

Habitat patch use, density, and territoriality of American Red Squirrels (*Tamiasciurus hudsonicus*) in the southwestern Rocky Mountains, Colorado

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Independent Research and Course
Summer 2016

Abstract

American Red Squirrels (*Tamiasciurus hudsonicus*) inhabit patches of conifer trees, relying upon the cones for food. They stockpile cones in middens, which are large piles of cones at the base of trees, and exhibit territorial behavior (alarm and warning calls) to protect their midden from squirrels and other mammals. Midden presence is an indicator of squirrel presence and can be used to predict squirrel population sizes within a patch of conifers, because each squirrel relies on the stockpile of cones in their middens to survive the winter. Previous studies have shown that Red Squirrels select conifer tree patches to occupy based on size, shape, and quality of tree availability. I investigated three questions related to the relationship between habitat patches and squirrel presence: 1) Is there a minimum patch size that squirrels will occupy? 2) Does squirrel density vary with patch size? 3) Does squirrel territoriality vary with patch shape or squirrel density? I searched nineteen patches of conifers of a range of sizes for middens, and observed 11 patches to note individual territorial behavior. I found that: 1) the smallest patch that a squirrel will occupy is 0.75 hectares in area, 2) more abandoned middens were found in smaller patches, indicating higher transience for squirrel occupation, 3) midden density did not vary with tree density or patch size. For the study on patch shape, I found fewer active middens in strip shaped patches, where there were also fewer territorial calls during observation periods, possibly explained by fewer neighbors and fewer territorial boundaries.

Introduction

The world contains patches of habitat for every species, which define how species can be dispersed across landscapes. Patches are instances of similar habitat of differing size, spread out across the Earth. These patches may be as small as an isolated drop of water or as large as an ocean, and they are defined as fulfilling the needs of a species so as to support its existence there. The patch size that an individual of a species requires also ranges from miniscule to gigantic. Many species' habitat patches overlap, and certain species often play such an important role in an ecosystem that they create vital habitat for other organisms. Patches are the way in which the world exists, but habitat fragmentation, or the loss of connected habitat and transformation of large habitat areas into smaller areas due to development often increases patchiness (Andrén 1994).

The effects of increased patchiness vary from species to species – some are severely inhibited in their ability to survive while others experience enhanced territories (Bayne & Hobson, 2000). Frequently, species that thrive due to fragmentation are generalists, or those who can quickly adapt to a multitude of circumstances. Other species that occupy more specific niches find it more challenging to succeed when less and less of that niche is available. Logically, larger patches, which contain more resources, support more individuals than smaller patches. Larger patches also hold more species diversity because they contain more niches, which is relevant at the ecosystem level.

The ability of species to colonize patches is conceptualized in the theory of island biogeography. Under the assumption that large patches are the original habitat of a species, as species migrate they will move first to close, large patches and last to small, distant patches

(Wilson & Bossert, 1971). It is therefore expected that larger patches have both higher species richness and density of individuals compared to smaller patches (Wilson & Bossert, 1971).

American Red Squirrels (*Tamiasciurus hudsonicus*) are generalists and diurnal species that rely on conifer tree species for food and shelter. Red Squirrels have one specific need, cones, which can be fulfilled by a multitude of tree species (Bayne & Hobson, 2000). The species is territorial because they require a cache of these cones, called a midden, to survive (Kemp & Keith, 1970). Territories range from 0.5 to 1 hectares in size (Bayne & Hobson, 2000) and are defended through territorial actions such as vocalizations and chasing away other squirrels (Gurnell, 1984). An individual squirrel may stockpile cones in more than one midden; in the Yukon, *T. hudsonicus* defended 2.5 middens each on average (Boon et al., 2008). Discrete middens, as defined by Gurnell, are larger and in a more confined and specific area, whereas diffuse middens may exist as a few medium or small caching areas (1984). Squirrels may protect multiple discrete and diffuse middens during one season (Gurnell, 1984). In estimating *T. hudsonicus* population, midden density calculations proved to be more suitable than direct animal observations due to the challenge of successfully observing all animals in an area (Mattson & Reinhart, 1996).

Different studies have shown that *T. hudsonicus* react variably to habitat fragmentation in their preference for habitat. When habitat became fragmented due to agriculture, Bayne and Hobson observed higher relative abundance of *T. hudsonicus* in fragmented patches than nearby contiguous forest (2000). Following the theory of island biogeography, individuals that disperse from a larger patch may remain in a closer, medium-sized patch until it becomes too crowded (Bayne & Hobson, 2000). This may produce a higher squirrel density in intermediate patches than in small patches and large, contiguous swathes of forest. Upon investigating the dispersal of

juvenile squirrels specifically, Haughland and Larsen found that *T. hudsonicus* born in denser, favorable forest habitat were less likely to explore unfavorable, thinned habitat than those born in the thinned habitat. Those born in the thin, less dense forest were more likely to explore more dense, and therefore more favorable, habitat (2004).

