Impact of ponderosa pine thinning on Abert's squirrel (*Scuirus aberti*) populations on Heil Valley Ranch

Submitted by:

Kelly J. Worden, PhD
Red Rocks Community College
13300 West Sixth Avenue
Lakewood, CO 80228

and

Catherine Kleier, PhD
Regis University
3333 Regis Boulevard, D-8
Denver, CO 80221

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Small Grants Program 2008
Boulder County Parks and Open Space
5201 St. Vrain Road
Longmont, CO 80503

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ABSTRACT:

This study provides baseline data on Abert's squirrel (*Sciurus aberti*) populations in thinned and unthinned stands of ponderosa pine on Heil Valley Ranch and tests methodologies that can later be employed in a much needed monitoring program of the species. Twenty seven 4-hectare (200mx200m) monitoring plots (8 in thinned stands, 19 in unthinned stands) were sampled for incidence of Abert's squirrel over-wintering feeding activity and general vegetation characteristics important to their populations. Abert's squirrel density for each monitoring plot was estimated using a recognized feeding sign index regression model. Feeding sign was found on all but 2 of our 27 monitoring plots with no difference in squirrel density between thinned and unthinned stands. Vegetation characteristics of the various stands indicate some differences between thinned and unthinned stands but only a slight, non-significant preference for stands with a high density of large ponderosa pines by Abert's squirrels. With knowledge of the current status of Abert's squirrel on Heil Valley Ranch and their associated habitat preferences, BCPOS will now be able to consider including forest structure that is beneficial to the squirrels in their treatments and management plans.

INTRODUCTION:

Abert's squirrel (*Sciurus aberti*) is considered a Management Indicator Species (MIS) by the US Forest Service with the potential to be used as an indicator of the effects of various management practices (Keith 2003). Generally assumed to be ecologically dependent on southwestern ponderosa pine forests for food, cover, and nest sites (Nash and Seaman 1977; Keith 2003; but see Edelman and Koprowski 2005), their presence, habitat use, and demographics can be indicative of forest health (Carey 2000; Koprowski 2005). The range of Abert's squirrel corresponds to that of dry, montane, interior ponderosa pine forests in the southwest (Keith 2003). In Colorado, ponderosa pine is often the dominant forest species in the foothills of the eastern slope particularly in the lower montane vegetation zone (Kaufman et al. 2006) and the distribution of Abert's squirrel reflects their reliance on these trees (see Davis and Bissell 1989). The habitat specificity of Abert's squirrel has led to its listing as a mammal of special concern by Boulder County (BCPOS 1996a) yet much of their ecology is not well understood (Keith 2003; Koprowski 2005).

Abert's squirrel habitat preferences have been described rather extensively and are summarized in Keith (2003). Ideal Abert's squirrel habitat is fairly open uneven-aged ponderosa pine forest (375-625 trees/ha) composed primarily of trees >30cm dbh with small clusters of even-aged groups including dense, young trees. High quality stands have a significant number of large trees (>50cm) and interlocking canopies between tree clusters to provide means of travel and protection. Nests are maintained and used throughout the year and generally located 9-15m above ground in trees ~40cm dbh occurring in tree clusters (Keith 2003). Nests have also been observed in witches' brooms caused by dwarf mistletoe (*Arceuthobium vaginatim*) infestation of ponderosa pines (Garnett et al. 2006) and, rarely, in cavities (Edelman and Koprowski 2006). The food of Abert's squirrels varies with availability and includes pine seeds, hypogeous fungi, apical buds, inner bark, and male and female pine cones (Keith 2003).

The structure of Abert's squirrel habitat, southwestern ponderosa pine forests, has changed dramatically since European settlement; human impact on ponderosa pine forests has dramatically altered forest structure. Prior to European settlement, ponderosa pine forests were open and park-like (Covington and Moore 1994; Moore et al. 1999). With logging, grazing, and wildfire suppression, however, these forests have typically become thick, uniform stands of even-aged pines. Present day ponderosa pine forests are often homogenous in structure and dominated by young trees with frequently >3,000 stems/ha (Mast 2003).

