

Using GIS techniques to test a model of the coexistence of the golden-mantled ground squirrel, *Callospermophilus lateralis*, and the least chipmunk, *Tamias minimus*

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Abstract

Predator-prey interactions extend beyond direct predation and can influence prey behavior and habitat use. This “ecology of fear” has been studied in a wide variety of taxa, and differences in perceived predation risk have been demonstrated to impact species coexistence. Previous research (Smith 1991, Baas 2011) on the golden-mantled ground squirrel (*Callospermophilus lateralis*) and the least chipmunk (*Tamias minimus*) has indicated that these species have differing foraging efficiencies at different distances from cover; *T. minimus* is more efficient close to cover, and does not venture too far from safety, while *C. lateralis* is able to exploit “riskier” habitat in the center of a meadow. The aim of this study was 1) to test the continued coexistence of *C. lateralis* and *T. minimus* to determine if their patterns of meadow usage are stable and 2) to use geographic information systems (GIS) to refine the methodologies used by Smith (1991) and Baas (2011). Raster analysis in GIS was utilized to locate meadows with appropriate habitat and determine the distance from cover and area of each meadow. Meadows were observed visually and with camera traps to record the presence of one or both sciurid species. Data was analyzed using logistic regression and it was found that both distance from cover and area of a meadow contribute to species composition. Results are consistent with past studies, indicating that the coexistence of these two species is stable. This research provides further evidence that the non-consumptive effects of predators promote species diversity.

Introduction

The effects of predators on prey species go beyond the direct removal of individual prey animals by predators. Predators and prey interact dynamically and respond to each other’s behavior, creating community structures that cannot be fully defined and understood using only the number of individuals who survive or are consumed (Holt 1984, Lima 2002). The non-lethal, or non-consumptive, effects of predators influence prey decision making; prey animals may adaptively change their behavior and habitat use in response to their perceived risk of predation, creating an ecology of fear (Lima 1998, Preisser et al. 2009).

Perceived predation risk has been demonstrated to impact prey behavior and habitat use in a wide variety of taxa. For instance, mule deer have been observed varying both their vigilance and foraging behavior in various levels of cover. Deer spent less time foraging, foraged

less efficiently, and displayed more vigilant behavior in microhabitats where they perceive more risk of predation (Altendorf et al. 2001). Another study found that the presence of piscivorous largemouth bass had unequal effects on different size groups of bluegill sunfish. The smaller sunfish chose to forage primarily in vegetative, less food-rich habitat where they were safer from predators, while larger sunfish utilized more “risky” open waters (Werner et al. 1983). Similar behavior has also been observed in rock hyraxes in South Africa. Hyraxes foraged most efficiently at intermediate distances from their rocky shelters, where sentinel individuals could easily alert them of predators (Kotler et al. 1999). In each of these cases, individuals varied in their perception of predation risk based on their microhabitat, morphology, and sociality. They altered their habitat use and behavior in response to these non-consumptive effects.

The ecology of fear also challenges assumptions about competition and coexistence of species that occupy similar ecological niches. The assumption that similar species will exclude each other and therefore inhabit different environments is not always true. Interspecific differences in perceived predation risk can allow for similar species to coexist. For example, heteromyid desert rodents were found to respond to both the actual presence of barn owls and indirect indicators of barn owl predation. Due to the morphological differences between kangaroo rats and pocket mice, kangaroo rats were able to forage more efficiently in “riskier” microhabitat, while pocket mice utilized “safer” habitat (Brown et al. 1988). Similar findings have also been recorded in three European tit species in coniferous forests. Crested tits and willow tits were only able to coexist with coal tits under predation by pygmy owls; in the absence of pygmy owls, the coal tit outcompetes and excludes its congeners (Kullberg & Ekman 2000). Interspecific morphological differences that result in variance in the perception of predation risk allow species with similar diets and habitats to coexist in ways that would not be possible without the presence of predators.

Theories about similar species responding to predation risk have been tested at Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado through studies of the golden-mantled ground squirrel (*Callospermophilus lateralis*) and the least chipmunk (*Tamias minimus*). The diets and behaviors of these sciurids are quite similar. Both species feed on seeds, flowers, fruits, bulbs, and herbage. They both inhabit montane meadows in western North America and use rocks to burrow under and as lookout points for predators (Verts & Carraway 2001, Bartels & Thompson 1993; R. Smith & C. Wells pers. comm.). Despite these similarities, these montane sciurids demonstrate different perceived predation risk. A study utilizing food trays placed at various distances from cover revealed that *T. minimus* foraged more efficiently 14m or less from cover, while *C. lateralis* foraged more efficiently 21m from cover. Additionally, both *C. lateralis* and *T. minimus* were observed in meadows containing area farther than 20m from cover, while smaller meadows without area 20m from cover only contained *T. minimus*. Based on these findings, it was hypothesized that in areas close to cover, *T. minimus* was able to outcompete *C. lateralis* with its foraging efficiency, while in areas far from cover, *C. lateralis* is able to. This indicates that there is a differentiating point between 14 and 20m from cover defining which

species has the competitive advantage due to their perceived predation risk, hypothesized to be around 18m (Smith 1991). This system was revisited in 2011 in a survey of twenty meadows. Observations of the two sciurid species supported the results and hypotheses reported by Smith (1991), with a differentiating distance of cover of 14m rather than 18m (Baas 2011).