At the Rocky Mountain Biological Laboratory in Gothic, CO, the coniferous forest is a mixture of Englemann Spruce (*Picea pungens*) and Subalpine Fir (*Abies lasiocarpa*) patches and individuals interspersed with Quaking Aspen (*Populus tremuloides*). Patch sizes vary greatly, from containing just a few trees to thousands. *Tamiasciurus hudsonicus* inhabits the Gothic Valley and therefore the location is well-suited for examining squirrel density, patch size, and territorial behavior.

Understanding how American Red Squirrels utilize different sizes and types of habitat has implications for contextualizing their ability to survive within a changing landscape. Squirrels' relationship with edginess of patches has been studied, but the influence of the shape of the patch on their territorial behavior has not been investigated. Additionally, past studies have not conducted observation hours to territorial behavior, rather they have noted calls on a shorter time scale.

This research answered the questions, What is the minimum patch size a squirrel will occupy? How does patch size influence *T. hudsonicus* density? How do patch size, shape, and density affect territorial behavior?

Methods

To analyze squirrel population densities, 20 patches of conifer forest of different sizes were searched. Patches of a range of sizes were selected using a vegetation layer and aerial photographs in ArcGIS (ArcGIS Desktop). I searched small patches in their entirety and at least 3 hectares of large patches. During these searches, I recorded all middens observed, both current and abandoned, and categorized them as such, uploading their GIS coordinates to iNaturalist. The middens are a proxy for population density (Mattson & Reinhart, 1996). Tree density and identification were also recorded in the patches. Tree density was measured with the point-quarter method (Brower et al 1998). Points were generated randomly and 2 measurements were taken per hectare of forest searched; these were averaged to find the average tree density in a patch. Observations of behavior were also conducted to note territoriality. During *T. hudsonicus*' most active hours (8:30 – 11:00 am, 1:00 – 6:00 pm) observations were conducted at middens currently being used by squirrels. Observations were made at 12 total patches, two groups of six that represented differing geometries, strips or squares, of similar sizes. There were 3 small and 3 large patches shaped both like strips and squares. Observations were 2 hours in duration and were conducted 2 times in each patch, once in the morning and once in the afternoon.

Results

Patches searched ranged in size from 0.4 hectares to 130 hectares, all of which had signs of squirrel occupation in either active or abandoned middens. The smallest patch size in which a current midden or squirrel was found was 0.4 hectares. In three out of four patches smaller than 0.75 hectares, no active middens were found. In contrast, seven out of eight patches between the sizes of 0.75 to 3.5 hectares contained active middens (Figures 1 and 2).

There was no effect of patch size on total midden density (F -ratio = 1.7343 p -value = 0.2053). Midden density ranged from 0.6 to 7.6 total middens (active and abandoned) per hectare. The average total midden density was 2.34 middens per hectare ($SD = 1.56$, $SE = 0.368$). There was a significant negative relationship between patch size and abandoned midden density (Figure 3, F -ratio = 5.1321, p -value = 0.0399).

Average tree density was 253.4 trees per hectare ($SD = 121.6$, $SE = 28.7$). There was no relationship between tree density and midden density (F -ratio = 0.0884, p -value = 0.7706). The number of trees per hectare had no bearing on the number of middens present per hectare (Figure 4).

There is a positive trend for the relationship between midden density and territoriality (F -ratio = 1.173, p -value = 0.3069), though neither patch size nor tree density showed any relationship with midden density (patch size: F -ratio = 2.3235, p -value = 0.1659 while tree density: F -ratio = 0.0884, p -value = 0.7706). More territorial calls were made in patches with higher midden density, though the relationship was not significant (F -ratio = 0.2118, p -value = 0.6576).

More territorial calls occurred in patches that were square-shaped than those that were strip-shaped ($t = -2.13649$, p -value = 0.03999, Figures 5 and 6). The average number of calls in 4

hours of observation at a strip patch is 38.8 (SD = 16.4, SE = 7.3) calls, while the average number for the same hours of observation at a square patch is 104 (SD = 96.7, SE = 69.0) calls. Though total midden density and abandoned midden density did not vary greatly between square-shaped and strip-shaped patches (total: $t = -0.29191$, $p\text{-value} = 0.3887$; abandoned: $t = 0.855172$, $p\text{-value} = 0.7922$), active midden density was consistently higher in square patches than in strip patches ($t = -1.7967$, $p\text{-value} = 0.053$, Figure 7).

Discussion

My results indicate that although there were squirrel middens in patches of all sizes, patches less than 0.75 hectares only had a 25% chance of being occupied by active middens, while those that ranged from 0.75 ha to 3.5 ha had an 87.5% chance of occupancy. Patches larger than 3.5 hectares in size all contained active middens. Patches greater than 0.75 hectares in size are therefore likely to be necessary for continuous squirrel occupancy in a patch. This result is consistent with previously measured territory sizes of red squirrels of 0.5 to 1 hectares (Bayne and Hobson, 2000).

