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**HABITAT PARTITIONING IN TWO SYMPATRIC SPECIES OF CHIPMUNK,
WARNER MOUNTAINS, CA**

A Thesis

Presented to

The Faculty of the Department of Biological Sciences
San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

By

Mary Helen Poffenroth

May 2006

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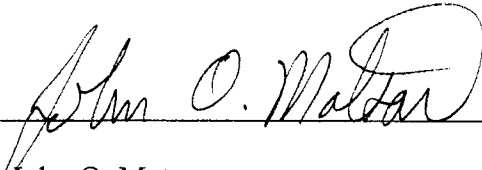
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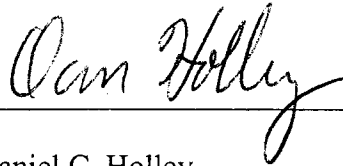
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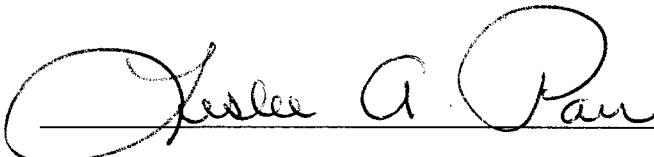
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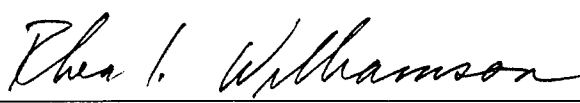


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ABSTRACT

HABITAT PARTITIONING IN TWO SYMPATRIC SPECIES OF CHIPMUNK,

WARNER MOUNTAINS, CA

by Mary H. Poffenroth

In the Warner Mountains, Modoc Co., California, two sympatric species of chipmunk partition their habitat primarily through the mechanism of competitive exclusion by social dominance and aggressive interactions. It has been suggested that the forest is the optimal habitat for both *Neotamias amoenus* and *Neotamias minimus*. In this study *N. amoenus* actively excludes *N. minimus* from the forest through successful aggressive interspecific interactions, leaving *N. minimus* to occupy primarily the arid sagebrush scrub. *Neotamias amoenus* was observed to be the more social species. *Neotamias minimus* appears to lack the level of social structure of *N. amoenus* and was not observed to win any aggressive encounters. Throughout this study *N. minimus* was observed to avoid interaction with *N. amoenus*.

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INTRODUCTION

In ecology, it is generally accepted that no two species can occupy the same area, utilizing the same resources during the same time (Savage 1958; Whittaker *et al.* 1973). The question then arises as to how animals with similar requirements, such as two or more closely related species, are able to occupy the same locality. The answer can sometimes be found by looking at competitive exclusion and interspecific interactions as a means of habitat partitioning (Brown 1971; Connell 1961).

By definition, competitive exclusion is simply the exclusion of one species by another from mutually desirable resources (Armstrong and McGehee 1980). When two similar species interact, it is deemed interspecific interaction. Competitive exclusion between species can occur through a variety of mechanisms including social, physical or chemical dominance of one species over another. Social dominance is defined as one individual or species having priority access to resources resulting from behavioral interactions such as successful attacks or chases by that dominant individual or species. Although dominance is usually discussed within a particular species, the same principles can apply to interspecific interactions between morphologically similar species (Morse 1974). Physical dominance is defined as one species being dominant over another species through morphological attributes such as size, weight or other physical adaptation. Chemical dominance is the dominance of one species over another through a chemical produced by that species. Chemical dominance, sometimes referred to as allelopathy, is most often documented in plants (Ornduff *et al.*, 2003).

Interspecific interaction has been well documented in many motile and non-motile species since the classic work of Connell (1961). Connell found that when two species of barnacles with similar ecological requirements were sharing one area, one displaced the other; that is the two species partitioned the habitat.

Chipmunks (genus *Neotamias*) are ecologically diverse rodents that can be found in a wide array of habitats across North America. Most are contiguously allopatric and actively participate in habitat partitioning (Heller 1971). A number of species may share a relatively small area, but distributions tend only to be abutting and overlapping is kept to a bare minimum (Patterson 1980).

