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LANDSCAPE-LEVEL ASSESSMENT OF ABERT'S SQUIRREL AND RED SQUIRREL IN MIXED CONIFER FOREST

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ABSTRACT—We examined feeding sign of Abert's squirrels (*Sciurus aberti*) and red squirrels (*Tamiasciurus hudsonicus*) each spring 2005–2009 in mixed conifer forests in northern Arizona, USA. We used high-resolution aerial photographs to assess vegetation characteristics where feeding sign surveys were conducted and analyzed the association of feeding sign frequency to vegetation characteristics to compare and contrast species habitat use. At the landscape level, we found considerable overlap in characteristics of forests used by the two species of native tree squirrels. Red squirrels used denser forests with fewer and smaller gaps than do Abert's squirrels, and Abert's squirrels used more ponderosa pine (*Pinus ponderosa*) than do red squirrels.

RESUMEN—Examinamos los restos de alimentación de las ardillas de Abert (*Sciurus aberti*) y de las ardillas rojas americanas (*Tamiasciurus hudsonicus*) cada primavera 2005-2009 en bosques mixtos de coníferas en el norte de Arizona, E.U.A. Utilizamos fotografías aéreas de alta resolución para evaluar las características de la vegetación donde se realizaron muestreos de restos de alimentación y se analizó la asociación de la frecuencia de los restos de alimentación con las características de la vegetación para comparar y contrastar el uso del hábitat por las especies. A la escala del paisaje, encontramos una considerable superposición en las características de los bosques utilizados por las dos especies de ardillas arborícolas nativas. Las ardillas rojas americanas utilizaron bosques más densos, con menos y más pequeños claros que las ardillas de Abert, mientras que las ardillas de Abert utilizaron más pino ponderosa (*Pinus ponderosa*) que las ardillas rojas americanas.

How species partition resources is a fundamental question in ecology that has dominated the field over the last century (Hutchinson, 1957; Schoener, 1974). Habitat partitioning through the differential use of habitats by species is an oft-cited explanation, with narrow habitat associations often considered to be particularly important where species with similar habitat requirements occur in close proximity (Schoener, 1968; Futuyma and Moreno, 1988). Abert's squirrels (*Sciurus aberti*) are large (~600 g) tree squirrels found in forests of the southwestern United States (Keith, 1965), often labeled a "ponderosa pine-obligate" (Dodd et al., 2006) due to reliance on the phloem of ponderosa pine (*Pinus ponderosa*) trees and because the species is found most often in forests dominated by ponderosa pines (Allred, 2011). Furthermore, modest digestive specialization has also been interpreted to support the ponderosa pine-obligate hypothesis (Murphy and Linhart, 1999). A U.S. National Natural Landmark was established in 1965 on the Kaibab Plateau on the northern rim of the Grand Canyon in Arizona for the Kaibab squirrel (*Sciurus aberti kaibabensis*), a subspecies of the Abert's squirrel, in

recognition of the general dependence on ponderosa pine forests (H. Eggleston et al., in litt.). However, Abert's squirrels are documented in other forest types (Ferner, 1974; Allred, 2011), including mixed conifer forests in the Pinaleno Mountains of southeastern Arizona (Hutton et al., 2003; Edelman and Koprowski, 2005). The population of Abert's squirrels was introduced into lower-elevation ponderosa pine forests (Davis and Brown, 1989) but has spread to higher-elevation mixed conifer and even spruce-fir (*Picea-Abies*) forests (Hutton et al., 2003). Little is known of the characteristics of mixed conifer forests used by Abert's squirrels outside the Pinaleno Mountains in natural systems where the species is native.