Additionally, the lack of a relationship between conifer forest patch size and midden density indicates that the number of middens (and therefore squirrels) per hectare does not change significantly as the size of the patch changes. A similar weak correlation between fragment size and abundance was found in forest fragments in Saskatchewan, Canada (Bayne & Hobson, 2000). However, the number of abandoned middens does vary significantly with patch size: there are more abandoned middens in smaller patches, and fewer abandoned middens in larger patches. This result indicates that Red Squirrels likely move into and out of smaller patches more frequently; there is greater transience of squirrel populations in small patches. In contrast, squirrel populations in larger patches are more stable. One potential reason for this is that larger patches contain more total resources and therefore have greater viability for supporting populations. Environmental stochasticity relates to this situation, too: if a small patch has a bad cone crop one year, a squirrel will be challenged to find other resources within its immediate surroundings, whereas squirrels in larger patches have adjacent accessible resources.

The lack of a relationship between tree density and patch size is useful in negating tree density as a potential confounding factor in this study. The lack of relationship between tree

density and midden density in combination with the lack of relationship between patch size and midden density indicates that squirrels are choosing territories based on area, not the amount of cone resources available (assuming that tree density represents equivalent cone resources). In this study, active midden density (0-3.8 middens per hectare) was greater than that reported by Mattson and Reinhart (1996), who found an active midden density range in Yellowstone of 0.2-0.8 middens per hectare. This regional variation may be due to differing available resources in the two areas, perhaps relating to tree density and available cone resources. Further comparative studies across regions should investigate midden densities and available resources.

There is a positive trend in the relationship between midden density and territoriality: as more squirrels are present, more calls are made to defend a single territory from more neighbors. This analysis applies to the instances of territorial behavior in strip-shaped and square-shaped patches as well. A strong trend showed that more calls were heard in square patches than in strip-shaped patches. Squirrels that inhabit square patches are more likely to have multiple neighbors than those that inhabit strip-shaped patches. Gurnell found that boundaries with unoccupied patches were less defended than those with occupied patches (1984), and my results provide strong evidence that patch geometry can dictate the occupancy around an individual squirrel's territory. These differing number of calls in square- and strip-shaped patches due to the presence of squirrel neighbors indicate that squirrel territorial behavior occurs in reaction to the presence of other squirrels, not randomly.

Higher active midden density found in square patches than strip patches does not currently have a clear explanation. One potential reason is that the elongate shape of a patch makes a territory more energetically difficult to defend: as Gurnell found, areas that are circular

are easiest both to defend and harvest (1984). A next step to understanding the difference in active midden density in strip versus square patches, other than having a larger-reaching and longer-term study, is to investigate juvenile dispersal from strip-shaped patches. Most juveniles disperse to within 100 meters of their natal territory (Kemp & Keith, 1970), but the strip shape of a patch may inhibit dispersal on such a small scale.

Other investigations to enlighten understanding of squirrel habitat use and behavior could be conducted with analysis of patch isolation, examination of individual midden size and differences in size between active and abandoned middens, and assessing the ratio of active to abandoned middens in a variety of patches. Differences within populations have potential for analysis, for example territorial behavior and use in males versus females or adults versus juveniles. Additionally, research on midden placement would be valuable in understanding how squirrels evaluate, establish, and access a territory. Anecdotal observations in this study noted potential edge preference for midden placement and avoidance of steep slopes or unsuitable substrates.

Tables and Figures

Figure 1

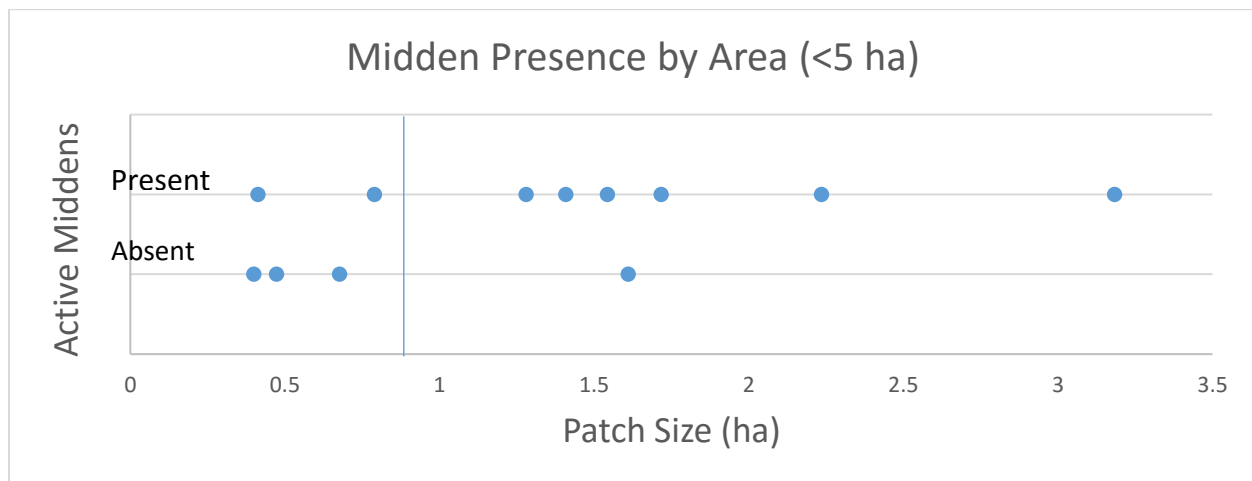


Figure 1: Active Midden Presence/Absence in patches less than 3.5 hectares in size. The top line indicates presence; the bottom indicates absence. The vertical line indicates the cutoff at which larger patches are very likely to contain an active midden.