The aim of this study is 1) to test the continued coexistence of *C. lateralis* and *T. minimus* to determine if their patterns of meadow usage are stable and 2) to use geographic information systems (GIS) to refine the methodologies used by Smith (1991) and Baas (2011). If this relationship is stable, meadows should either contain only *T. minimus* or both *T. minimus* and *C. lateralis*; there should be no meadows in which only *C. lateralis* exists. Utilizing GIS will allow for both the distance from cover and area of each meadow to be determined, allow for predictions about species composition to be made about meadows prior to visiting them, and increase the sampling effort by locating additional meadows not visible in the previous studies.

Methods

Locating meadows with GIS

To identify my study sites, I analyzed available raster data sets in ArcGIS to locate meadows where one or both ground squirrel species are likely to appear. I used RMBL's 1m resolution Basic Landcover Map of the East River Valley area (Breckheimer). I reclassified this dataset so terrain categories where meadow, bare soil, and rocky areas where ground squirrels are likely to exist have a value of 1, and all other terrain categories have a value of zero. I also used RMBL's 1/3m resolution Canopy Height Map (Breckheimer) and reclassified it so canopy 1m or shorter has a value of 1, and canopy higher than 1m has a value of zero, as ground squirrels are unlikely to inhabit canopy higher than 1m. I then multiplied these reclassified raster layers together so any area where squirrels are likely to occur (meadows and rocky areas with a canopy height $\leq 1\text{m}$) has a value of 1, and all other areas have a value of 0. This raster was converted into a polygon layer of suitable meadows. I located 34 meadows along the Judd Falls, 401, and Deer Creek trails to survey. Repeated buffer operations at 1/2m increments were applied to these polygons to determine the maximum distance from the edge of each meadow.

Determining species presence or absence

At each meadow, I first observed using binoculars during most likely active periods (8:00-11 AM) and recorded if *T. minimus* and/or *C. lateralis* were present. I collected a GPS location of the spot where the animal was sighted. If both species were present, I recorded that data and moved on to the next meadow.

If I could not visually confirm the presence of both species, I placed a camera bucket trap. I followed similar camera trapping methods to Macias (2019) and Novoa (2021). Each trap consisted of a 26.5L (7 gal) plastic bucket with a motion-activated camera attached to a fitted lid.

Two round holes were cut in the side of each bucket to allow small animals to pass through. A camouflage tarp was placed over each bucket. Cameras were Browning Strike Force HD Pro X, set to one shot per trigger, a 10 second interval, and 20MP resolution. Photos were stored on Ultra San Disk SD Cards. These camera trapping methods were demonstrated to be effective in photographing ground squirrels in the Gothic area by both Macias (2019) and Novoa (2021). One camera trap was placed near the edge of each meadow in a location likely to be frequented by both species (near rocks/cover, near active burrows if possible). They were baited with a mixture of peanut butter, oats, and horse feed, and left out for three to four days before being moved to a different meadow. The photos were reviewed and the presence or absence of each species in each meadow was recorded.

Results

Of the 34 meadows surveyed, 17 had only *T. minimus* present, 16 had both *T. minimus* and *C. lateralis*, and one had neither species present (Figure 1). In meadows containing one or both species, maximum distance from cover strongly predicted whether the meadow would contain only *T. minimus* or if it would contain both (logistic regression, $z = 2.477$, $p = 0.0133$, Figure 2). Meadows with only *T. minimus* present had a significantly lower maximum distance from cover than meadows containing both species (t-test, $t = -2.8476$, $df = 19.752$, $p = 0.01003$, Figure 3). Meadows containing only *T. minimus* had an average maximum distance from cover of $10.47 \pm 1.22\text{m}$ and meadows with both species present had an average maximum distance from cover of $19.78 \pm 3.03\text{m}$. Additionally, the total area of each meadow was also a strong predictor of whether the meadow would contain only *T. min* or both species (logistic regression, $z = 2.468$, $p = 0.01358$ Figure 4). The average total area of meadows containing only *T. minimus* was significantly lower than the average total area of meadows containing both species (t-test, $t = -3.5058$, $df = 15.793$, $p = 0.002977$, Figure 5).

Using the average maximum distance from cover of 10.47m for a meadow containing only *T. minimus*, a buffer of 10.47m was applied to each meadow to determine the internal area of each meadow greater than 10.47m from the edge (Figure 6). This internal area also strongly predicted whether a meadow would contain only *T. minimus* or if it would contain both species (logistic regression, $z = 2.275$, $p = 0.0229$ Figure 7). Meadows with only *T. minimus* had a significantly lower average internal area greater than 10.47m from cover than meadows with both *T. minimus* and *C. lateralis* (t-test, $t = -2.468$, $df = 15.233$, $p = 0.02589$ Figure 8).

