

Testing predictions of the coexistence of golden-mantled ground squirrels, *Spermophilus lateralis*, and least chipmunks, *Tamias minimus*, in meadows with various distances from cover

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Abstract:

Differing sensitivities to predation risk contribute to diversity by allowing similar organisms to coexist. Such is the case with the golden-mantled ground squirrel, *Spermophilus lateralis*, and the least chipmunk, *Tamias minimus*. These sciurids are both abundant in the area surrounding the Rocky Mountain Biological Laboratory in Gothic, Gunnison County, Colorado. Because of predation risk, *T. minimus* tends to forage closer to cover, while *S. lateralis* forages more efficiently farther from cover (Smith 1991). This phenomena was revisited to support the theory that these two species differ in sensitivities to predation risk. Meadows with various distances from cover were observed during the sciurids' active hours. Most meadows with less than 14 meters from cover contained only *T. minimus*, and most meadows with equal to or greater than 14 meters from cover contained both *T. minimus* and *S. lateralis*, showing the importance of predation risk to species coexistence.

Introduction:

Due to competition for resources, the assumption is that similar species may exclude each other, and therefore occupy different habitats. However, examples do exist of species with similar morphology living in the same environment. For example, two bat species *Scotophilus dinganii* and *Scotophilus mhlanganii* are very similar in morphology. However, they coexist by occupying different roosts with *S. dinganii* in buildings and *S. mhlanganii* in trees (Jacobs and Barclay 2009). What is necessary for species coexistence is habitat variation, which allows each species to specialize.

Predation can have great impacts in the lives of prey species due to lethal as well as non-lethal effects. Unlike the models which present either predators or prey as behaviorally static, these groups interact dynamically and respond to each other's behavior (Lima 2002). The non-lethal effects of predators, termed non-consumptive effects (NCEs) can change aspects of the entire prey community, not simply the individuals who are eliminated (Preisser et al, 2009). For example, in the presence of largemouth bass, smaller sunfish resided in nutrient-poor water because of the risk of predation. The larger sunfish did not face as much of a threat and remained in nutrient-rich water with less competition from the smaller sunfish (Werner 1983). Another interesting study observed that birds that did not require cover for escaping predators actually avoided cover. When woody cover was increased, birds that required cover became more abundant and birds that did not became less abundant. The opposite occurred when cover was decreased (Lima 1998). These non-consumptive effects of predators serve to enhance species diversity by selecting for differences among organisms, allowing coexistence of otherwise similar species. Due to differences in prey reaction to predators, predators add variation to habitats, allowing species to dominate specific niches that would not exist without the predator presence (Brown et al. 1988).

Two species that have been shown to exhibit differences in predator-induced habitat selection include the golden-mantled ground squirrel, *Spermophilus lateralis*, and the least chipmunk, *Tamias minimus*. Both *S. lateralis* and *T. minimus* were found in the Rocky Mountains near Gothic, Gunnison County, Colorado. The behavior and diet of these two sciurids has been studied by multiple professors and undergraduates (Smith 1991, Williams 1997, Young 1997, Arellano 1994, Hernick 2010, Hutcheson 1993). *S. lateralis* and *T. minimus* both fed primarily on seeds, fruits, nuts, bulbs, herbage, insects, carrion, and the common dandelion, *Taraxacum officinale* (Carleton 1966). These species were found concurrently in the