Figure 2

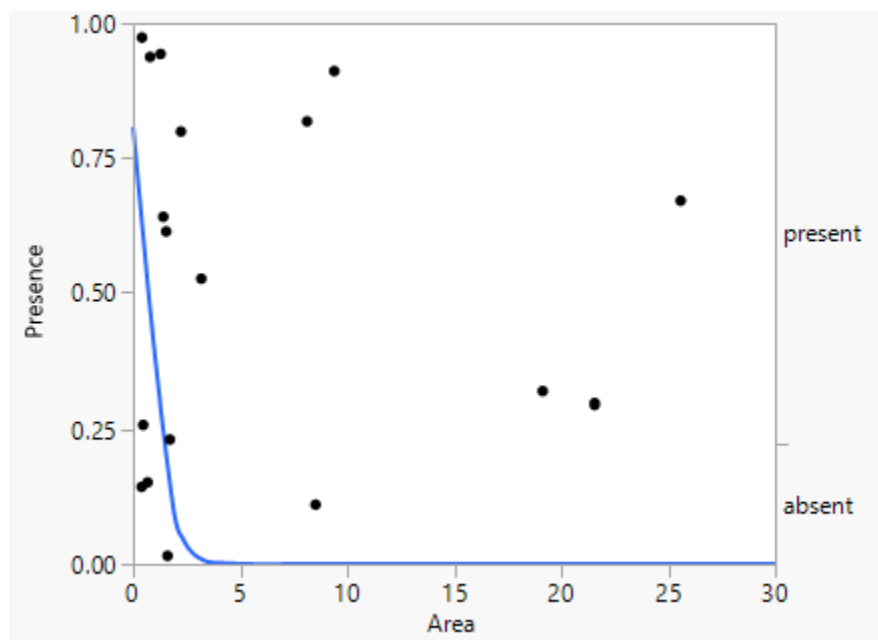
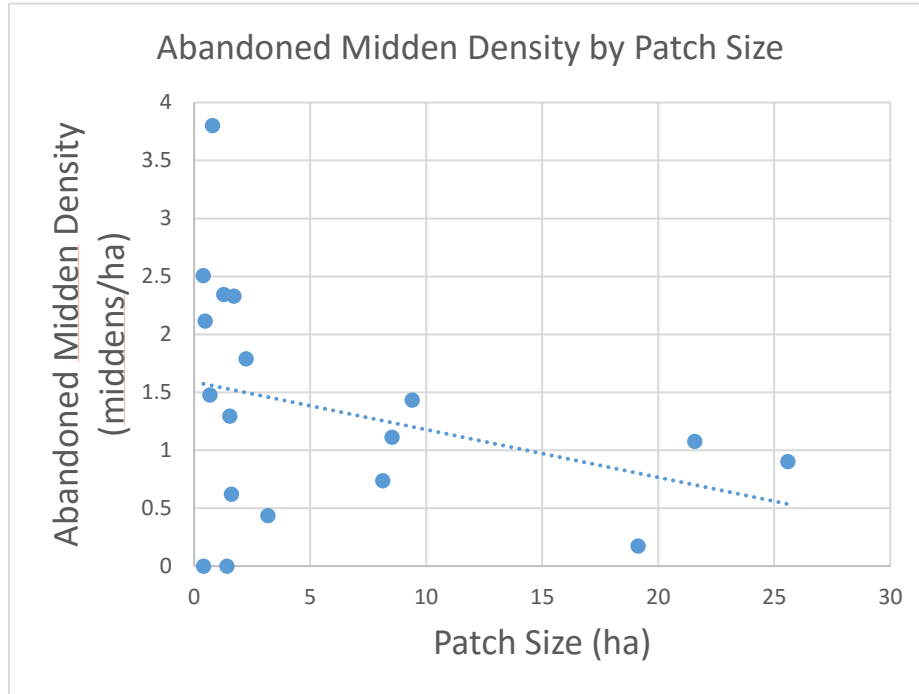