Of the 16 meadows with both species present, three of them had maximum distances from cover below 10.47m. A study on *C. lateralis* in Gothic, Colorado found that these squirrels maintain an average home range of 1.02 ± 0.15 ha (Aliperti et al. 2021). Assuming this home range takes a roughly circular shape, the radius of this area would be approximately 57m. Applying a 57m external buffer to each meadow that was recorded to contain *C. lateralis*, as illustrated in Figure 9, the three small meadows containing both species fall into the buffer areas

of neighboring meadows, implying that *C. lateralis* individuals seen in those meadows may have been passing through to forage and do not burrow in those locations. With this in mind, the same calculations were repeated excluding these three datapoints. Maximum distance to cover was an even stronger predictor of species composition (logistic regression, $z = 2.956$, $p = 0.00311$, Figure 10), and meadows containing only *T. minimus* had a significantly lower average maximum distance from cover than meadows containing both species (t-test, $t = -3.9313$, $df = 15.97$, $p = 0.001196$, Figure 11). The total area of each meadow remained a strong predictor of species composition (logistic regression, $z = 2.754$, $p = 0.00589$, Figure 12), and the average total area of each meadow was significantly less for those containing only *T. minimus* compared to those containing both species (t-test, $t = -4.0977$, $df = 12.547$, $p = 0.001351$, Figure 13). Finally, the internal area greater than 10.47m from cover was a very strong indicator of the species composition of a meadow (logistic regression, $z\text{-value} = 2.581$, $p = 0.00987$, Figure 14), and the average internal area was significantly lower in meadows containing only *T. minimus* compared to meadows with both species present (t-test, $t = -2.617$, $df = 12.135$, $p = 0.02233$, Figure 15).

Discussion

These results support the idea that differences in perceived predation risk are an integral component of species coexistence. Due to their differences in harvesting rates and running speeds, *T. minimus* and *C. lateralis* are able to utilize their habitat differently, as they vary in their perceived predation risk. The fact that these species are able to coexist rather than exclude each other makes sense in this context, and is consistent with other studies on interspecific coexistence. Ritchie (2002) proposes that mobile species are actually highly likely to coexist because of their abilities to move and make decisions. *T. minimus* and *C. lateralis* make choices, based on perceived predation risk, that allow them to partition their habitat, hence their coexistence. Understanding these interspecific differences and their implications allow for better understanding of the structure and diversity of ecological communities. Furthermore, the presence of predators and subsequent differences in microhabitat usage promote species diversity within an ecosystem. Although difficult to observe, microhabitat partitioning has been suggested to promote sympatry among small mammals (Jorgensen 2004). This heterogeneity, driven by predators, allows for more species to coexist than would if predators were not present.

Predictions made by Smith (1991) and Baas (2011) about species composition within a meadow are also supported by these results. *C. lateralis* cannot outcompete *T. minimus*, supported by the fact that no meadows containing only *C. lateralis* have been observed in this or in previous studies. Smith and Baas also hypothesized that if *T. minimus* foraged more efficiently than *C. lateralis*, then in meadows with no “risky” habitat far from cover, only *T. minimus* would exist. This prediction was also supported by these results, as the 17 meadows containing only *T. minimus* had a significantly smaller average maximum distance from cover than the 16 meadows

containing both species. The average maximum distance from cover for a meadow containing only *T. minimus* of 10.47m is consistent with Smith's proposed range of 7-21m based on a food-tray based experiment determining foraging efficiency and is consistent with Smith and Baas's estimations of 18m and 14m, respectively. The consistency of these results over several decades suggests that this mechanism of coexistence between *C. lateralis* and *T. minimus* is stable. The composition of these ground squirrel species has remained the same, indicating that there has not been significant change in predation or meadow composition in the area. If predation in the area were to change significantly, the composition of these two ground squirrel species would also change. This is supported by the results found by Kullberg and Ekman (2000): when pygmy owls were present as a predator, three species of European tits were able to coexist on the islands studied. However, when pygmy owls were not present, the coal tit outcompeted the other two species entirely (Kullberg & Ekman 2000). If the overall predation risk for ground squirrels in the East River Valley were to decrease, *T. minimus* may outcompete *C. lateralis* and potentially exclude them entirely. If predation were to increase, *T. minimus* may stay even closer to safety within a meadow, giving *C. lateralis* more internal area in a meadow in which it can outcompete *T. minimus* and the two species may coexist in meadows currently only inhabited by *T. minimus*. Instances of interspecific coexistence like this one may reveal information about the status of predators in the area if changes are noted over time.