The North American red squirrel (*Tamiasciurus hudsonicus*) is a small (<250 g) tree squirrel found in conifer forests throughout northern North America and the Rocky Mountains of the western United States (Steele, 1998). Despite their extensive range overlap in forested environments of the western United States, Abert's and red squirrels may spatially segregate by macrohabitat (Allred, 2011). Red squirrels favor spruce-fir and, to a

lesser extent, mixed conifer forests, whereas Abert's squirrels prefer ponderosa pine (Ferner, 1974; Allred, 2011). Red squirrels use both mixed conifer and ponderosa pine forests in some parts of their range but not in others (Ferner, 1974; Patton and Vahle, 1986). However, in the Pinaleno Mountains, an isolated population of red squirrels (a federally endangered subspecies, *Tamiasciurus hudsonicus grahamensis*) competes with Abert's squirrels within mixed conifer forests (Edelman and Koprowski, 2009).

Although extensive overlap exists in microhabitat use by Abert's and red squirrels in the Pinaleno Mountains within mixed conifer forests, red squirrels use more-densely forested areas dominated by *Abies lasiocarpa* whereas Abert's squirrels use more-open forest and those that contain greater tree species diversity (Edelman et al., 2009). Herein, we discuss our examination of feeding sign of Abert's and red squirrels within the Kaibab National Forest each spring 2005–2009 in conifer forests. We used these data to document and contrast characteristics of forests used by Abert's and red squirrels in northern Arizona where both species are native.

MATERIALS AND METHODS—We surveyed feeding sign of squirrels in ponderosa pine and mixed conifer forest of the Kaibab National Forest in northern Arizona. Annual forest-wide surveys were sponsored by the Kaibab National Forest and conducted in early spring, 2005–2009, by the Rocky Mountain Bird Observatory. Data were collected in association with a study of avian community ecology by Rocky Mountain Bird Observatory (D. J. Hanni et al., in litt.). Transects ($n = 83$) ranged in length 750–3,539 m (mean = $2,883 \pm 147$ m) and were stratified by dominant vegetation type, either ponderosa pine or mixed conifer (includes Douglas-fir [*Pseudotsuga menziesii*], white fir [*Abies concolor*], blue spruce [*Picea pungens*], limber pine [*Pinus flexilis*], Engelmann spruce [*Picea engelmannii*], *A. lasiocarpa*, and spruce-fir) as determined by Kaibab National Forest stand inventory data (United States Department of Agriculture [USDA] Forest Service, 2009). Transects were oriented randomly relative to an access point near roads, and the initial survey point was located at a random distance from the access point. Transects were located >50 m apart to ensure independence. Red squirrels defend a territory of 0.2 ha minimum (Smith, C. C., 1968; Reynolds et al., 1992); a circular area of 0.2 ha is 50 m in diameter. Therefore, transects ≤ 50 m apart are likely to intersect the same individuals' defended territories and are not independent. We surveyed a subset of transects each year (total number of surveys = 160) and recorded feeding sign of squirrels within 5 m on each side of transects. Abert's sign included branch clippings and peeled twigs, and red squirrel sign included middens (piles of conifer cone scales left over from previous feeding in which red squirrels cache fresh cones). Data collected on numbers of cones and cone scales were not used because we did not distinguish Abert's and red squirrel feeding sign of this type. We counted feeding events, where each group of each type of sign was counted once per 20-m section. However, old and fresh branch cuttings could be distinguished by color of pine needles and, when detected together, were counted as separate feeding events. We pooled numbers of

feeding events for each transect and computed feeding events/kilometer surveyed. We averaged results across years for transects surveyed in more than 1 y. Feeding events/kilometer are comparable to frequency of occurrence of feeding sign (Dodd et al., 2006), which is strongly correlated with Abert's squirrel densities (Dodd et al., 2006) and red squirrel abundance (Smith, M. C., 1968; Mattson and Reinhart, 1996).