Because of our dramatic impact on ponderosa pine forests and the associated threat of severe fires, insect infestations, and low ecosystem health, efforts to restore ponderosa pine forests to pre-settlement conditions are widespread throughout the southwest; these efforts most often include aggressive thinning and prescribed burns (Covington and Moore 1994; Covington et al. 1997; Moore et al. 1999; Allen et al. 2002). While forest management practices do not often consider tree squirrels (Dodd 2003; Keith 2003), studies on several species in different habitats have converged on the conclusion that promotion of a mosaic landscape is the most successful conservation approach (Carey 2000; Dodd et al. 2003; Koprowski 2005 and refs. therein). Nonetheless, the impact of various forestry management practices on Abert's squirrel has not been widely studied (Dodd 2003; Koprowski 2005). Intensive thinning treatments may be detrimental to Abert's squirrel because they remove interlocking canopy trees, dramatically decrease tree density often resulting in densities of <60 trees/ha, decrease both the number of large trees and forest structure diversity, and alter the availability of fungi (Mast et al. 1999; Allen et al. 2002; Keith 2003; Dodd et al. 2006). On the other hand, restoration initiatives that involve only "thinning-from-below" (removal of saplings) may improve Abert's squirrel habitat as characteristics of presettlement forests are achieved; recently, the recruitment and survival of Abert's squirrel showed a negative correlation with the number of small saplings (Dodd et al. 2006).

The current ponderosa pine community at Heil Valley Ranch is relatively disturbed compared to pre-settlement conditions primarily due to fire suppression and logging (BCPOS 1996a; Kaufmann et al. 2006). Without low intensity fires thinning out seedlings and saplings, the forest is relatively closed, continuous, and lacking in complexity, composed primarily of young (<100 years old) trees. Restoration efforts on Heil Valley Ranch include both prescribed burns and thinning of ponderosa pine forests (BCPOS 1996b). The thinning implemented focuses on removing understory trees, seedlings, and saplings that normally would have been killed by ground fires. Forest management plans indicate that the objectives are to reduce the density of forest stands, returning them to a more natural density thereby decreasing the likelihood of catastrophic fires and insect infestations. Additional objectives relevant to Abert's squirrel habitat include retaining large trees (>50cm dbh) and maintaining mosaics of stand density, size, and age (BCPOS 1996b). In addition to forest management, BCPOS (1996b) has described general management goals for wildlife in this area as including protection and management of effective wildlife habitat especially natural food, cover, and nest sites. The density of Abert's squirrel on the property is unclear but they are known to be fairly common (BCPOS 1996a; Mark Brennan pers. comm.).

As ponderosa pine forest restoration continues on BCPOS, the effect on Abert's squirrel needs to be examined. While forest restoration practices will not likely eliminate the species, understanding the impact of the management techniques on the density of Abert's squirrel is important. This study provides a baseline for data on Abert's squirrel in thinned and unthinned stands of ponderosa pine on Heil Valley Ranch and tests methodologies that can later be employed in a much needed monitoring program of the species. With knowledge of the current status of Abert's squirrel on Heil Valley Ranch and their associated habitat preferences, BCPOS will be able to consider including forest structure that is beneficial to the squirrels in their treatments and management plans, a rare practice in Colorado (Keith 2003).

METHODS:

Feeding Sign

Squirrel density on Heil Valley Ranch was estimated using a monitoring technique developed by the Arizona Game and Fish department (Dodd undated, Dodd et al. 1998) that has subsequently been successfully implemented by others (e.g. Frey 2005, 2006). Based on signs of Abert's squirrel over-wintering feeding activity, this method is an indirect population index that is reliable, consistent, efficient, economical, and low-impact (Dodd 1998, Frey 2003, 2004, 2005, 2006). Feeding sign includes cone bracts and cores, terminal needle bundles, and short twigs with outer bark removed that are dropped to the ground while feeding (Rasmussen et al. 1975; Dodd undated; Dodd et al. 1998). An individual Abert's squirrel generally clips 10 to 1000 twigs from a single ponderosa pine tree though clippings in excess of 1200 have been documented (Keith 2003).

Crucial to this monitoring technique is accurate identification of Abert's squirrel over-wintering feeding sign, but there is reportedly a relatively steep learning curve when beginning to identify the source of sign, age of sign, etc. (Jennifer Frey, pers. comm.). Fortunately, Jennifer Frey and colleagues offered to share their expertise; prior to initiating fieldwork, Worden and

Kleier traveled to northern New Mexico to receive training on how to identify Abert's squirrel feeding sign. Care was taken to become adept at distinguishing Abert's squirrel sign from that of red squirrels, porcupine, other animals, and other factors (Rasmussen et al. 1975).

Monitoring Plots and Data Collection

In consultation with BCPOS forestry personnel, twenty seven 4-hectare monitoring plots were established in 9 different areas of Heil Valley Ranch (Figure 1). The locations of the sampling areas and the plots within were selected primarily based on logistical considerations including distributing plots among different areas of the property, ensuring representative habitat, and ease of access. Within each of the 9 areas, 2 to 4 monitoring plots were established.