Chipmunks achieve nearly non-overlapping ranges through various mechanisms of competitive exclusion such as aggression (Chappel 1978; Meredith 1976; Sheppard 1971). For example, in an innovative observational study using artificial feeding stations, Brown (1971) found that *Neotamias dorsalis* excluded *N. umbrinus* from the open, rocky areas of the juniper-pinyon woodland of the northwestern Great Basin. *Neotamias dorsalis* achieved this by being substantially more aggressive and intolerant of intruders. Although *N. dorsalis* would fervently chase *N. umbrinus* back into its arboreal woodland habitat, there was rarely any physical damage inflicted. However, for the social and docile *N. umbrinus*, the threat alone was usually enough reason to flee (Brown 1971). One must speculate that *N. dorsalis*' dominance is shown not only through aggressive interactions, but also through avoidance by *N. umbrinus*. While avoidance is seldom included in competitive exclusion discussions, it plays an important role in the maintenance of boundaries. Avoidance occurs when the subordinate species simply

avoids an area defended by the dominant species because of past altercations that occurred there (Morse 1974, Sheppard 1971).

Another facet of habitat partitioning is adaptation. Brown (1971) found that although *N. dorsalis* excludes *N. umbrinus* from the open, rocky portion of the juniper-pinyon woodland through social dominance, *N. umbrinus* passively excludes *N. dorsalis* from the woodland habitat by being better adapted to arboreal conditions. During a confrontation, *N. umbrinus* will flee from *N. dorsalis* and escape to the nearest tree. Once the canopy becomes sufficiently dense, *N. dorsalis* can no longer follow chase. In this case the habitat is being partitioned on the basis of vegetation density and *N. umbrinus*' arboreal adaptations (Brown 1971).

Physiological adaptations may also play an active role in habitat partitioning. For example, *N. minimus* of the Sierra Nevada, being more tolerant of high temperatures and arid conditions, is able to occupy the sagebrush zone when the usually more dominant species *N. alpinus*, *N. amoenus*, and *N. speciosus* are present (Heller and Gates 1971; Heller 1971).

Neotamias minimus is the most widely distributed of all North American chipmunks and is capable of occupying a wide spectrum of habitats such as sagebrush scrub, woodland, and alpine (Sheppard 1971, Hall 1981, Bergstrom 1992, Verts & Carraway 2001). *Neotamias amoenus*, although less widespread than *N. minimus*, can be found abundantly throughout open brush and dense forests in the Pacific Northwest, Idaho, Montana, and Wyoming (Hall 1981, Sheppard 1971, Meredith 1976, Sutton 1992). In the Warner Mountains, *N. amoenus* can be found primarily in the conifer forests, while *N.*

minimus predominately occupies the sagebrush scrub, with both species being abundant in an intermediate area containing a relatively even mixture of conifers and sagebrush. It is in this overlapping intermediate area that a unique opportunity is available to observe frequent interspecific interactions between the two species and to test the hypothesis of competitive exclusion.

Interspecific aggression is an important factor in habitat partitioning between closely related species. The importance of interspecific dominance through interspecific aggression between contiguous species has been supported and well documented by Brown (1971), Chappell (1978) Heller (1971), Meredith (1976), Orians and Wilson (1964), Sheppard (1971), and others. Specifically, it has been documented that *N. amoenus* is dominant over *N. minimus* through aggressive interactions in a laboratory setting (Sheppard 1971; Meredith 1976).

Both in the field (Chappell 1978, Heller 1971, Sutton 1992) and in the laboratory (Meredith 1976, Sheppard 1971), *N. amoenus* was found to be more aggressive and dominant than *N. minimus*. Meredith (1976) speculated that avoidance, the act of one individual conspicuously altering or reversing direction at the sight of another individual of the opposing species, might occur once dominance had been established due to prior aggressive encounters and that future aggressive encounters would become dramatically less abundant.