We used high-resolution aerial photographs (USDA Farm Service Agency National Agriculture Imagery Program [NAIP], 2010) and USDA Forest Service vegetation type layer (USDA Forest Service, 2009) to sample vegetation characteristics along the same transects where surveys of feeding sign were conducted. We sampled these vegetation characteristics within 10 m on each side of transect lines: proportions canopy cover, high-quality habitat, and each vegetation type present (see below). We classified 1-m-resolution 4-band NAIP images (USDA Farm Service Agency NAIP, 2010) into 2 classes (trees and ground) with a maximum likelihood-supervised classification process. Our classification procedure was somewhat unreliable in areas shaded by cliffs or outcroppings, as well as in some large meadow areas; transects in these areas were few, and each was subsequently verified for correct classification. To create a measure of canopy cover, we calculated the proportion of trees within 10 m on each side of transect lines. We identified areas with dense tree cover as high-quality habitat for both species of tree squirrels (Dodd et al., 2006; Prather et al., 2006; Merrick et al., 2007) and calculated the proportion of high-quality habitat within 10 m of transects. To identify high-quality habitat, we aggregated the classified 1-m-resolution images (trees = 1, ground = 0) into 20-m cells. We assigned mean value of component cells to the 20-m aggregated cell so that the proportion of trees for each 20-m cell was computed. We defined high-quality habitat at a threshold, where high quality was defined as ≥ 0.6 tree cover for aggregated cell value. This threshold was chosen from field experience on the Kaibab Plateau and published habitat preferences (Merrick et al., 2007; Allred, 2011). By computing both a measure of canopy cover and proportion of high-quality habitat, we can examine the effects of both tree cover and tree distribution (Fig. 1). Sampled vegetation characteristics should have remained consistent over the 5 y between the first surveys and the aerial photographs from which we sampled vegetation characteristics, except where fires have occurred. We eliminated transects where fires have occurred after feeding sign surveys were conducted and prior to aerial photography. Parameter estimates are given \pm half-width 95% confidence interval unless otherwise noted.

We identified the proportion of transect (buffered by 10 m on each side) covered by each vegetation type: ponderosa pine, mixed conifer (consolidated USFS types of Douglas-fir, white fir, and blue spruce), spruce-fir (consolidated USFS types of Engelmann spruce and *A. lasiocarpa*), grasslands, aspen (*Populus tremuloides*), pinyon-juniper (*Pinus monophylla*, *Pinus edulis*, *Juniperus monosperma*, *Juniperus osteosperma*, *Juniperus deppeana*, *Juniperus scopulorum*, consolidated USFS types of pinyon-juniper and juniper woodland), scrub (consolidated USFS types of oak woodland [*Quercus* species], treeland, and other hardwoods).

We used principal components analysis (Manly, 2005) to reduce the many habitat variables into a more interpretable number and because some of the variables covaried. We used multiple logistic regression to assess association of mean feeding sign for all years on each transect to the principal components