Following the general recommended sampling design (Dodd undated, Dodd et al. 1998, Frey 2003, 2004, 2005, 2006), each monitoring plot is a 5x5 grid with points 50m apart (effectively, 5 parallel transects forming a 200x200m plot). Within each plot, $1m^2$ quadrats were used to quantify the abundance of Abert's squirrel over-wintering feeding sign. Quadrats were placed every 12.5m along each of the 5 transects, giving a total of 85 samples per monitoring plot. The presence of any Abert's squirrel feeding sign within or touching the quadrat was recorded. A handheld GPS unit was used to determine the location of the first plot corner and a compass bearing used to generate the transects (see appendix A for specific plot locations and bearings). While working, visual surveys were made and the presence of tree squirrels and any other evidence of current or past use of the stand by Abert's squirrels recorded.

In addition to examining feeding-sign, general vegetation characteristics reported to influence Abert's squirrel populations were measured following similar methodology employed by Dodd (2003) and Dodd et al. (2003). Within each monitoring plot, the point-centered-quarter method was used at 5 randomly selected points located throughout the grid at least 50m from each other (1 point per transect). In each quarter (determined by cardinal directions), the identity, diameter at breast height, and distance from the sampling point of the nearest two trees was recorded. This method resulted in a total of 40 trees measured per plot and allowed calculation of basal area by tree species and density corresponding to size classes. Density was calculated according to Mueller-Dombois and Ellenberg (1974; also see Mitchell 2007). In addition, at each sampling point a spherical densiometer was used to assess canopy cover in the 4 cardinal directions.

Due to the difficulty distinguishing active Abert's squirrel nests from inactive ones, no quantification of nesting structures was conducted in this study. As stated above, Abert's squirrels often use witches' brooms created by dwarf mistletoe infestations for nests. While we a few mistletoe infestations were observed during the study, we were not able to determine if they were being used as nests.

Data Analysis

Data analysis includes estimating Abert's squirrel density for each monitoring plot using a feeding sign index regression model developed by Dodd and used by Frey (2003, 2004, 2005, 2006; Figure 2). This model corresponds to the relationship between the percentage of $1m^2$ sampling quadrats containing feeding sign and the density of the population. The relationships between the habitat variables and squirrel density were assessed using regression analyses.

Schedule

While Dodd et al. (1998) found that mid-March to late May provides the most consistent relationship between feeding sign and squirrel density, monitoring often needs to be delayed to avoid snow on the ground (see Frey 2003, 2004, 2005, 2006). Our sampling began May 29th and concluded June 17th. While accurate sampling was maintained throughout our study, it became more difficult to recognize older feeding sign as sampling progressed. It is, therefore, recommended that future sampling be completed as soon as possible in the spring. It should also be noted that we found evidence of active feeding on twigs and cones throughout the study suggesting that the squirrels rely on these food sources well into the spring.

RESULTS:

Abert's squirrel feeding sign was found in 25 (92.6%) of the 27 monitoring plots; only one plot in thinned forest and one plot in unthinned forest had no evidence of Abert's squirrel feeding sign. The frequency of occurrence of each feeding sign type is indicated in Table 1. Because cones can be chewed by other animals after falling to the ground, the frequency of feeding sign excluding cones (peeled twigs and terminal branches only) was also calculated. While there was generally more sign found in unthinned stands, the difference is not significant for any of the different feeding sign types.

When considering all types of feeding sign in all plots, Abert's squirrel density ranged from 0 to 0.376 individuals per hectare with a mean of 0.061. When cones are excluded from the analysis, Abert's squirrel density ranged from 0 to 0.215 per hectare with a mean of 0.032. The difference in squirrel density when estimated using all feeding sign types and when using only peeled twigs and terminal branch clippings is significant when all plots are considered together ($p<0.01$). This difference is maintained when considering only unthinned stands ($p<0.01$) but is not significant when considering only thinned stands ($p=0.22$). For both estimates, the density of Abert's squirrels tends to be higher in unthinned stands but the difference is not significant (Figure 3).

The vegetation characteristics for thinned and unthinned ponderosa pine stands are summarized in Table 2. All trees were divided into size classes according to DBH measurements as follows: small = 0 to 20cm; medium = 20.5 to 50cm; large = >50.5cm. While unthinned stands have larger values than thinned stands for all variables, the only statistically significant difference is in canopy cover; plots located in unthinned stands have greater canopy cover than plots in thinned stands. When examining the relative density of the different sizes of ponderosa pine trees, the varying structure of the thinned and unthinned stands becomes more clear; in areas that have been thinned, medium sized trees make up the majority of the stand while in unthinned areas, the proportion of medium and small sized trees is nearly equal (Figure 4).

Abert's squirrel density has a weak negative relationship with the density of ponderosa pines in the small size class and a weak positive relationship with all of the other measured vegetation characteristics; however, none of these relationships are statistically significant. The strength of each relationship is indicated in Table 3.