Pacific Northwest, southern Canada, and the Mountain States (Carleton 1966). They exhibited similar predator-affected behavior in their feeding habits, such as preferring peanut halves, which can be eaten in an upright posture, to peanut bits, which must be eaten on all fours, when further from cover (Hutcheson 1993). However, they showed differing sensitivities to the threat of predation. For example, they differed in giving up densities (GUDs) with reference to distances from the edge of meadows. The GUD is a common method used to measure a rodent's perception of potential gain versus cost. *T. minimus* foraged more efficiently in feeding trays placed 0 and 7 meters from cover, whereas *S. lateralis* foraged more efficiently in a feeding tray placed 21 meters from cover. A tray 14 meters from cover was alternately foraged more efficiently by *T. minimus* and *S. lateralis*, leading to the hypothesis of a differentiating point between 14 and 21 meters, which was supported by a survey of meadows (Smith 1991). In meadows containing area less than or equal to 18 m from cover, *T. minimus* was predominant. In meadows containing area greater than 20 m from cover, both species were observed. This indicated that in areas close to cover, *T. minimus* outcompeted *S. lateralis* for resources. However, *S. lateralis* was better able to escape predators due to faster running speeds and greater body mass and therefore took advantage of areas further from cover than *T. minimus* (Smith 1991).

This study follows a similar method as Smith (1991) for two reasons: 1) To test more thoroughly the predictions made in Smith (1991) and 2) To ensure that the pattern was not specific to a single generation of *S. lateralis*. This study addressed two specific predictions: 1) If *S. lateralis* could not outcompete *T. minimus*, then, no meadows would contain *S. lateralis* only. 2) If *T. minimus* foraged more efficiently than *S. lateralis*, and therefore outcompeted *S. lateralis* in habitat closer to protective cover, then in meadows with no "risky" habitat more than 18 m from cover, only *T. minimus* would exist.

Methods:

I observed twenty meadows ranging along the Copper Creek Trail, Virginia Mine trail, 401 trail, and around Judd Falls during the active hours of *S. lateralis* and *T. minimus* to determine their presence or absence. The meadows surrounding the Rocky Mountain Biological Laboratory in Gothic, Gunnison County, Colorado, are mostly montane meadows within the vegetational zones of sagebrush, aspen, and upland herb as characterized in Langenheim (1955). I generally observed between 7:30am and 10:30am and between 3:00pm and 5:30pm, with variations due to weather. Initial observations involved visiting meadows for one to two hours. I started observations by finding a convenient position that maximized visibility of the meadow while minimizing detection from sciurids or hikers. Using binoculars (Nikon Action EX, 8x40 8.2°), I noted present species and behaviors in a composition book. If I observed both species at one meadow, I did not revisit that meadow. However, if I did not observe one or both species, I did revisit that meadow, often at a different time of day. I recorded the general activity of the sciurids along with the species and time sighted. I observed meadows for a total of 83.2 hours, with an average of 3.3 hours per meadow and 4.1 hours per meadow with absences. I observed the last five meadows for one morning period due to time constraints.

I obtained the distance from cover by finding the shortest line between two sources of cover that went through the point in the meadow that was furthest from sources of cover. This distance was then divided by two to obtain the radius. Cover was defined as large bushes, conifers with low branches, tree lines, or dense, high foliage. Measurements were obtained using a tape measure or, for the larger meadows, using a Measure Distance Tool (Free Map Tools

2011, <http://www.freemaptools.com/measure-distance.htm>). Meadows were also mapped for the RMBL database using a Geo-XT system (Trimble Navigation, Sunnyvale, CA) by mapping one point near the center of each meadow and noting the approximate radius of the meadow.

The distance from cover available in the meadow was compared to the presence or absence of either species using a logistic regression in SAS JMP v 8 (SAS Institute, Cary, NC). The distance from cover was also compared to the presence of *T. minimus* and the presence of both *T. minimus* and *S. lateralis* using a logistic regression in SAS JMP. The distances from cover in meadows with only *T. minimus* and in meadows with *T. minimus* and *S. lateralis* were compared using a t-test also performed in SAS JMP.

Results:

Most meadows had at least one species present. For the four meadows with neither species present, distance from cover did not predict their absence (logistic regression, $\chi^2 = 1.307093$, $p = 0.2529$). However, distance from cover strongly predicted the species composition of a meadow with either *S. lateralis* and *T. minimus* or only *T. minimus* (logistic regression, $\chi^2 = 6.260224$, $p = 0.0123$; Figure 1). Meadows with only *T. minimus* had mean distance from cover significantly less than meadows with both *T. minimus* and *S. lateralis* (t-test, $t = 2.624608$, $p = 0.0171$; Figure 2).