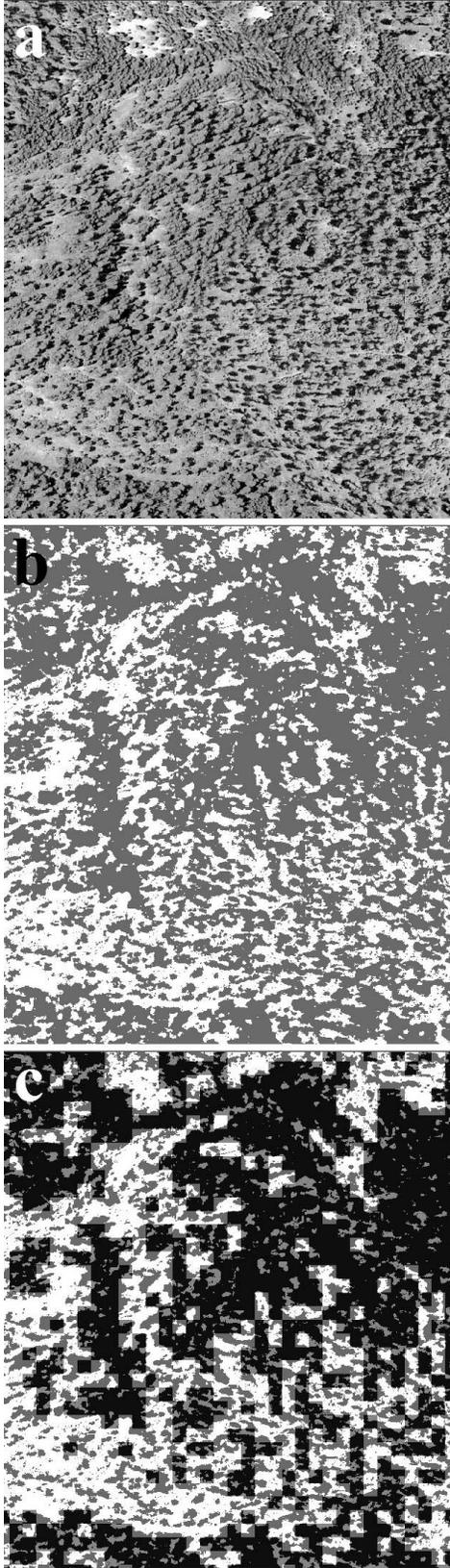


FIG. 1—Vegetation characteristics for analysis of Abert's squirrel (*Sciurus aberti*) and red squirrel (*Tamiasciurus hudsonicus*) use of forests. Grayscale representation of high-resolution 4-band National Agriculture Imagery Program images from 2010

and used an information theoretic approach emphasizing Akaike's Information Criterion (AIC) values for model selection (Burnham and Anderson, 2002). Because feeding sign of tree squirrels varies temporally and because not all transects were surveyed in all years, we used the mean feeding sign for all years as response variables. All transects surveyed, including those with feeding sign = 0, were analyzed in the regressions for each species. To partially correct for data skew detected by visual examination of data distributions, we log transformed the habitat quality and feeding sign data.

RESULTS—Feeding sign of squirrels was found on 79 of 83 transects (95%). Abert's feeding sign was found on 75 transects (90%), red squirrel feeding sign was found on 39 transects (47%), and both were found on 35 transects (42%). The percentage of ponderosa pine vegetation surrounding transects ranged 0–100% (mean = $56.9 \pm 9.1\%$). The percentage of spruce-fir vegetation ranged 0–99.7% (mean = $14.2 \pm 5.5\%$). While at least one transect was almost entirely mixed conifer (96.0%) or grass (86.2%), these vegetation types averaged $14.8 \pm 5.5\%$ and $3.1 \pm 2.4\%$, respectively. Aspen, scrub, and pinyon-juniper vegetation occupied 55.9%, 44.2%, and 54.4%, respectively, of at least one transect but averaged only $6.9 \pm 2.6\%$, $2.1 \pm 1.7\%$, and $2.0 \pm 1.8\%$, respectively. The proportion of tree cover for all transects ranged 0.23–0.96 (mean = 0.69 ± 0.03) and proportion of high-quality habitat ranged 0–0.97 (mean = 0.68 ± 0.05). On transects where Abert's squirrel feeding sign was found, the proportion tree cover ranged 0.25–0.96 (mean = 0.71 ± 0.03) and proportion high-quality habitat ranged 0.07–0.97 (mean = 0.70 ± 0.04). On transects where red squirrel feeding sign was found, the proportion tree cover ranged 0.44–0.89 (mean = 0.73 ± 0.03) and proportion high-quality habitat ranged 0.27–0.97 (mean = 0.75 ± 0.05). Neither the proportion tree cover nor the proportion high-quality habitat differed between transects on which Abert's feeding sign was found and transects on which red squirrel feeding sign was found ($t_{112} = 0.87$, $P = 0.39$, and $t_{112} = 1.31$, $P = 0.19$, respectively).