Because the characteristics of the different 9 sampling areas (each with 2 to 4 monitoring plots) vary, it is helpful to examine them separately. Appendix B provides information on each of the sampled areas. There is a significant difference between the sampled areas in ponderosa pine density ($p=0.001$) and basal area ($p=0.005$), and in the density of small sized ($p=0.019$) and medium sized ($p<0.001$) ponderosa pines. There is no statistically significant difference in the density of large sized ponderosa pines among the sampled areas ($p=0.114$). When the sampling areas are ranked according to Abert's squirrel density, with the exception of area C5, it seems Abert's squirrel prefers forest with relatively high density of large sized ponderosa pines.

DISCUSSION:

Although this study found no differences between Abert's squirrel densities in thinned and unthinned ponderosa pine stands, there are several important observations that should be noted. These include a discussion of the sampling protocol, a further inquiry into the differences between thinned and unthinned forest plots, and a discussion of implications to natural resource and visitor management.

There were two aspects of the study protocol that require further investigation. First, the analyses presented here were based on Abert's squirrel densities using all types of feeding sign. These values may be slight overestimates as both red squirrels and Abert's squirrels remove cone scales and discard the cores. While no red squirrels were observed during the study, it is possible that some of the cone cores considered Abert's squirrel feeding sign were created by other small mammals. Though no observations of other mammals feeding on cones in this nature were observed, we were not specifically looking for this behavior. Additionally, as previously noted, the study took place in late May and early June. An earlier start time would allow for observation of over-wintering feed sign only and reduce the likelihood of overlooking sign that has aged. In addition, as terminal branches begin to brown after they fall from the tree, distinguishing between the recent winter's and the previous winter's feed sign was difficult. For these reasons, we recommend beginning sampling as soon as the ground is clear of snow, ideally completing monitoring no later than the first week of June.

Many studies have indicated that Abert's squirrels prefer forests that include trees over 40cm DBH (Keith 2003). It is important to note that this study at Heil Valley Ranch showed no differences in the density of large trees between the thinned and unthinned stands. Therefore, although the tree density may differ, the major determining factor for the squirrels, large trees, was not different, and so a difference in overall density may not have been expected. The forest data also show that while there are more medium sized trees in the thinned plots, this difference did not affect squirrel densities. So, while some authors have argued that thinning is good for squirrel densities (Keith 1965) and others have argued that thinning is bad for squirrel densities (Koprowski 2005), our study indicates that thinning will not have an effect if the density of trees with DBH over 40cm remains the same.

Still, forest thinning might affect other aspects that could influence squirrel densities. It has been reported that goshawks prefer a greater tree density in addition to forests that contain many large trees (Drennan and Beier 2003). As goshawks are known predators of Abert's squirrel (Reynolds 1963), there may be fewer squirrels in forests with higher densities due to predation pressure from goshawks. Although there was no difference between thinned and unthinned forests in this study, we explicitly did not investigate areas near known goshawk territory. Another study noted that non-native plants responded positively to thinning in a ponderosa pine forest (Griffis et al. 2001). While this may not be an issue for Abert's squirrels, it may provide an unwanted management problem.

In terms of overall management for BCPOS, we recommend investigating the Abert's squirrel population over a long-term time scale. As noted previously, there were not differences in densities of large trees in the thinned and unthinned forests, so it may be too early to see a difference in squirrel populations. Additionally, because two of the areas sampled this year are supposed to be thinned, this is an excellent opportunity to see if the thinning activity results in any change to the squirrel population. Lastly, the presence of people didn't seem to effect the squirrels. Although this was not part of our study, we did notice squirrels occurring both adjacent and far away from trails, so apparently this is not a concern, though, again, it was not a primary objective of the study.

CONCLUSION:

In conclusion, we recommend continuing monitoring of Abert's squirrel. We also recommend that future sampling start earlier, look only for feed sign of terminal branches (or conduct a different study to determine if other species are feeding on cones), and to especially monitor areas that have been thinned.

TABLES:

Table 1. Frequency of Abert's squirrel feeding sign on 1m^2 quadrats in monitoring plots located in thinned (N=8) and unthinned (N=19) ponderosa pine stands (85 quadrats/plot). There is no significant difference between thinned and unthinned stands for any feeding sign type.

Percent of Occurrence Per Monitoring Plot (mean ± SE)		
Feeding Sign Type	Thinned	Unthinned
Peeled Twigs	1.47 ± 0.53	1.30 ± 0.40
Terminal Branch Clippings	3.09 ± 1.11	3.96 ± 1.45
Cone Cores	3.53 ± 1.79	5.64 ± 1.54
Twigs and Branches Only	3.09 ± 1.11	4.58 ± 1.51
All Sign	5.29 ± 2.07	7.99 ± 2.12

Table 2. Vegetation characteristics of thinned and unthinned ponderosa pine stands. Size classes are according to DBH measurements as follows: small = 0 to 20cm; medium = 20.5 to 50cm; large = >50.5cm. * indicates significant difference at $p<0.05$.

