbers. Spearman's rank-order correlation was chosen because it assed the monotonic relationship, where both variables increase or decrease together, between two variables that was not linear in nature.

RESULTS





Figure 4: Proportion of traps with ants as a function of elevation. All transects taken together: Spearman Rank Correlation Coefficient (ρ) = -0.107, p = 0.634, n = 22. Boulder transect: ρ = 0.577, p = 0.175, n = 7. Big Thompson transect: ρ = -0.119, p = 0.793, n = 8. Lizard Head transect: ρ = -0.517, p = 0.2, n = 7.

The presence of ants tended to decrease as elevation increased, although not

significantly when all three transects were considered together (Fig. 4). The Boulder transect exhibited a slight, but not significant, positive relationship between elevation and ant presence (Fig. 4). Both the Big Thompson and Lizard Head transects exhibited slight negative correlations, but neither was statistically significant (Fig. 4).



Figure 5: Minimum mammals known alive as a function of elevation. All transects taken together: $\mathbf{\varrho} = -0.190$, p = 0.395, n = 22. Boulder transect: $\mathbf{\varrho} = 0.0357$, p = 0.964, n = 7. Big Thompson transect: $\mathbf{\varrho} = -0.238$, p = 0.582, n = 8. Lizard Head transect: $\mathbf{\varrho} = -0.214$, p = 0.662, n = 7.

Peaks in mammal abundance at the Boulder and Big Thompson transects appeared at 2200 m and 3000 m, with lower abundance at 1800 m, 2500 m, and beyond 3200 m (Fig. 5). The opposite trend was seen in mammal abundance at the Lizard Head transect, with peaks at 1500 m, 2500 m, and 3500 m and lower abundance at 2200 m and 3000 m (Fig. 5). Overall, the three transects together exhibited a slight negative correlation between variables that was not statistically significant (Fig. 5). The Big Thompson and Lizard Head transects exhibited slight negative correlations, but neither was statistically significant (Fig. 5). The Boulder transect showed no correlation between elevation and minimum number of mammals known alive (Fig. 5).



Figure 6: Relationship between proportion of traps with ants and minimum mammals known alive. All transects taken together: $\mathbf{\varrho} = 0.0266$, p = 0.907, n = 22. Boulder transect: $\mathbf{\varrho} = 0.126$, p = 0.788, n = 7. Big Thompson transect: $\mathbf{\varrho} = 0$, p = 1, n = 8. Lizard Head transect: $\mathbf{\varrho} = 0$, p = 1, n = 7.

Presence of ants showed no correlation with mammal abundance along any of the three transects (Fig. 6). Spearman's Rank Correlation Coefficient was effectively 0 for each correlation indicating no relationship between the variables (Fig. 6).



Figure 7: Proportion of traps with ants as a function of temperature. All transects taken together: $\mathbf{\varrho} = 0.0814$, p = 0.719, n = 22. Boulder transect: $\mathbf{\varrho} = -0.577$, p = 0.175, n = 7. Big Thompson transect: $\mathbf{\varrho} = 0.119$, p = 0.793, n = 8. Lizard Head transect: $\mathbf{\varrho} = 0.571$, p = 0.2, n = 7.

The presence of ants in relation to the temperature patterns taken from the elevational data of each site exhibited a very slight positive, albeit non-significant correlation for all three transects taken together (Fig. 7). The Boulder transect exhibited a negative correlation that was not statistically significant (Fig. 7). The Big Thompson transect displayed a slight, but not significant, positive correlation (Fig. 7). The Lizard Head transect displayed a positive correlation that was not statistically significant (Fig. 7).



Figure 8: Proportion of traps with ants as a function of precipitation. All transects taken together: $\mathbf{\varrho} = -0.157$, p = 0.485, n = 22. Boulder transect: $\mathbf{\varrho} = 0.541$, p = 0.210, n = 7. Big Thompson transect: $\mathbf{\varrho} = -0.119$, p = 0.793, n = 8. Lizard Head transect: $\mathbf{\varrho} = -0.571$, p = 0.2, n = 7.