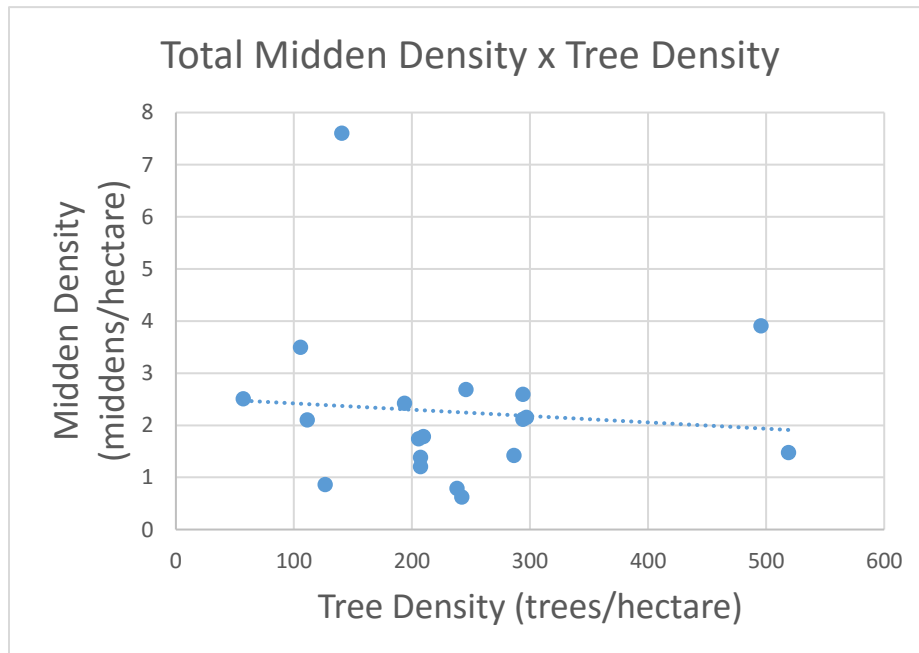
Figure 2: Logistic Regression of presence and absence data for all patches. On the left of the blue line is area in which active middens are unlikely to occur, to the right is the area in which active middens are very likely to occur. Chi Square value = 7.04, p-value = 0.008.

Figure 3



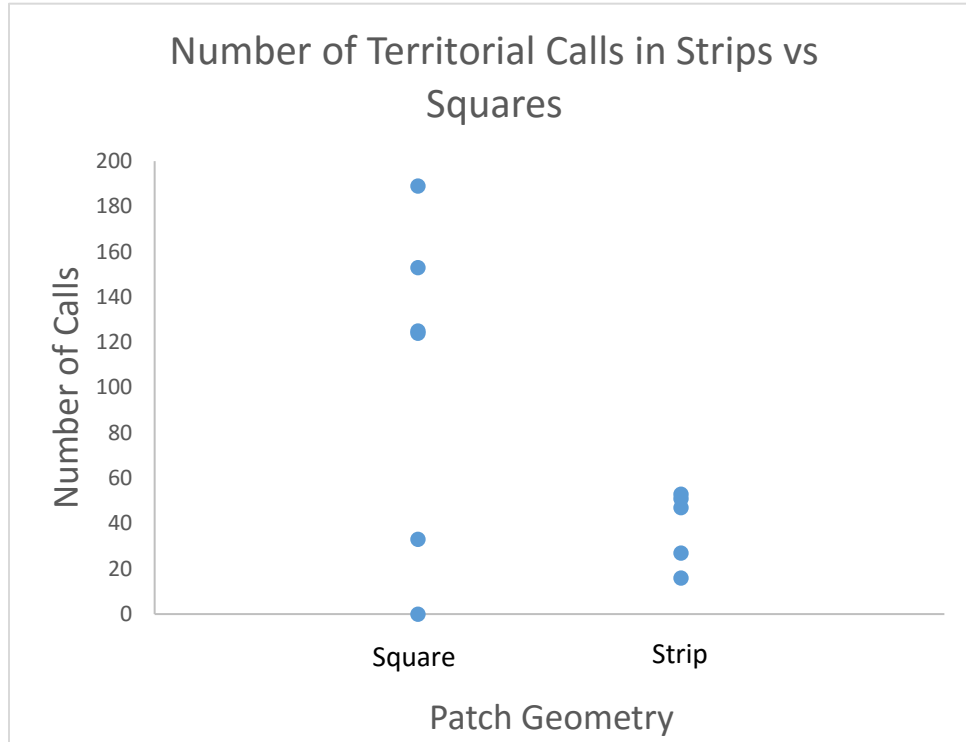
An increase in patch size significantly correlated with a decrease in the number of abandoned middens found per hectare (F-ratio = 5.3123, p-value = 0.0399).

Figure 4



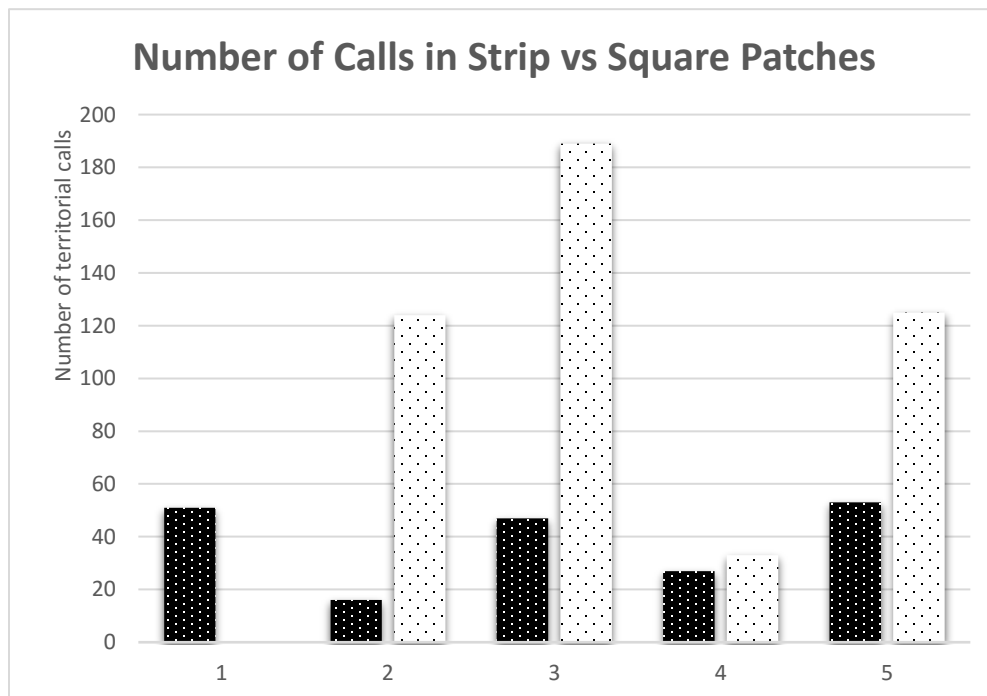
Total Midden Density response to Tree Density. There was no significant relationship between tree density and midden density (F-ratio = 0.088, p-value = 0.77).