This study addressed the question of how two closely related species, *N. amoenus* and *N. minimus*, partition their habitat in the Warner Mountains, Modoc County, California. From previous studies (Brown 1971, Chappell 1978, Heller 1971, Meredith 1976, and

Sheppard 1971) it is likely that competitive exclusion through interspecific aggression and avoidance may be the mechanisms by which these two species are able to partition their habitat.

METHODS

Study Site---All data were collected from a single site in the Warner Mountains, Modoc National Forest, Modoc County, California. The site was located approximately 13 km East of Blue Lake Campground at an elevation of 2105 meters above sea level (N 41° 11', W 120° 14').

The study site consisted of three habitats: coniferous forest, sagebrush scrub, and an area of ecotone between the two. The conifer forest community is an area consisting mostly of lodgepole pine (*Pinus contorta*), Jeffrey pine (*Pinus jeffreyi*), and white fir (*Abies concolor*) with very little or no sagebrush scrub in the ground cover. Ground cover consisted of grasses, forbs, a few bushes, and mule ears (*Wyethia helenioides*), yellow bush lupine (*Lupinus arboreus*) and indian paintbrush (*Castilleja coccinea*). The sagebrush scrub community contained mostly big basin sagebrush (*Artemisia tridentata*) with only a few scattered conifers. The intermediate (ecotonal) community was defined as an area with a mixture of both big sagebrush and conifers.

Habitat Utilization--- Chipmunk utilization of the three habitats was determined by live trapping. One hundred folding aluminum Sherman live traps (7.6 x 9.0 x 23.4 cm) with galvanized steel doors were placed in a 190 x 90 m grid. The grid consisted of ten trap-lines placed 20 m apart with ten traps per line set 10 m apart. The grid was oriented so that the trap-lines ran northeast to southwest. Each of the four corners was marked

with an aluminum stake for the duration of the study. Each of the 100 traps was flagged and sequentially numbered (1 to 100) starting in the forest.

The grid was placed so that each habitat type was sampled. The conifer forest and sagebrush scrub contained three trap lines each, while the ecotone area contained four (Figure 1).

A total of thirteen days of trapping was conducted (three each in July and September, and seven in August). Traps were baited using a combination of oats, dried fruit, raw almonds, and raw sunflower seeds. Traps were set at 0700 hrs and checked and closed by 1000 hrs.

Captured animals were identified to species and gender, ear tagged with a numbered monel small animal ear tag and weighed. Any significant conditions such as obvious pregnancy, lactation, or scrotal distention were recorded. The animals were then released.

Behavioral Interactions---Artificial feeding stations (similar to those described by Brown 1971) were utilized to observe possible interspecific and intraspecific interactions. Feeding stations consisted of a small food pile located in an area where both species were known to occur and that had an unobstructed view. Dried fruits, raw almonds, raw sunflower seeds, and uncooked oats were used to attract visitors to the feeding station. A total of four feeding stations were established.

Observations were conducted approximately 10 m away from the feeding station. A Winchester spotting scope (15-45 x 50 mm), Bushnell 10 x 25mm compact binoculars,

Olympus handheld micro-cassette recorder, and Olympus Camedia C-750 digital camera were used to assist in the collection of data.

A Sony Digital 8 Camcorder was used to record ninety-minute spans of continuous real time data of chipmunk interactions while at the feeding station. These included feeding, grooming, social, and aggressive behaviors. All observed behaviors and interactions, both interspecific and intraspecific, were recorded along with the respective times and dates.

An aggressive interaction was defined as an event between two or more individuals of the same or different species that included biting, chasing, vocalization directed at a specific individual, or fighting. An individual was deemed a winner of the aggressive interaction if that individual was successful in defending its position. The individual that abandoned the position was deemed the loser of the event. An event where an individual made a clear and distinct attempt to travel towards a feeding station but was halted by the presence of another individual or group and then clearly changed course was considered an avoidance interaction.