Geospatial analysis techniques proved to be extremely beneficial in studying this mechanism of coexistence. GIS software made it possible to find and measure numerous meadows very quickly, much faster than if the meadows were located on foot and measured by hand in the field. Furthermore, buffer operations allowed for the analysis of the internal area of a meadow in which *C. lateralis* may be able to outcompete *T. minimus*. The significant differences between this "risky" area in meadows containing only *T. minimus* compared to those containing both species indicates that linear distance from cover alone is not the only factor contributing to these species' coexistence. In order for these species to exist together in the same meadow, the meadow must have sufficient area far from the edge to support *C. lateralis*. Multiple studies use similar GIS techniques to analyze habitat and draw conclusions about species composition, and the geospatial technology used is constantly improving (Skidmore 2017). One review of geospatial technology for wildlife habitat evaluation proposed that GIS methods offer definite advantages over conventional methods, including the limitation of individual bias, faster data collection and analysis, and many additional tools and comparison possibilities that are difficult or nearly impossible with ground survey methods (Kushawa & Roy, 2002). The results of this study are yet another example of the advantages of GIS techniques.

Beyond meadow size and distance from cover, there are additional habitat features that may also impact meadow use by both species. One study by Kitchings and Levi (1981) found that distances to overstory and understory trees, vegetation density, available rocky surface, and a variety of other environmental factors allowed for the descriptive discrimination of small mammal habitat. They suggest that variations in these parameters are important for habitat

analysis as they correlate with food supplies and nesting sites (Kitchings & Levi 1981). This study lacked sufficient geospatial data on available rocks, which serve as lookout points and burrowing sites for both ground squirrel species. Data layers containing the vegetation density and the specific species of forage present were also unavailable. These habitat features contribute to the food and nesting site availability for both species. Obtaining this information, potentially via advanced remote sensing techniques, could improve understanding of the distribution of *T. minimus* and *C. lateralis* and allow for more accurate predictions about their presence.

The same GIS methods used in this study could also be expanded to additional locations in order to see if a similar pattern of coexistence exists broadly. This study focused on meadows in the Gothic, Colorado that were easily accessible on foot in order to place and retrieve the camera bucket traps. Adjusting observation methods could allow for similar surveys to be conducted throughout the East River Valley to determine if the same patterns of coexistence apply. Future studies could also take place in any area where the range of *T. minimus* and *C. lateralis* overlap, which could reveal if the same mechanism of coexistence exists in a broad region or if site-specific differences alter this relationship. Additionally, lack of geospatial and raw data from the studies performed by Smith (1991) and Baas (2011) prevented the direct comparison of the same meadows over time. All data from this study will be stored in the RMBL database to allow for future studies to make these comparisons and draw further insights into the distribution and coexistence of *T. minimus* and *C. lateralis*.

The results of this study support the results found by Smith (1991) and Baas (2011) in explaining the mechanism of coexistence of *T. minimus* and *C. lateralis* based on their differences in perceived predation risk. The coexistence of these species has appeared to remain stable over the past several decades. Utilizing GIS techniques, both linear distance from cover and internal area far from cover were found to be significant in predicting species composition of a meadow. This study provides additional evidence that the indirect effects of predators on prey species influence coexistence and promote habitat heterogeneity and species diversity, further emphasizing the importance of predators to an ecosystem.

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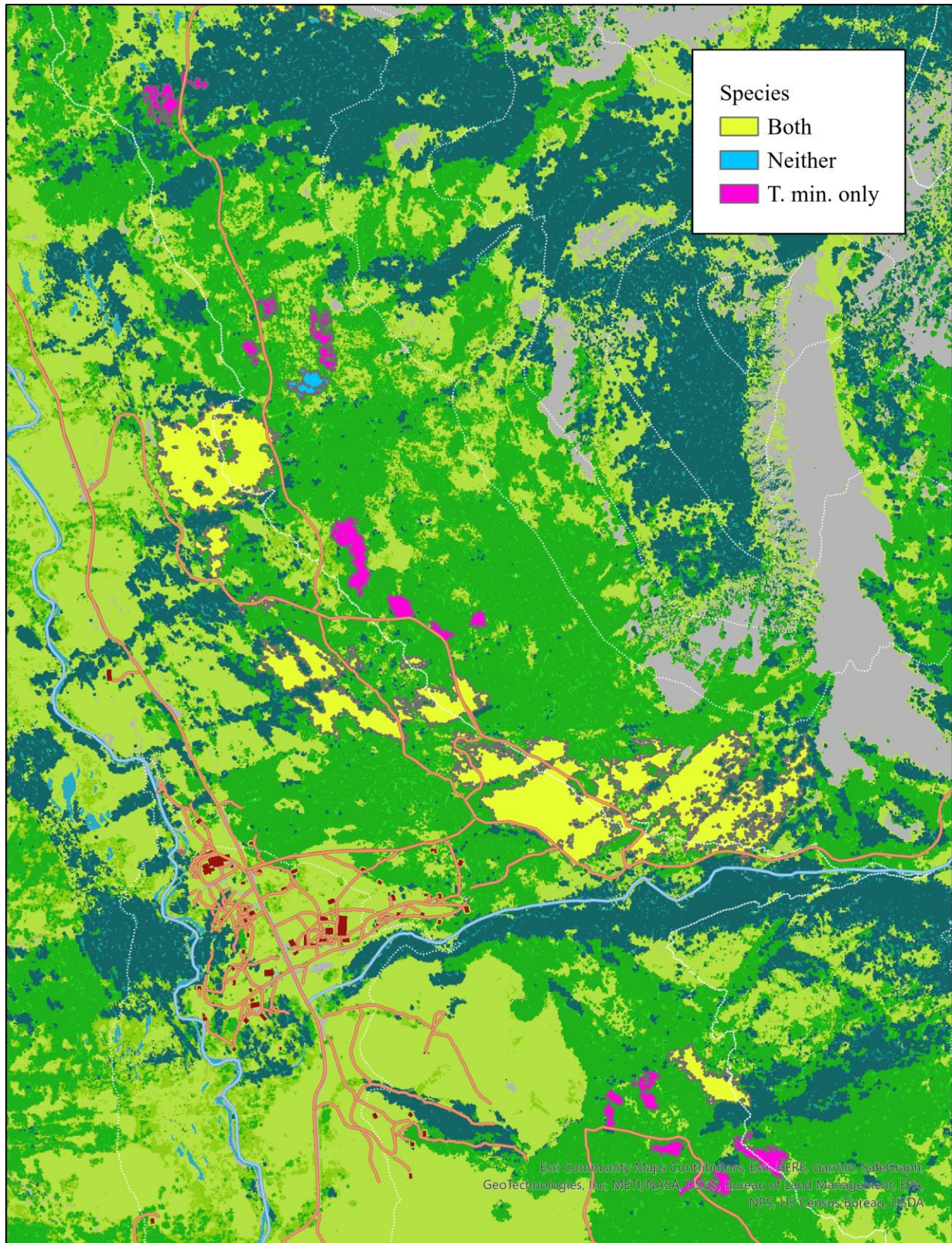