S. lateralis individuals were most often noted standing or sitting on rocks (Table 1). *T. minimus* individuals were most often noted moving and running through meadows (Table 2). Simply from observations made during hiking to meadows and other activities, *T. minimus* individuals were often seen on the trails and the remainders of their foraging, clumps of dandelion seeds, were often observed. Sightings of *S. lateralis* on trails were much rarer, except in the area around Judd Falls, and the leavings from their foraging, full heads of dandelions, were rarely, if ever, observed. *T. minimus* were noticed on the edges of meadows for more than half of the total sightings. *S. lateralis* were most often noted in the middle of meadows, perched on rocks.

Discussion:

The first prediction stated that if *S. lateralis* could not outcompete *T. minimus*, then no meadows would contain *S. lateralis* only. This prediction was supported by these results. Any meadow with *S. lateralis* also contained *T. minimus*. The second prediction stated that if *T. minimus* foraged more efficiently than *S. lateralis*, then in meadows with no “risky” habitat more than 18 m from cover only *T. minimus* would exist. This prediction was also supported by these results, with a slight difference in distance from cover. Of six meadows with less than 14 meters from cover and *T. minimus*, only one contained *S. lateralis*. Of 15 meadows with more than or equal to 14 meters from cover and *T. minimus*, only three did not contain *S. lateralis*. These results indicated that *T. minimus* outcompeted *S. lateralis* in meadows with no “risky” area far from cover. The significant difference between the distance from cover in meadows with only *T. minimus* and those with both *T. minimus* and *S. lateralis* indicated that meadow size was an important factor.

A previous study by Smith (1995) indicated that two reasons for the difference in distance from cover while foraging were harvesting rates and running rates. *S. lateralis* both harvested faster and ran faster (3.14m/s) than *T. minimus* (2.13m/s). Several studies cited by Smith showed that smaller body size tended to support more efficient foraging and larger body size supported predator avoidance. This trend allowed these two ground squirrel species to

dominate different areas of meadows (Smith 1995). A similar trend was exhibited in a study of kangaroo rats and pocket mice. The rats' larger hindlimbs and larger auditory bullae allowed it to detect and escape predators easier than the smaller limbs and smaller auditory bullae of the pocket mice. Alternatively, these traits likely prevented the kangaroo rats from moving through dense shrubs as easily as the pocket mice. Therefore, the kangaroo rats tended to forage in open areas more often than the pocket mice (Brown et. al. 1988). Another possible factor that influenced presence/absence was the home range of the species. *T. minimus* had a larger home range (2.10 ha) than certain species of *Spermophilus* (1.4 or 0.17 ha) (Swihart et. al., 1988), which could have explained its presence in smaller meadows. It may have taken advantage of several small meadows to obtain resources, whereas *S. lateralis* had to be more selective and reside in meadows with enough concentrated resources to meet its metabolic needs. *T. minimus* also had more flexibility in diet. Carleton (1966) found that as the dandelion abundance declined west of Gothic, the golden-mantled ground squirrel was replaced with the rock squirrel, but the chipmunk remained present (Carleton 1966). This flexibility possibly allowed the chipmunk to occupy a larger range of habitats than the ground squirrel.

Alternatively, smaller meadows may not be able to support a sciurid the size of *S. lateralis*. The smaller meadows also were likely not rocky enough to provide adequate housing for *S. lateralis*. Large rocks were shown to be important for *S. lateralis* burrow location. In one study, a greater proportion of burrow entrances were found near rocks than would have been expected had burrows been placed randomly. The average sizes of rocks chosen were larger than the average sizes of rocks at the study sight (Bihr and Smith 1998). Therefore, meadows without adequate numbers or sizes of rocks likely would not contain *S. lateralis* regardless of distance from cover.