There was a slight negative, albeit non-significant correlation between precipitation and presence of ants when all sites were taken together (Fig. 8). The Boulder transect displayed a positive correlation that was not statistically significant (Fig. 8). The Big Thompson transect displayed a slight, but not significant, negative correlation (Fig. 8). The Lizard Head transect displayed a negative correlation that was not statistically significant (Fig. 8).

DISCUSSION

In the three elevational transects in Colorado, no significant relationship was seen between ant and small mammal abundances or between climatic factors, such as temperature and precipitation and ant abundance. The prediction that competition is occurring between ants and small mammals along these temperate elevational gradients is not supported by these data and therefore the null hypothesis, that there is no signal of a competitive interaction occurring between ants and small mammals, can be accepted.

Rodent and Ant Competition

There was no direct evidence for competition between small mammals and ants in this study. Studies, in which significant competition was detected between small mammals and ants, have been conducted mostly in desert sites (Brown and Davidson, 1977; Brown et al., 1979a; Brown et al., 1979b) and predicted from limited studies in the tropics (Heaney, 2001). In desert studies, either a limiting resource (available in a finite amount that multiple individuals compete for) was utilized by either group, or one group predominated over another at different elevations leading to various modes of competitive interaction. In tropical regions, large abundances of both ants and small mammals are present, leading to increased incidence of competition due to the size of home ranges of the individuals.

Work by Brown and Davidson (1977) and Brown et al. (1979a, 1979b) in arid desert ecosystems in Arizona shows significant competition between seed-eating small mammals and ants. In these desert ecosystems, seeds are the primary source of food for both groups and, due to droughts, seeds can be severely limited in availability. Seeds

become a limiting resource for the abundance and distribution of both ants and rodents. In exclusion experiments by Brown et al. (1977), the number of ant colonies and number of individual rodents increased substantially in plots where the other species was excluded, particularly in drought years, suggesting strong competitive interactions.

At tropical sites, primarily in the Philippines, Heaney (2001) found complex interactions between ants and rodents that affected community organization along elevational gradients. Bait in traps set for capturing small mammals at lower elevation sites was consumed nearly 100% of the time (Heaney, 2001). At these tropical sites, ants are usually the first organisms to find bait and small mammal populations occur in high abundances only at sites where ants are rare or absent (Heaney, 2001).

In temperate areas, rodents and ants are able to use a wider array of available food resources, including a consistent availability of seed resources, than in desert sites. Rodents that consume insects or leafy material, such as deer mice (*Peromyscus*) and New World harvest mice (*Reithrodontomys*), shift to the latter food resources, leaving seeds to more specialized granivores, such as kangaroo mice (*Microdipodops*) and pocket mice (*Perognathus*) (Armstrong, 1994; Brown et al., 1979a). A similar effect is in place in these non-desert areas for ants that are generally opportunist feeders foraging on nectar, leafy matter, scavenging, and capturing prey, in addition to feeding on seeds (Brown et al., 1979a; Kaspari et al., 2000b). The tendency of these two groups of organisms to become effective generalists outside of desert environments allows for individual species to fill different niches in the ecological community potentially lessening competition between the groups. The "niche limitation hypothesis" assumes members of a species pool to be specialized to different parts of a resource spectrum to avoid competitive

interactions (Kaspari et al., 2000b). Similarly, Ideal Free Distribution theory states that animals will distribute themselves according to the quality of food resource patches available (Abrahams, 1986; Fretwell and Lucas, 1969). In temperate areas, with a generally lower abundance of species than in tropical regions, a greater amount of space is available for use. The species-area relationship is a largely accepted ecological concept that can be applied to both species richness and population abundance (Arrhenius, 1921; Conner and McCoy, 1979; Storch et al., 2005; Wright, 1983). As the size of an area increases, a greater amount of resources is available, which then leads to increased local population sizes, or abundance (Bakawski et al., 2010; MacArthur and Wilson, 1963; Storch et al., 2005; Rowe, 2009). This could be what is occurring in temperate regions, with fewer limiting resources than in desert (with limiting food resources) or tropical (with limiting space resources) sites, and why there is no evidence of competition for resources between ants and small mammals in the present study.