The first three principal components (PCs) accounted for nearly all variation (Table 1). PC1 generally characterized tree cover and distribution while PC2 generally characterized vegetation type. Values of PC1 presented a continuum from a few trees with gaps at low values to many trees evenly distributed at high values. PC2 values presented a continuum from ponderosa pine at low values to spruce-fir at high values. Although the proportion of mixed conifer vegetation was not included in PC2, mixed conifer vegetation does fall within the continuum

←

(a); Classification into trees (gray) and ground (white) to characterize tree cover (b); high-quality habitat for both species darkened, as defined as ≥ 0.6 tree cover within aggregated 20-m cells (c). Kaibab National Forest, Coconino County, Arizona, USA.

TABLE 1—Factor loadings for principal component (PC) analysis; all variables are proportions computed for the area 10 m on each side of transects of feeding sign surveys of Abert's (*Sciurus aberti*) and red squirrels (*Tamiasciurus hudsonicus*), Kaibab National Forest, Coconino County, Arizona, USA, 2005–2009.

Vegetation variable (proportions)	PC1	PC2	PC3	PC4
Tree cover	0.69	−0.16	0.18	−0.68
High-quality habitat (inverse)	−0.69	0.13	0.20	−0.68
Ponderosa pine	−0.14	−0.70	0.68	0.20
Spruce-fir	0.15	0.69	0.68	0.18
Proportion of variance	0.479	0.418	0.084	0.019
Cumulative proportion	0.479	0.897	0.981	1.000

of vegetation type. The proportion of mixed conifer is inversely correlated to the proportion of ponderosa pine plus the proportion spruce-fir (Pearson's correlation coefficient $r = -0.79$, $t_{81} = -11.51$, $P < 0.001$) and was unnecessary to include in the PCA. Mixed conifer forests as well as grass meadows, aspen forests, and scrub are better represented in PC3, where high values represent a high proportion of ponderosa pine or spruce-fir and low values represent low proportions of ponderosa pine or spruce-fir and high proportions of other vegetation types. PC4 represented primarily a measure of tree cover and habitat quality; a transect having high tree cover but a low proportion of high-quality habitat had a low PC4 value, and a transect with low tree cover but a high proportion of high-quality habitat had a high PC4 value.

Using the best-performing model, mean feeding sign of Abert's squirrels for all years was associated with PC1 and PC2 (multiple linear regression, whole model $F_{2,78} = 11.28$, $P < 0.001$, $r^2 = 0.22$, $AIC_c = 85.10$, Table 2), with increased feeding sign associated with increased tree cover and more high-quality habitat (effect likelihood ratio test, $F_{1,79} = 18.17$, $P < 0.001$) and more ponderosa pine vegetation (effect likelihood ratio test, $F_{1,79} = 4.99$, $P = 0.03$). Two other models could also be considered because their $\Delta AIC_c \leq 2$. These top-performing models included PC1 and PC2 and differed only in whether PC3 or PC4 was included (Table 2).

Using the best-performing model, mean feeding sign of red squirrels for all years was associated with PC1 and PC2 (multiple linear regression, whole model $F_{2,80} = 11.28$, $P < 0.001$, $r^2 = 0.35$, $AIC_c = 91.12$; Table 2), with elevated feeding sign associated with more tree cover and increased high-quality habitat (effect likelihood ratio test, $F_{1,81} = 13.50$, $P < 0.001$) and more spruce-fir vegetation (effect likelihood ratio test, $F_{1,81} = 30.50$, $P < 0.001$). Two other models could also be considered because their $\Delta AIC_c \leq 2$. These top-performing models included PC1 and PC2 and differed only in whether PC3 or PC4 was included (Table 2).

The strength of the effect of PC1 (more tree cover and

TABLE 2—Model selection statistics and performance measures for models using multiple linear regression to explain associations of Abert's (*Sciurus aberti*) and red squirrel (*Tamiasciurus hudsonicus*) feeding sign to vegetation characteristics represented by principal components (PC) 1–4, Kaibab National Forest, Coconino County, Arizona, USA, 2005–2009. Models with $\Delta AIC_c > 7$ are not shown.