Figure 5



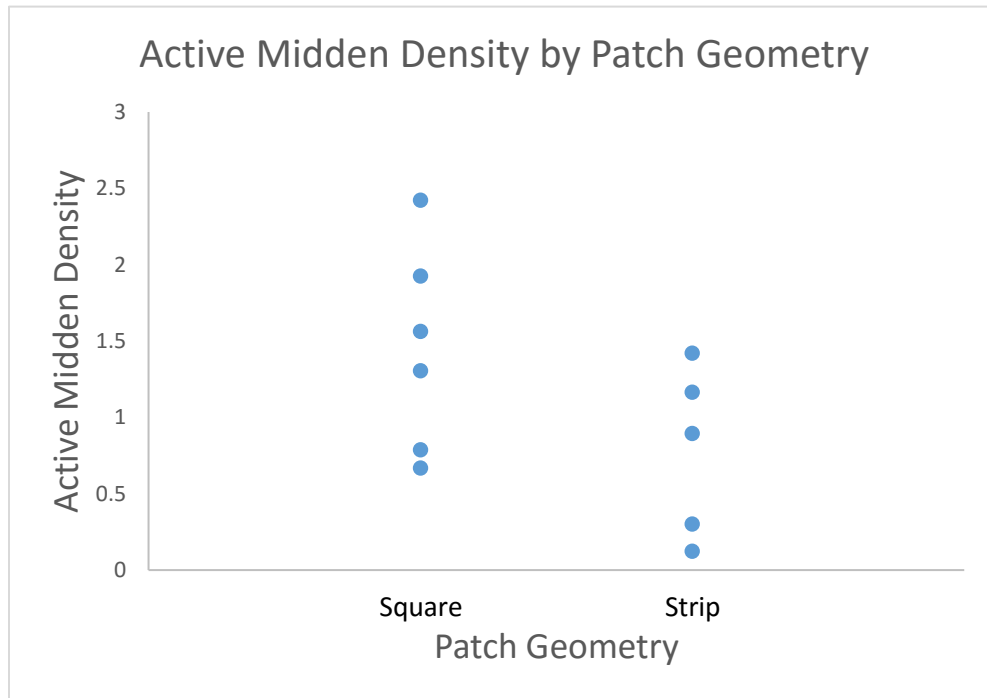
Influence of Patch Geometry (strip versus square) on number of territorial calls made in a patch. Significantly more calls were made in square-shaped patches than in strip-shaped patches (p -value = 0.0399, $t = -2.13649$).