Vegetation Characteristics (mean ± SE)		
	Thinned	Unthinned
Canopy Cover (%)	26.86 ± 5.25	43.17 ± 4.30*
Ponderosa Pine:		
Basal Area (m^2/ha)	9.13 ± 2.00	14.55 ± 1.75
Total Density (#/ha)	167.51 ± 48.18	320.51 ± 66.23
Small Density	63.64 ± 50.54	168.49 ± 51.12
Medium Density	101.58 ± 31.91	146.97 ± 20.95
Large Density	2.30 ± 1.10	5.05 ± 1.39

Table 3. Relationship of Abert's squirrel density to vegetation characteristics. The direction and strength of the relationship is indicated by the correlation coefficient (r).

	r	p-value
Canopy Cover (%)	0.206	0.303
Ponderosa Pine:		
Basal Area (m^2/ha)	0.202	0.312
Total Density (#/ha)	0.020	0.919
Small Density	-0.049	0.807
Medium Density	0.142	0.479
Large Density	0.340	0.083

FIGURES:

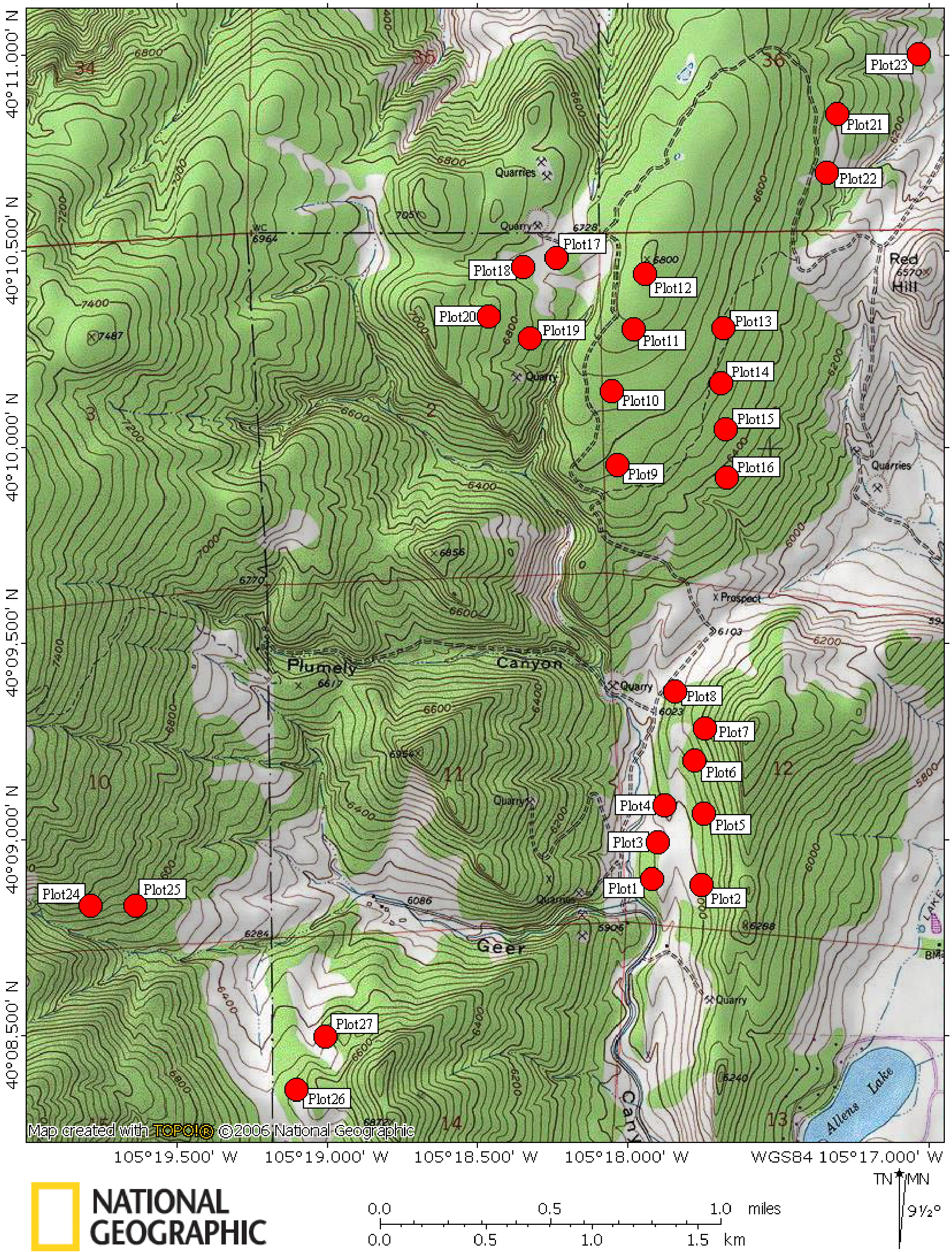

Figure 1. Location of monitoring plots on Heil Valley Ranch. See Appendix A for additional information.