Figure 1. Map of the 34 meadows surveyed near Gothic, Colorado, color-coded by species presence.

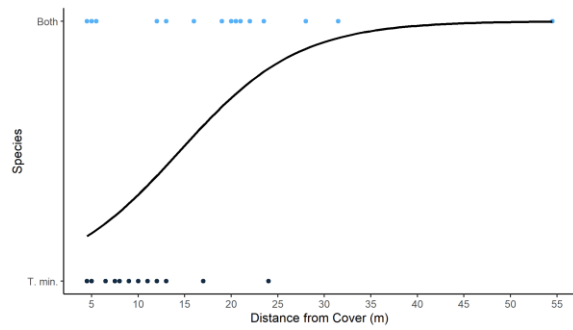


Figure 2. Distance from cover (m) of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*, with logistic regression curve.

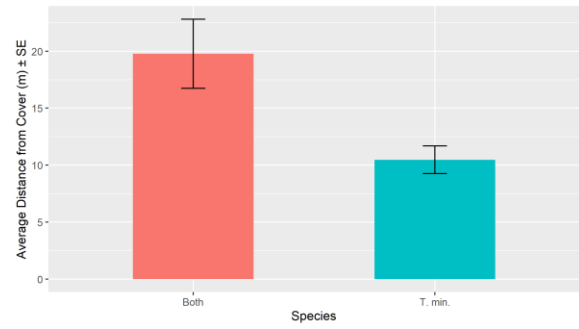


Figure 3. Average distance from cover (m) $\pm$ standard error of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*.

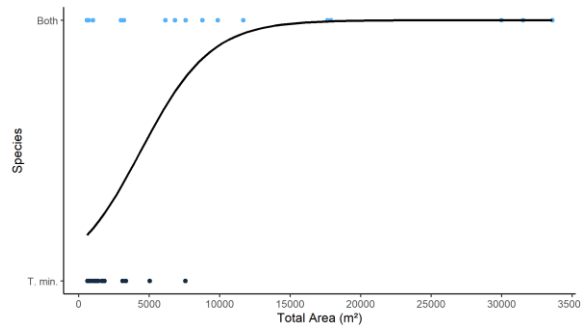


Figure 4. Total area (m²) of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*, with logistic regression curve.

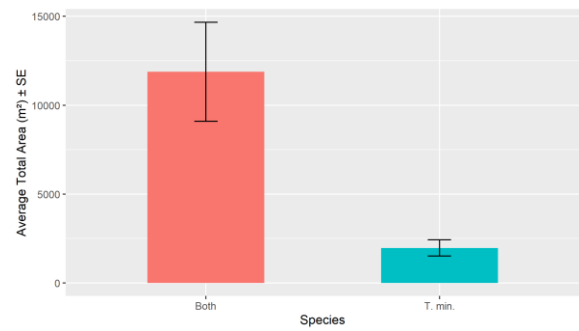


Figure 5. Average total area (m²) $\pm$ standard error of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*.