Model	K ^a	AIC ^b	AIC _c ^c	ΔAIC_c ^d	w_i ^e	R ²
Abert's squirrels						
PC1 and 2	2	85.05	85.100	0.000	0.306	0.22
PC1, 2, and 3	3	85.12	85.272	0.172	0.281	0.24
PC1, 2, and 4	3	86.81	86.962	1.862	0.121	0.23
PC1, 2, 3, and 4	4	86.97	87.278	2.178	0.103	0.24
PC1 and 3	2	87.43	87.480	2.380	0.093	0.20
PC1	1	88.07	88.070	2.970	0.069	0.17
PC1, 3, and 4	3	89.4	89.552	4.452	0.032	0.20
PC1 and 4	2	90	90.050	4.950	0.025	0.18
Red squirrels						
PC1 and 2	2	91.07	91.120	0.000	0.494	0.35
PC1, 2, and 3	3	92.62	92.772	1.652	0.216	0.36
PC1, 2, and 4	3	92.77	92.922	1.802	0.201	0.36
PC1, 2, 3, and 4	4	94.32	94.628	3.508	0.085	0.36

^a K = number of parameters.

^b AIC = Akaike's Information Criterion values.

^c AIC_c = Akaike's Information Criterion values corrected for small samples.

^d ΔAIC_c = AIC_c relative to the most-parsimonious model.

^e w_i = AIC model weight.

more high-quality habitat) on mean feeding sign was about the same for Abert's and red squirrels (parameter estimates for PC1 = 0.57 and 0.50, respectively). However, the effect of vegetation type (ponderosa pine for Abert's and spruce-fir for red squirrels) was stronger for red squirrels than for Abert's squirrels (parameter estimate for PC2 = 0.80 for red squirrels and PC2 = −0.34 for Abert's squirrels).

While Abert's squirrel feeding sign was found primarily on ponderosa pine-dominated transects represented by low PC2 values and somewhat more heavily (larger bubble size in Fig. 2) on transects with many trees and few gaps represented by high PC1 values, feeding sign of Abert's squirrels was found on transects throughout a wide variety of vegetation type, tree cover, and distribution. Red squirrel feeding sign was found on transects dominated by ponderosa pine or by spruce-fir or in-between these two extremes on transects dominated by mixed conifer. This variation represented the full range of PC2 values. However, little feeding sign of red squirrels was found on transects with low PC1 values, those with few trees or large gaps.

DISCUSSION—Abert's and red squirrels used conifer forests throughout a wide spectrum of conifer vegetation types, tree cover, and tree distribution. At the landscape level, overlap in use of forests by red and Abert's squirrels