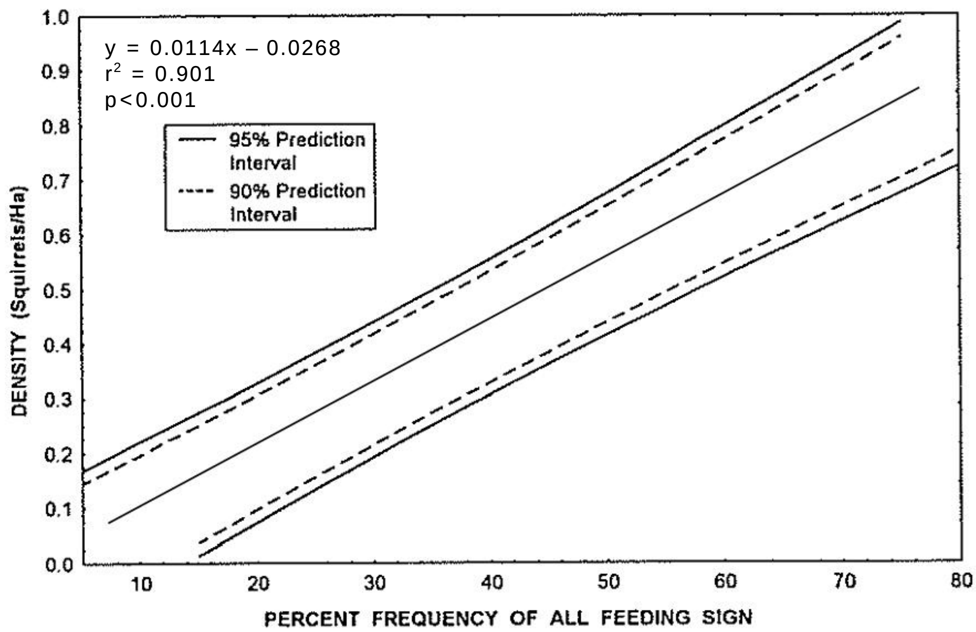

Figure 2. Adapted from Dodd 1998. Regression model between percent feeding sign and Abert's squirrel density developed from data collected in north-central Arizona.

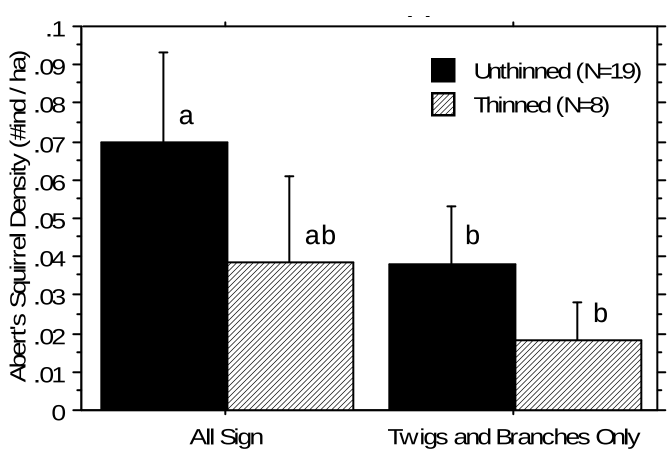

Figure 3. Abert's squirrel density (number of individuals per hectare) in thinned and unthinned ponderosa pine stands as estimated by all over-winter feeding sign and by peeled twigs and terminal branch clippings only (mean±SE). Different letters indicates significant differences ($p<0.05$).