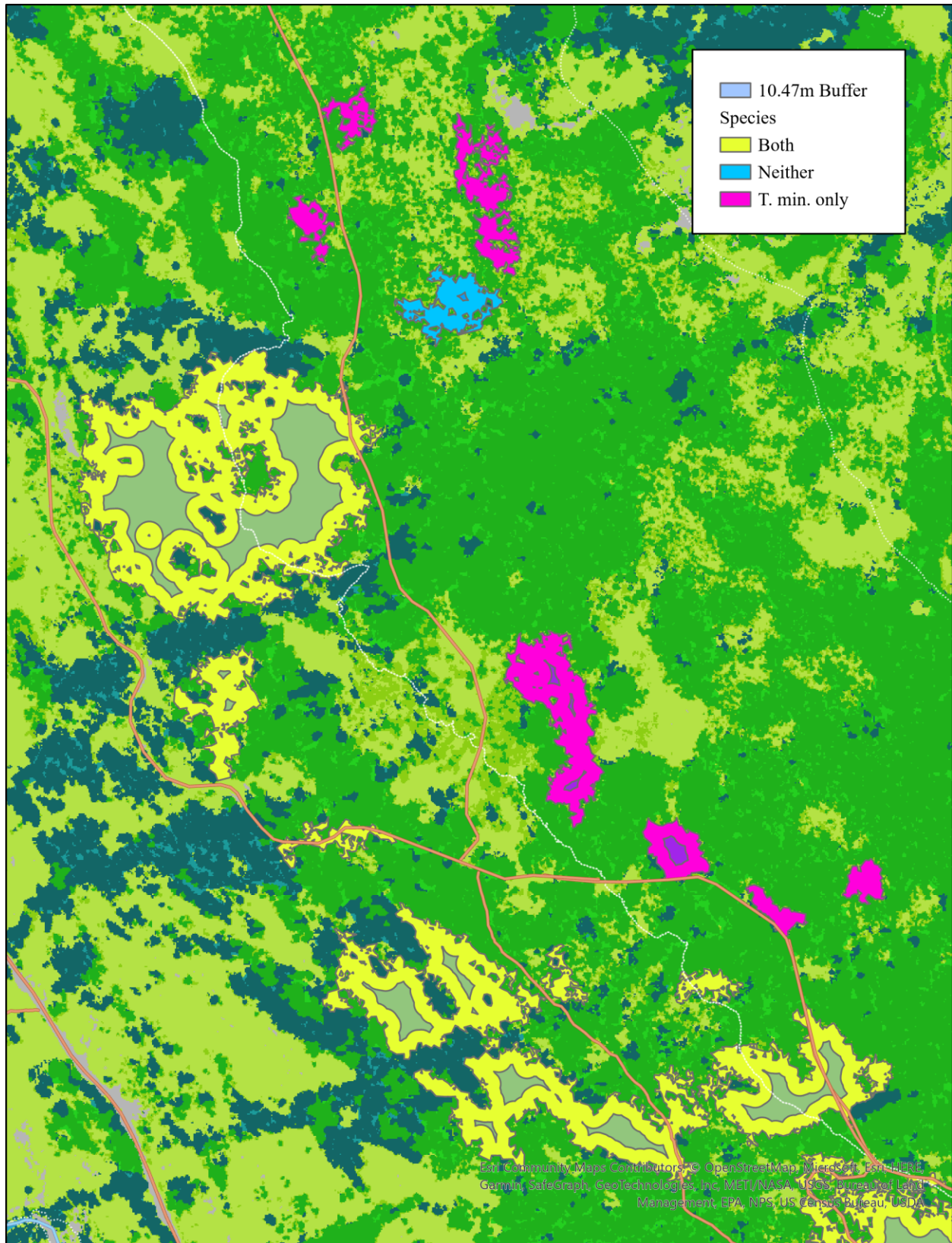


Figure 6. Map demonstrating an internal buffer of 10.47m applied to each meadow.

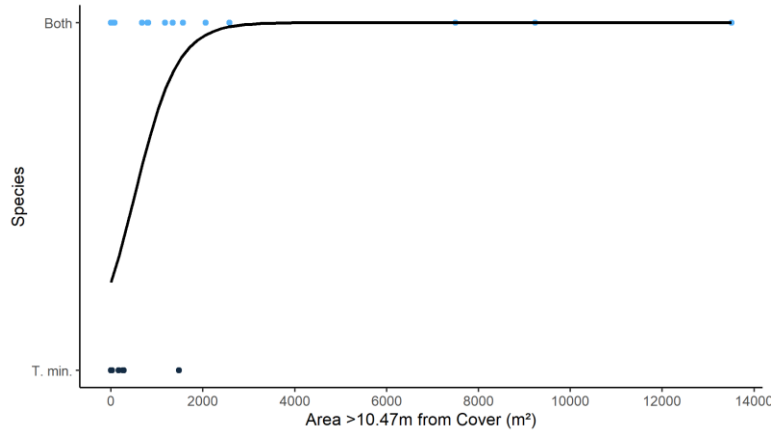


Figure 7. Area >10.47m from cover (m²) of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*, with logistic regression curve