The lack of ability to predict absence of both species from distance from cover suggested that an undetermined factor had a role. This factor could be the previously mentioned lack of rockiness or resources. One study by Kitchings and Levi (1981) looked at the habitats in which the rodents *Blarina brevicauda*, *Tamias striatus*, *Peromyscus leucopus*, and *Ochrotomys nuttalli* were found. They found that distances to overstory and understory tree, foliage and vegetation density, as well as several other factors, allowed for descriptive discrimination between the habitats of these species (Kitchings and Levi 1981). For this study, the meadows in which neither were observed included a meadow with few large rocks, which served as sites for burrows and look-out points, one with much overgrowth, which greatly limited visibility of predators, and two that were small openings in the forest. The small openings were difficult in determining chipmunk use due to lack of knowledge of when *T. minimus* individuals were foraging elsewhere. More than simply the size of the meadow likely effects the presence of these sciurids.

One challenge encountered in this study was accounting for travel of sciurids between meadows. Often, it was difficult to determine whether a *S. lateralis* or *T. minimus* individual was passing through a meadow or foraging in it. As mentioned in the results, the most common activities of *S. lateralis* and *T. minimus* were standing on rocks and moving about respectively. Foraging behavior was not one of the main activities observed. This travel factor became especially difficult when considering meadows that were within about 50 meters of each other, allowing overlap of meadows within home ranges. A suggestion for future studies would be to ensure that the meadows observed are far enough away from other meadows so that the home range of the sciurids does not overlap several meadows. Alternatively, longer observation hours that would document the foraging activities of the sciurids could be implemented.

A future step for this study will be comparing the presence/absence of the two species in the meadows from this year's study and the meadows from the study in Smith (1991). For meadows that were studied in both, comparisons of presence/absence of sciurids could yield insight into the stability or transience of these populations in the meadows. Another factor to be considered in future studies is habitat. A study by Kitchings and Levi (1981) showed the importance of habitat for various species of small rodents (Kitchings and Levi 1981). *Tamias* species have a larger habitat range than *Spermophilus* species (Rickart 2001), so *S. lateralis* may be absent from large meadows which contain *T. minimus* on account of habitat and not size. Therefore, it may be useful to use the method in Kitchings and Levi (1981) to make notes on habitat and compare those notes with presence versus absence. Observing long, narrow meadows would also be beneficial. Meadows of this shape would allow determination of whether *S. lateralis* absence is due to competition from *T. minimus* or resource availability.

These results support the results in Smith (1991) in showing how predation risk contributes to the coexistence of these two species. As in studies of trophic cascades, non-consumptive effects of predators were found to have an impact in niche differentiation. Further studies will hopefully elicit the degree to which distance from cover is a factor in the coexistence of *T. minimus* and *S. lateralis* in Rocky Mountain meadows.