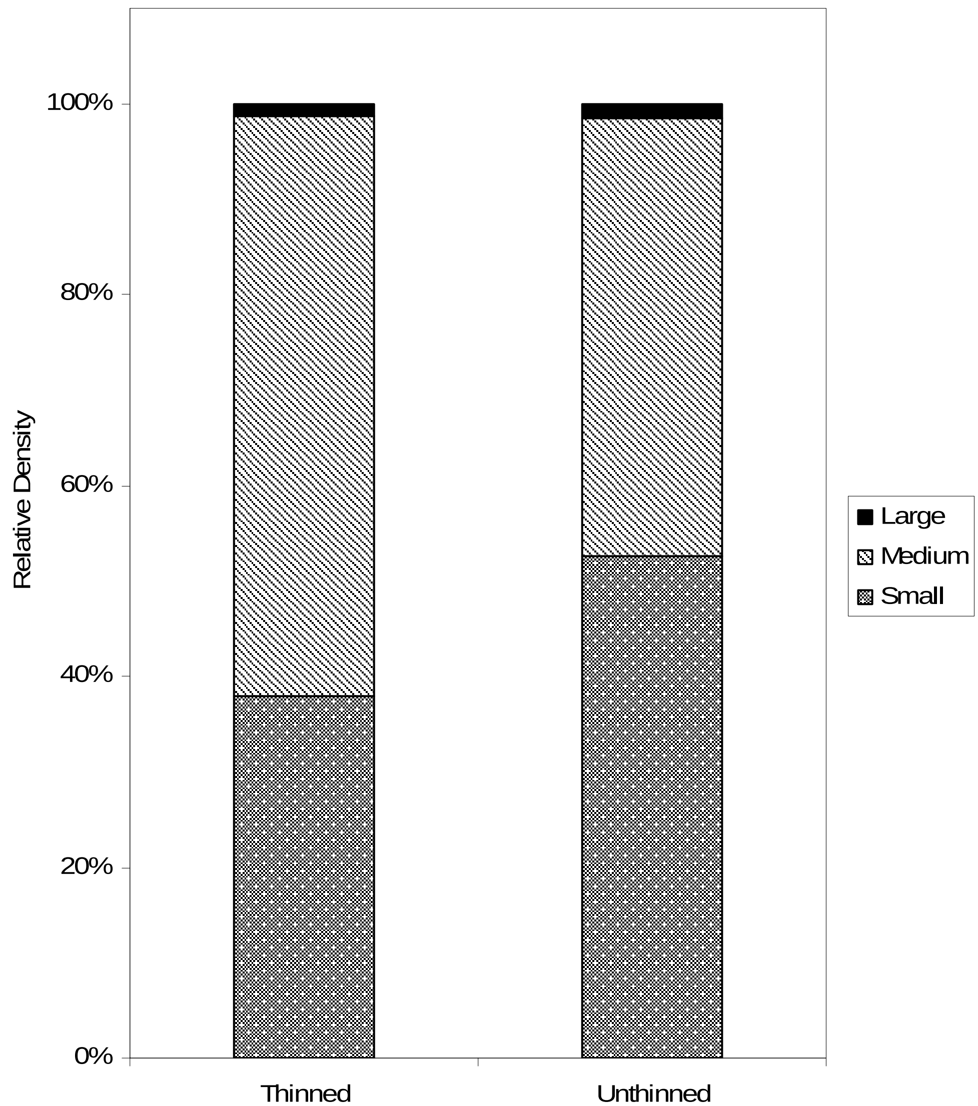

Figure 4. Relative density of different sizes of ponderosa pine trees in thinned and unthinned forest. Size classes are according to DBH measurements as follows: small = 0 to 20cm; medium = 20.5 to 50cm; large = >50.5cm.

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Appendix A. Abert's squirrel monitoring plots on Heil Valley Ranch.