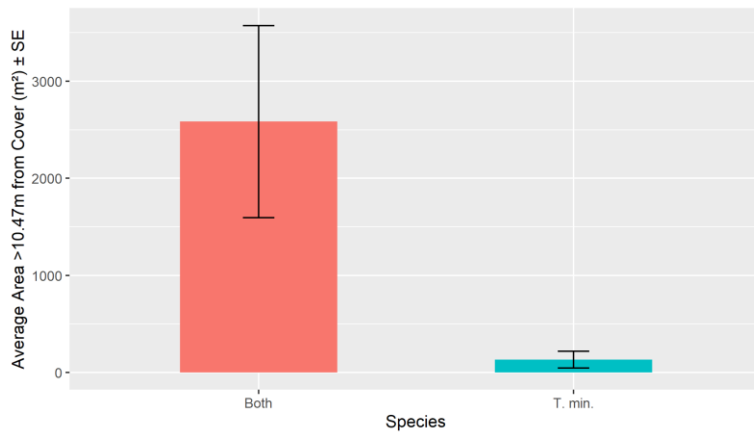


Figure 8. Average area >10.47m from cover (m²) $\pm$ standard error of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*.

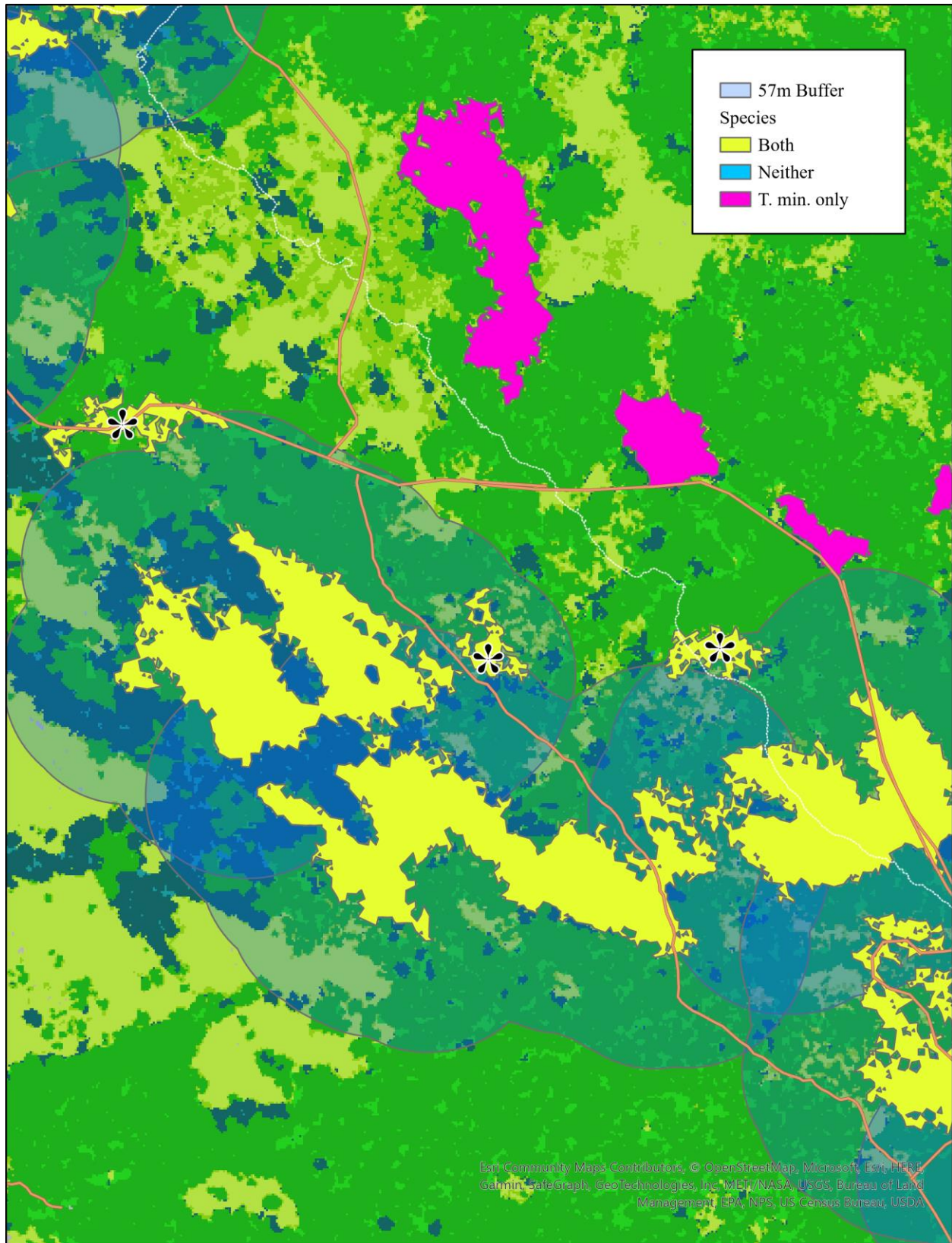


Figure 9. Map showing 57m buffer around meadows containing *C. lateralis*, with three meadows chosen to be excluded marked with * symbols.