Figure 6



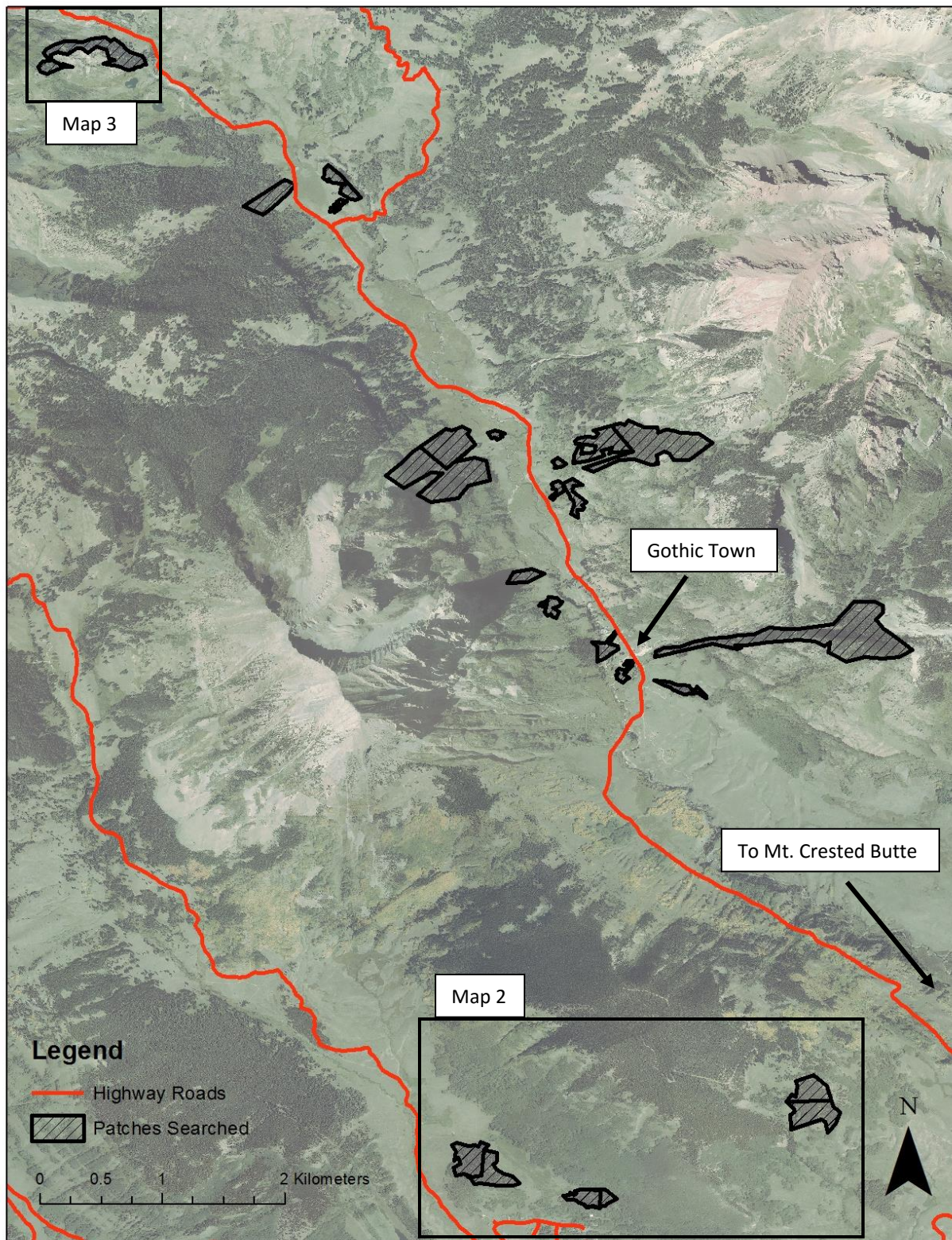
Distribution of the number of calls made in square patches (white dotted) versus the number made in strip patches (black dotted). Each number represents a set of patches that are of similar size.