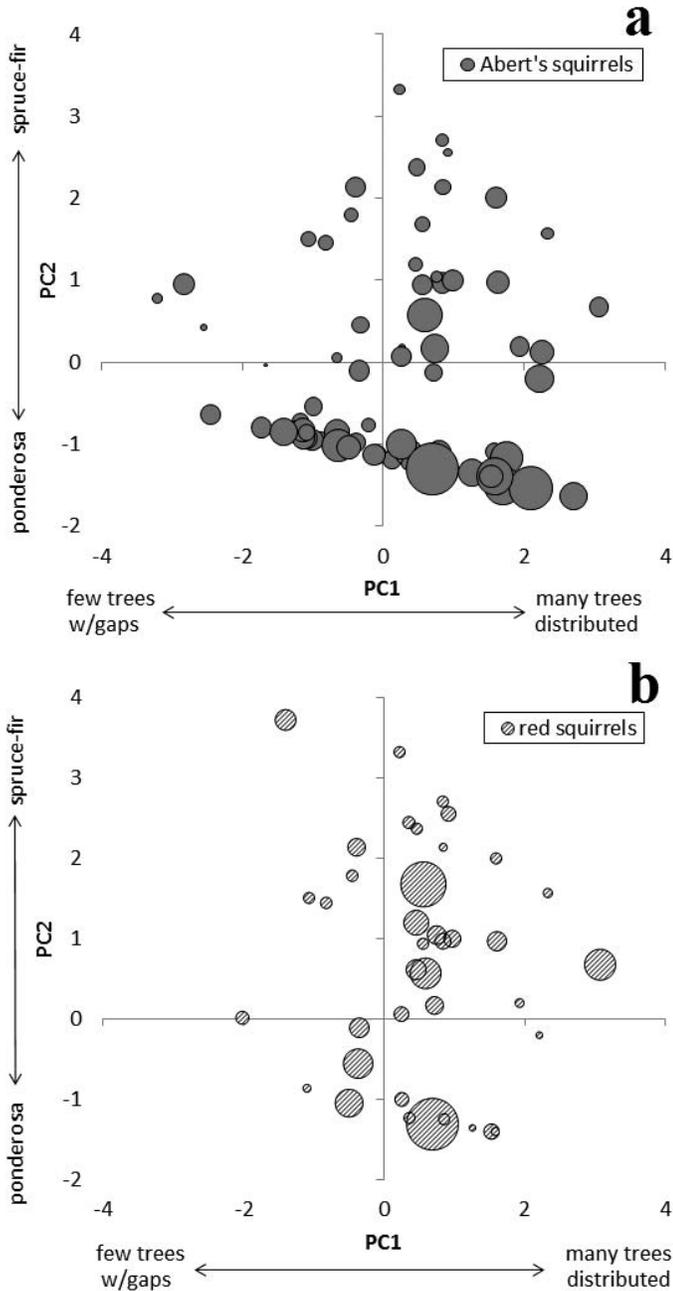


FIG. 2.—Mean feeding sign (scaled) of Abert's, *Sciurus aberti* (a) and red squirrels, *Tamiasciurus hudsonicus* (b) for each transect relative to principal component (PC) PC1 (x-axis) and PC2 (y-axis). Bubble size represents value of scaled mean feeding sign. Kaibab National Forest, Coconino County, Arizona, USA, 2005–2009.

was high; we found sign of both species on 42% of transects. However, red squirrels used denser forests with fewer and smaller gaps than did Abert's squirrels, and red squirrel feeding sign was more-evenly distributed throughout the continuum of spruce-fir to ponderosa pine vegetation types than was Abert's squirrel feeding sign. Abert's squirrels used more ponderosa pine than did red squirrels but commonly used spruce-fir forests as well

as other forests types. Abert's squirrel feeding sign was more-evenly distributed throughout the continuum of tree cover and distribution than was red squirrel feeding sign.

A notable difference between forest use by Abert's squirrels and red squirrels was the minimum proportions of tree cover and high-quality habitat used. Abert's squirrels fed in forests with a lower percentage tree cover ($\geq 25\%$) than did red squirrels ($\geq 44\%$) and in forests with lower percentage high-quality habitat ($\geq 7\%$) than did red squirrels ($\geq 27\%$). Abert's squirrels are known to use open forests with low tree density and sparse undergrowth (Dodd et al., 2006; Edelman et al., 2009). Although the mean proportions of tree cover and high-quality habitat for forests where Abert's and red squirrels fed were only slightly higher than for all transects surveyed, the minimums suggest thresholds for both species of tree squirrel, and the thresholds were lower for Abert's squirrels than for red squirrels. In mixed conifer forests in southern Arizona, introduced Abert's squirrels use more-open forest with greater tree species diversity for nesting sites than do native red squirrels (Edelman et al., 2009).