Plot #	Area	Date	Forest Condition	Location of Starting Corner			Transect Direction	Plot Elevation (m)	Notes
				Location on Plot	North	West			
1	C1	5/29/2008	Unthinned	SW	40°08.852'	105°17.956'	N/S	1817	To be thinned 2008 (PA1U1)
2	C1	5/29/2008	Unthinned	SW	40°08.860'	105°17.809'	N/S	1840	To be thinned 2008 (PA1U1)
3	C1	5/30/2008	Unthinned	SW	40°08.950'	105°17.950'	N/S	1819	To be thinned 2008 (PA1U1)
4	C1	5/30/2008	Unthinned	NE	40°09.134'	105°17.826'	N/S	1831	To be thinned 2008 (PA1U1)
5	C2	6/4/2008	Unthinned	SW	40°09.012'	105°17.789'	N/S	1854	To be thinned 2008 (PA1U2)
6	C2	6/4/2008	Unthinned	SE	40°09.159'	105°17.724'	N/S	1857	To be thinned 2008 (PA1U2)
7	C2	6/4/2008	Unthinned	NE	40°09.324'	105°17.681'	N/S	1902	To be thinned 2008 (PA1U2)
8	C2	6/6/2008	Unthinned	NE	40°09.417'	105°17.804'	N/S	1854	To be thinned 2008 (PA1U2)
9	T1	6/6/2008	Thinned (1995-2006)	SW	40°09.873'	105°18.078'	N/S	2004	
10	T1	6/6/2008	Thinned (1995-2006)	SE	40°10.099'	105°17.983'	N/S	2031	
11	T1	6/6/2008	Thinned (1995-2006)	SW	40°10.265'	105°18.094'	N/S	2057	
12	T1	6/6/2008	Thinned (1995-2006)	SE	40°10.409'	105°17.834'	N/S	2073	
13	C3	6/10/2008	Unthinned	NE	40°10.414'	105°17.604'	N/S	2004	
14	C3	6/10/2008	Unthinned	NW	40°10.209'	105°17.747'	N/S	1988	
15	C3	6/10/2008	Unthinned	NE	40°10.063'	105°17.588'	N/S	1966	
16	C3	6/10/2008	Unthinned	NW	40°09.942'	105°17.717'	N/S	1938	
17	T2	6/11/2008	Thinned (2006)	NE	40°10.505'	105°18.172'	N/S	2053	
18	T2	6/11/2008	Thinned (2006)	SE	40°10.405'	105°18.294'	N/S	2058	
19	C4	6/11/2008	Unthinned	NE	40°10.325'	105°18.268'	N/S	2053	
20	C4	6/11/2008	Unthinned	SE	40°10.291'	105°18.438'	N/S	2092	
21	C5	6/16/2008	Unthinned	NW	40°10.888'	105°17.345'	N/S	1950	
22	C5	6/16/2008	Unthinned	NE	40°10.713'	105°17.316'	N/S	1920	
23	C5	6/16/2008	Unthinned	SE	40°10.951'	105°16.967'	N/S	1867	
24	C6	6/16/2008	Unthinned	SW	40°08.782'	105°19.815'	E/W	2049	
25	C6	6/16/2008	Unthinned	NW	40°08.869'	105°19.703'	E/W	2029	
26	T3	6/17/2008	Thinned (2007)	SW	40°08.310'	105°19.151'	N/S	1994	Burned
27	T3	6/17/2008	Thinned (2007)	SW	40°08.420'	105°19.072'	N/S	1981	Burned

Appendix B. Mean±SE for measurements of the 9 sampled areas on Heil Valley Ranch as ranked by density of Abert's squirrels.

Area	# of plots	forest condition	**Abert's squirrel density (#/ha)**	% feeding sign/plot	% canopy cover	Ponderosa pine: Basal Area (m2/ha)	Ponderosa pine: Total Density (#/ha)	Ponderosa pine: Small Density (#/ha)	Ponderosa pine: Medium Density (#/ha)	Ponderosa pine: Large Density (#/ha)
C6	2	unthinned	**0.315** ± 0.060	30.00 ± 5.29	62.70 ± 3.70	21.45 ± 1.13	433.17 ± 12.39	199.57 ± 21.34	223.08 ± 44.25	10.52 ± 10.52
T2	2	thinned	**0.101** ± 0.087	11.18 ± 7.65	18.90 ± 5.70	5.12 ± 1.36	50.22 ± 19.81	9.55 ± 7.95	36.84 ± 10.43	3.83 ± 1.43
C2	4	unthinned	**0.080** ± 0.033	9.12 ± 3.13	44.03 ± 6.23	12.46 ± 1.85	160.15 ± 36.71	46.76 ± 12.37	105.00 ± 26.20	8.39 ± 2.22
C1	4	unthinned	**0.047** ± 0.030	5.88 ± 2.96	28.10 ± 7.70	9.28 ± 3.14	117.10 ± 44.54	36.95 ± 13.63	72.09 ± 32.30	8.06 ± 1.16
C4	2	unthinned	**0.027** ± 0.027	4.71 ± 2.35	52.70 ± 9.50	21.46 ± 3.93	740.09 ± 236.47	446.52 ± 188.25	293.57 ± 48.22	0.00 ± 0.00
C3	4	unthinned	**0.020** ± 0.020	3.24 ± 2.06	53.68 ± 11.53	20.28 ± 4.26	563.77 ± 168.39	366.86 ± 163.75	196.92 ± 27.52	0.00 ± 0.00
T1	4	thinned	**0.020** ± 0.012	3.24 ± 1.55	37.75 ± 5.11	13.76 ± 1.83	292.92 ± 15.41	112.06 ± 18.42	178.75 ± 26.60	2.10 ± 2.10
C5	3	unthinned	**0.018** ± 0.018	3.14 ± 1.96	28.74 ± 8.47	7.55 ± 2.52	126.33 ± 44.75	35.60 ± 11.22	87.72 ± 34.45	3.02 ± 3.02
T3	2	thinned	**0.013** ± 0.013	3.53 ± 1.18	13.05 ± 9.55	3.88 ± 1.79	33.97 ± 11.08	20.87 ± 16.29	11.95 ± 4.07	1.15 ± 1.15