Ants and the Elements of Elevation: Temperature and Precipitation

The lack of evidence for elevational effects on ant and small mammal abundance in the present data is curious, as many prior studies along elevational gradients have shown decreases in abundance and/or species richness at higher elevations (Andrews and O'Brien, 2000; Currie, 1991; Currie et al., 2004; Evans et al., 2005; Heaney, 2001; Kaspari et al., 2000a; Kaspari et al., 2000b; Kaspari et al., 2003; Kerr and Packer, 1997; Lomolino, 2001; McCain, 2005; McGlynn et al., 2010; Mittelbach et al., 2001; Waide et al., 1999). Much of the support for predictions that both ant and mammal abundance decrease at high elevations is based on studies of climatic variables. Temperature and precipitation are considered two major factors driving ant abundance along elevational

gradients in indirect ways. In previous studies, species richness and population abundance were shown to increase in areas of higher productivity for each site studied (Andrews and O'Brien, 2000; Currie, 1991; Currie et al., 2004; Evans et al., 2005; Hawkins et al., 2003; Kaspari et al., 2000a; Kaspari et al., 2000b; Kaspari et al., 2003; Kerr and Packer, 1997; McGlynn et al., 2010; Mittelbach et al., 2001; Waide et al., 1999). Ants are a thermophilic (thriving at high temperatures) group reaching high abundances in warmer habitats (Kaspari et al., 2000a; Kaspari et al., 2000b). Precipitation is also a player in the productivity of an area, as increased levels of precipitation yield increases in plant resource availability including seeds and leafy vegetation (Andrews and O'Brien, 2000; Brown, 2001; Heaney, 2001; Lomolino, 2001; McCain, 2005). Despite the absence of a significant relationship between either temperature and precipitation and ant abundance, the present survey does not question the thermophilic nature of ants as a taxon (Kaspari et al., 2000a; Kaspari et al., 2000b).

Future Areas of Expansion

This study revealed no evidence of competition between ants and rodents via comparing abundances of ants and mammals. Two of these sites, GLV and El Diente (both at 3700 m) were excluded from the study completely as they were not pitfall trapped at all due to the abundance and activity of marmots in the area. Beaver Ponds and Sunshine Canyon were included in the study even though they were outliers in the data due to disturbance from bears or other mammal activity at the site.

If I were to do this study again, I would consider utilizing (i) exclusion plots similar to those utilized by Brown et al. (1979a; 1979b) in desert granivory studies, or (ii)

conducting trapping along an elevational gradient in a tropical region. Exclusion plots would allow for measurement of changes in abundances of small mammals and ants in plots where the potential competitor is excluded. Any changes in the abundances of the respective other groups would indicate competition between the two. Tropical regions, on the other hand, exhibit less seasonal variability than temperate regions and would allow for assessment at any point in the year that could be extrapolated to the rest of the year (Nadkarni and Wheelwright, 2000). Tropical regions also exhibit much greater abundances of both ants and small mammals, which would allow for a greater sample size and potentially stark contrasts in the abundances of each group (Heaney, 2001).

Additional methods for analyzing the data collected in the present study, and expanding on the competitive aspect, could be to limit the species considered to seed specialists. As the species of ants are identified (as part of a separate study not yet completed), granivores could be separated out and compared to those mammals specializing on seed resources, largely Heteromyidae species (including kangaroo rats, kangaroo mice, and pocket mice) (Brown et al., 1979a). Another way to reanalyze data would be to assess the traps located near ant colonies and for mammal activity in those areas.

Competition has been studied predominantly for species similar in size or close in taxonomic relationship (Aguiar et al, 2001; Kozár, 1987; Mountainspring and Scott, 1985). Ecological communities are complex webs of many interactions between every member of that community. Understanding the interactions that make up this entire web is crucial to understanding the life history of any single species in that ecosystem. As issues of conservation become much more pressing with global climate change, species

will begin to shift into areas historically outside of their home ranges. The competitive interactions between not only similar species but also key and abundant different species in an ecosystem, like ants and rodents, will likely play a role in the survival of these species as some species become more widespread.

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