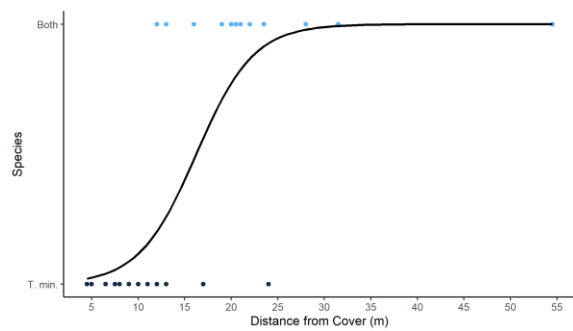


Figure 10. Distance from cover of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*, with logistic regression curve. Excludes three datapoints of meadows with both species where the home range *C. lateralis* in neighboring meadows likely overlaps.

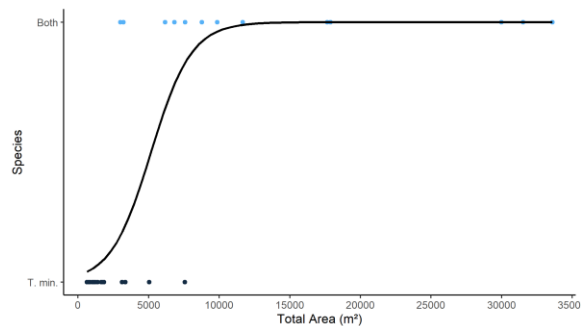


Figure 12. Total area (m²) of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*, with logistic regression curve. Excludes three datapoints of meadows with both species where the home range *C. lateralis* in neighboring meadows likely overlaps.

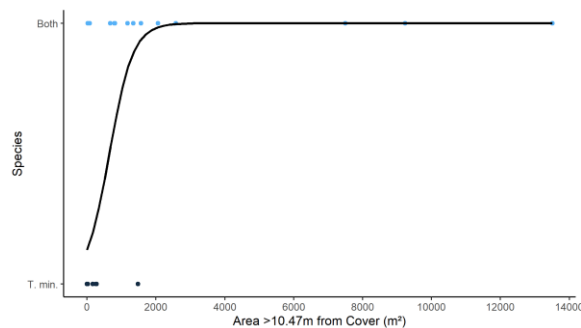


Figure 14. Area >10.47m from cover (m²) of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*, with logistic regression curve. Excludes three datapoints of meadows with both species where the home range *C. lateralis* in neighboring meadows likely overlaps.

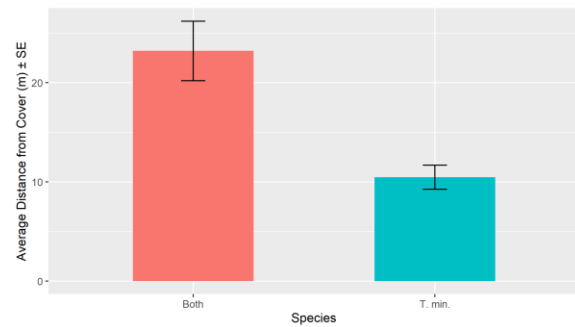


Figure 11. Average distance from cover (m) ± standard error of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*. Excludes three datapoints of meadows with both species where the home range *C. lateralis* in neighboring meadows likely overlaps.

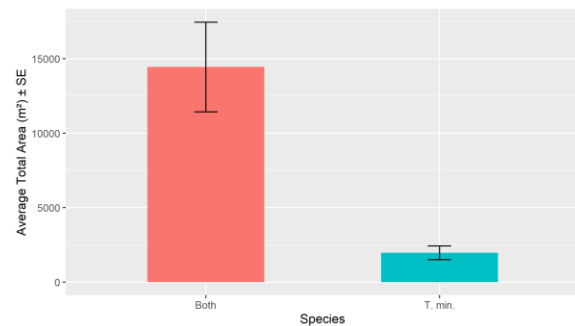


Figure 13. Average total area (m²) ± standard error of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*. Excludes three datapoints of meadows with both species where the home range *C. lateralis* in neighboring meadows likely overlaps.

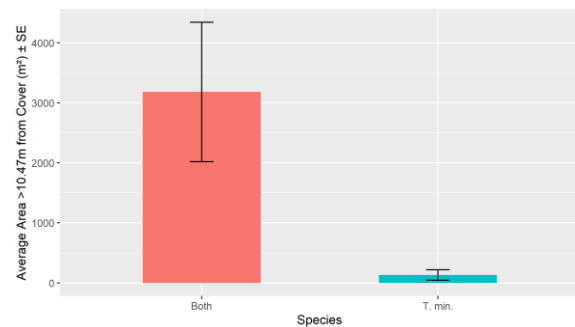


Figure 15. Average area >10.47m from cover (m²) ± standard error of meadows containing *T. minimus* or both *T. minimus* and *C. lateralis*. Excludes three datapoints of meadows with both species where the home range *C. lateralis* in neighboring meadows likely overlaps.