Although the distance between the observation seat and the feeding station was relatively close, because of their size and quickness, this was the maximum distance that allowed the two species to be distinguished. To verify that this distance did not have an effect on the subjects, the number of visits to the feeding station while under human observation were compared to the number of visits to the feeding station under video monitoring. There was essentially no difference between the two.

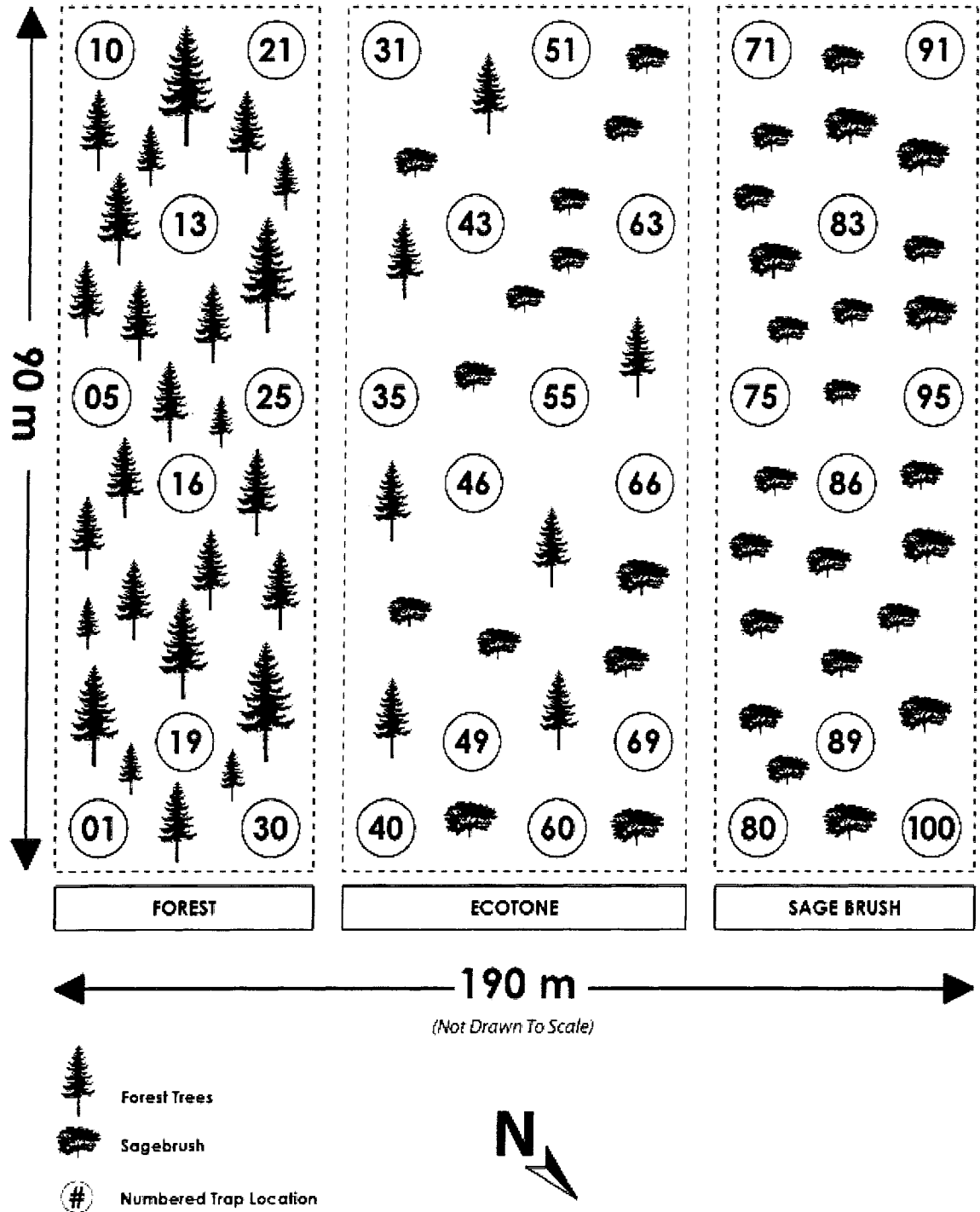


Figure 1. Schematic map of the study area showing selected trapping stations, approximate distribution of major vegetation, and the layout of "forest", "ecotone", and "sagebrush scrub" habitats (map not drawn to scale).