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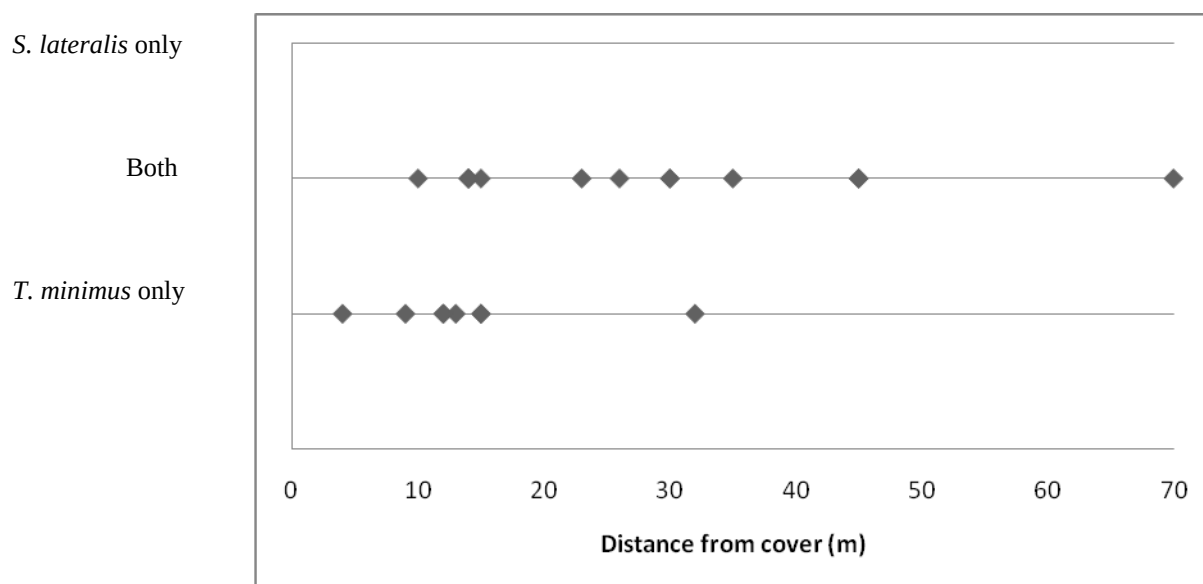


Figure 1 Distance from cover (m) versus presence of *T. minimus* and *S. lateralis*

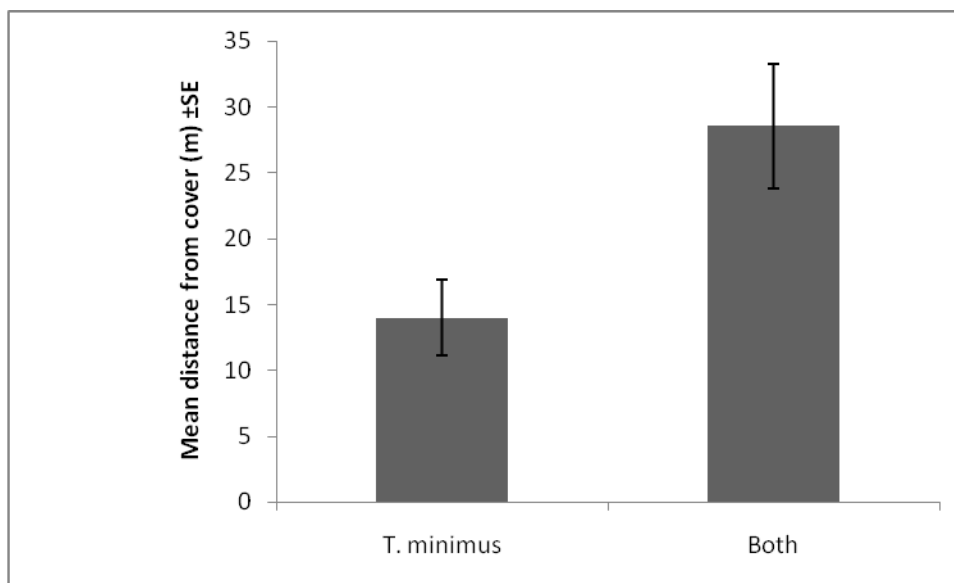


Figure 2 Average distances from cover (m) for meadows containing only *T. minimus* and meadows containing both *T. minimus* and *S. lateralis*

Table 1 *S. lateralis*: Common activities and number of times a golden-mantled ground squirrel was observed performing that activity

<i>S. lateralis</i> activity	Number of times activity was observed
Grazing and foraging	9
Running through meadow	8
Looking around alertly; standing/sitting on rocks	14
Rolling in dirt	2
Shaking tail	3
Scratching and cleaning	3

Table 2 *T. minimus*: Common activities and number of times a chipmunk was observed performing that activity

<i>T. minimus</i> activity	Number of times activity was observed
Running across meadow; moving about	18
Perched on rock; attentive	14
Eating on rock	7
Foraging and eating	11
Chasing each other	4
Shaking tail	5
Scratching and cleaning	8