Figure 7

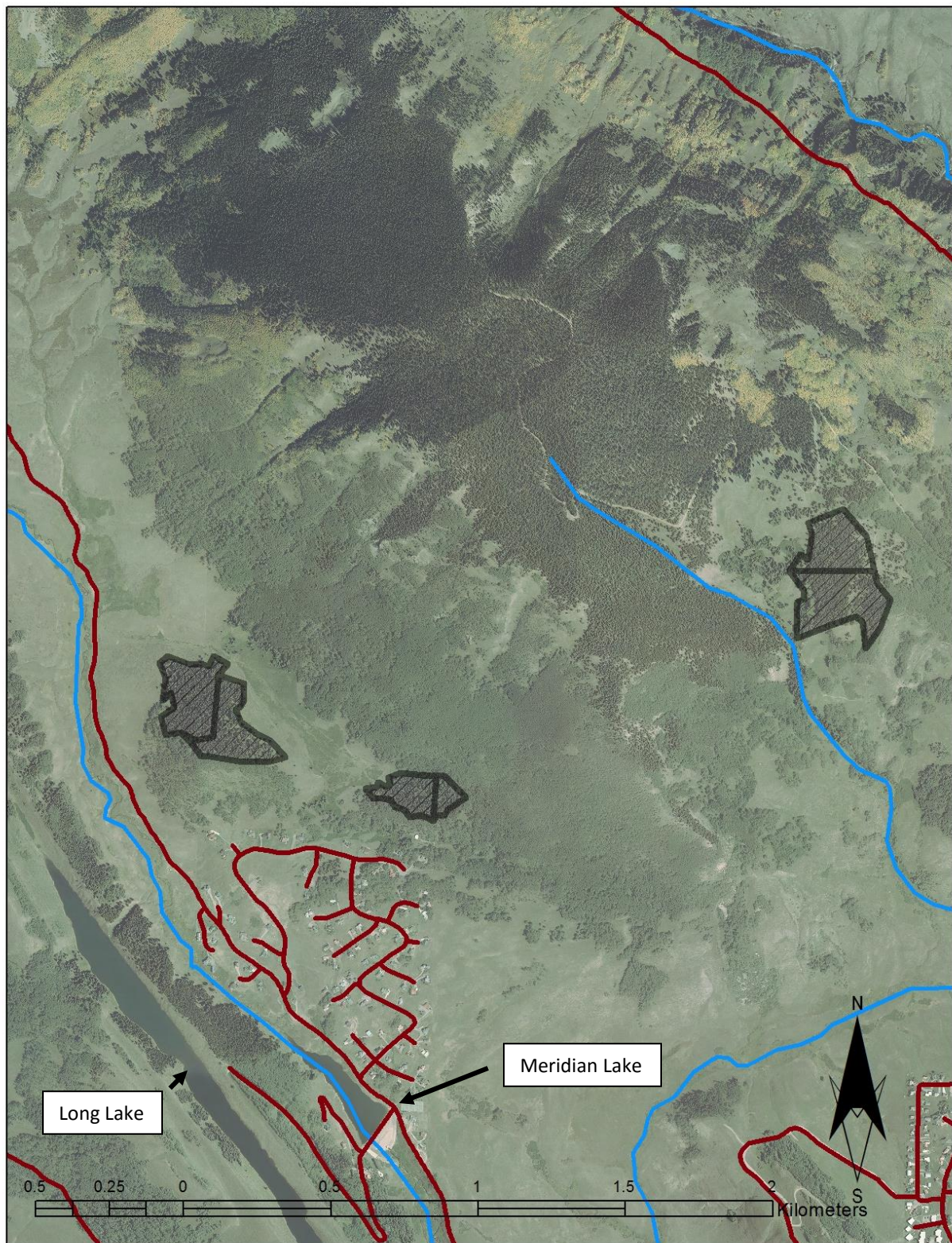


Higher active midden density was found in square patches than in strip patches (p-value= 0.053, $t = -1.7967$).

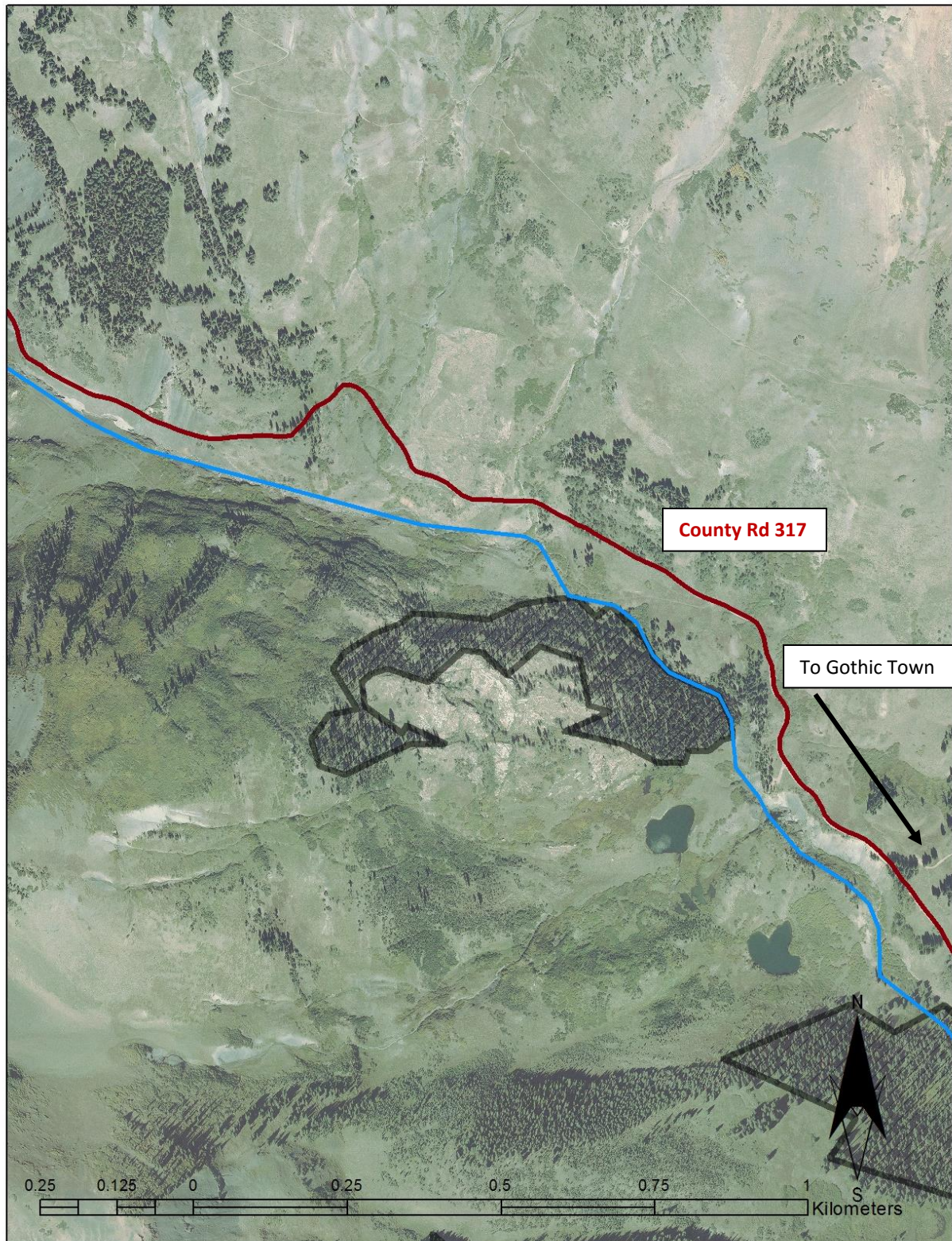
Map 1: All research sites



Map 2: Square-shaped Patches in Washington Gulch
Lines through the middle indicate area searched compared to total area.



Map 3: A strip-shaped patch southwest of Schofield Pass



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