All fieldwork and handling of animals was conducted under Animal Protocol #793 approved by the San Jose State University Institutional Animal Care and Use Committee and California Department of Fish and Game scientific collecting permit (#SC-007372).

RESULTS

General Morphology---Although these two chipmunks closely resemble one another, they are distinguishable on the basis of several characteristics. *Neotamias minimus* has an average total length of 167-225 mm, average tail length of 70-114mm, and an average weight of 32-50g. *Neotamias amoenus* has an average total body length of 186-238mm, average tail length of 72-109mm, and an average body weight of 36-50g. In this study (N=179), *N. amoenus* and *N. minimus* ranged in actual observed weight from 39-59g (n=117) and 31-56g (n=62), respectively.

The major differences that make them distinguishable in the field are that *N. minimus* is generally smaller and paler than *N. amoenus* with the fur located on the underside of the tail being more yellowish, the rostrum being shorter, and having a tawny tuft of fur at the base of the ear. *Neotamias amoenus* is in turn distinguishable from *N. minimus* by not having the above features and having a more reddish undertail and broader, lighter dorsal stripes (Hall, 1981; Kays and Wilson, 2002).

Habitat Utilization---A total of 1300 trap-days yielded 179 captures. Both *N. amoenus* and *N. minimus* were abundant in the study area with 65% of captures consisting of *N. amoenus* and 35% of captures consisting of *N. minimus*. Males were more readily captured than females and 52% of the sample was recaptures. Trapping effort was most successful in the forest area, Traps 1-30 (Figure 1), with 52% of the

captures, with the ecotone and sagebrush accounting for 30% and 18%, respectively. In the forest area, *N. amoenus* was the most abundant, comprising 89% of the sample (Table 1). There was no significant difference in the distribution of these two species in the ecotone area (Traps 31-70, Figure 1). In the sagebrush area (Traps 71-100), *N. minimus* was the species most caught and consisted of 84% of the captures.

Behavioral Interactions---A total of 80 interspecific interactions between *N. amoenus* and *N. minimus* were recorded at the artificial feeding stations Table 2. Of the 80 total interactions, 65% were aggressive with *N. amoenus* clearly the aggressor, while the remaining 35% were avoidance behaviors taken by *N. minimus* in response to the aggression perpetrated by *N. amoenus*.

Table 1 – Habitat Utilization Chi Square Goodness of Fit

| | <i>N. amoenus</i> Captured | <i>N. minimus</i> Captured | df | X ² | P |
|------------------|-------------------------------|-------------------------------|----|----------------|-------|
| Forest | 84 | 10 | 1 | 58.24 | <.001 |
| Ecotone | 28 | 25 | 1 | .17 | >.05 |
| Sagebrush | 5 | 27 | 1 | 15.12 | <.001 |

Table 2 – Interspecific Interactions Chi Square Test for Independence

| | <i>N. amoenus</i> | <i>N. minimus</i> | df | X ² | P |
|---------------------------------------|-------------------|-------------------|----|----------------|-------|
| Aggressive Interactions Won | 52 | 0 | 1 | 75.69 | <.001 |
| Number of Interactions Avoided | 0 | 28 | | | |

DISCUSSION

Habitat Utilization---Chappell (1978) stated that *N. minimus* would colonize forest habitat left vacant by *N. amoenus*. This was supported by Sheppard (1971) when he suggested that although the forest was the optimal habitat type for both *N. amoenus* and *N. minimus*, *N. amoenus* excludes *N. minimus* through successful interspecific aggressive encounters. Both Meredith (1976 and 1977) and Sheppard (1971) demonstrated that *N. amoenus* prefers forest areas while *N. minimus*, when occurring near *N. amoenus*, is restricted to areas of sparse cover such as the alpine or sagebrush scrub.