Absolute differences in feeding sign frequencies for the two species can be attributed at least partially to the types of feeding sign used in these surveys. Red squirrels each defend a single midden and there is little or no sharing of middens during the winter–spring season (Steele, 1998). Abert's squirrels exploit only a subset of trees for phloem to eat, but each squirrel must visit many trees, which may be spaced widely apart (Snyder, 1992). Both types of feeding sign are easily detected in spring; therefore, there should be no difference in detectability for each feeding “event” of each species. But the likelihood of a transect intersecting at least one of the many feeding trees per Abert's squirrel is higher than for one midden per red squirrel; therefore, the detectability of species may differ even if the detectability of feeding sign does not. Both types of feeding sign, however, are used as an index for population density and analyzed separately by species to address these concerns.

Thinning forests mechanically, using prescription burns, or a combination are used by forest managers to restore forests to healthier and more fire-resilient condition after decades of fire suppression (Covington et al., 1997; Agee and Skinner, 2005). Recruitment and survival of Abert's squirrels is inversely associated with numbers of small, sapling-sized (2.5–12.4-cm diameter at breast height) trees, suggesting that removal of small trees may be important for Abert's squirrels (Dodd et al., 2006). Red squirrels may decrease after fuels-reduction thinning (Bull and Blumton, 1999), but short-term population densities may not change after low-severity prescription fire that retains large-diameter trees (Russell et al., 2010). Overall, due to the thresholds of tree cover and high-quality habitat presented herein, fuel-reduction

treatments necessary for forest health and resiliency may favor Abert's squirrels over red squirrels in forests where they co-occur, but a forest mosaic that retains areas of high canopy cover should reduce impacts to both species (Prather et al., 2006). Previous studies show that high-quality habitat for Abert's squirrels has a canopy cover >50% (Dodd et al., 2003), and analysis suggests that maintaining a threshold at or above 24–42% of high-quality habitat may be important for Abert's squirrels (Dodd et al., 2006). Red squirrels tend to be found in areas with >70% canopy cover and high stem densities (Vahle and Patton, 1983; Patton and Vahle, 1986; Merrick et al., 2007; Edelman et al., 2009).

Although Abert's squirrel winter feeding sign was associated with ponderosa-pine vegetation and red squirrel feeding sign was associated with spruce-fir vegetation, feeding sign of both species was found on transects throughout the continuum of vegetation types. In addition, the association of red squirrel feeding sign to vegetation type was stronger than for Abert's squirrels. Our vegetation data represent map categories for vegetation, and there are likely many individual, and clusters of, ponderosa pine trees within mixed conifer forest and, to a lesser extent, spruce-fir forest. Abert's squirrels clearly use areas that are classified as mixed conifer and spruce-fir as well as other vegetation types. Introduced Abert's squirrels in the Pinaleno Mountains of southeastern Arizona live in mixed conifer forest with as little as 2% ponderosa pine (Hutton et al., 2003; Edelman and Koprowski, 2005). Abert's squirrels are known to occur in a diversity of habitats from high-elevation alpine meadows to low-elevation pinyon pine (Allred, 2011), suggesting that the species is not as restricted in habitat use as previously described (Edelman and Koprowski, 2009). Because Abert's squirrels commonly use higher-elevation mixed conifer and even spruce-fir forests, and because climate models predict that ponderosa pine may expand its range into higher elevations (Rehfeldt et al., 2006), forest managers may consider including some areas of higher-elevation forests in management plans for the Kaibab squirrel as well as the other subspecies of Abert's squirrels. For instance, The Kaibab Squirrel Area National Natural Landmark currently excludes most mixed conifer and spruce-fir forests on the Kaibab Plateau. In addition, forest-thinning policies should include considerations of threshold minimums for tree cover and proportion of high-quality habitat (Vahle and Patton, 1983; Dodd et al., 2006) for forest used by tree squirrels. Planning for posttreatment forest structure heterogeneity within specific vegetation cover types could benefit tree squirrels as well as other wildlife species.

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