It is evident that *N. amoenus* and *N. minimus* occupy distinct habitat types. In the forest areas the most abundant species was *N. amoenus*, with a small number of *N. minimus*. In the arid sagebrush, *N. minimus* was the most abundant. In the ecotonal area there was no significant difference in the numbers of *N. amoenus* and *N. minimus* (Table 1). These data support the conclusion that *N. amoenus* appears to be excluding *N. minimus* from the forest. Chappell (1978) also states that it is the ability of *N. minimus* to tolerate a higher heat load and lower water loss that allows it to live in less than optimal

conditions. The conditions of the arid sagebrush may be excluding *N. amoenus* or may be helping to restrict *N. minimus*. This physiological aspect was not explored in this project but future studies in this area may help to further confirm competitive exclusion between these two species.

Behavioral Interactions---The artificial feeding stations were highly successful in attracting both species at the same times during the day. The most successful station was located in an ecotonal area easily accessible to both species. Once both species began utilizing the feeding stations a clear hierarchy was established both intra- and interspecifically. *Neotamias amoenus* proved to be the more aggressive and social species of the two.

Many intraspecific aggressive interactions were observed between *N. amoenus* individuals at the feeding stations. There were times when some individuals would feed in a group and other times where a dominant *N. amoenus* would chase off conspecifics and feed alone. *Neotamias amoenus* was frequently observed traveling in groups of two to four individuals. Other animals would visit the feed station from time to time including golden mantle ground squirrels (*Spermophilus lateralis*) and Steller's jay (*Cyanocitta stelleri*). These animals would either share the station peacefully or choose to successfully chase away a single or pair of chipmunks. However, if there was a group of at least three *N. amoenus*, they would be successful in chasing away their opponent and taking control of the feeding station. This demonstrated how advantageous it is for *N. amoenus* to be not only aggressive as previously shown (Chappell 1978; Meredith 1976; Sheppard 1971) but to travel in social groups. In future studies, it would be

important to look at the effects of social grouping in conjunction with the aggressive nature of *N. amoenus* in relation to their success in excluding other species.

Although *N. minimus* visited the feeding stations far less often than *N. amoenus*, that does not mean *N. minimus* was not in the immediate area. Avoidance, the act of an individual changing course or direction in response to the presence of an individual of the opposing species (Sheppard 1971), was prevalent in *N. minimus* and accounted for 35% of the total behavioral observations (Table 2). In every avoidance encounter recorded, *N. minimus* would change course or direction in order to avoid *N. amoenus*.

Neotamias minimus appears to be a solitary species. It did not approach a feeding station in a group. Only when there were no other animals (such as birds, chipmunks, or golden mantle ground squirrels) within close proximity (at least 5 m) of the feeding station did an individual *N. minimus* approach the station. This species showed no obvious signs of intra- or interspecific aggression or social interaction throughout the study.

CONCLUSION

It appears that *N. amoenus* excludes *N. minimus* from the forest area through competitive exclusion mechanisms of social dominance and aggressive interactions. Although it is obvious in this study that both species are capable of existing in all three habitats (forest, ecotone, sagebrush scrub) *N. amoenus* continues to primarily occupy the forest while *N. minimus* is found mostly in the sagebrush scrub. *Neotamias amoenus* is the more aggressive species. *Neotamias amoenus* has also demonstrated that it is a more social animal than *N. minimus*. *Neotamias minimus* was not observed to have won any

aggressive bouts with *N. amoenus* and appears to lack the social structure seen in *N. amoenus*. *Neotamias minimus* was always observed traveling and feeding alone, providing a target for the aggressive *N. amoenus*. These very important aspects, aggression by *N. amoenus* and avoidance by *N. minimus*, have led to the current habitat partitioning between these two species observed in this study.

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