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COMPOSITION OF CAVITY-NESTING BIRD COMMUNITIES IN MONTANE ASPEN WOODLAND FRAGMENTS: THE ROLES OF LANDSCAPE CONTEXT AND FOREST STRUCTURE

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Abstract. We compared cavity-nesting bird communities in aspen (*Populus tremuloides*) woodland fragments classified on the basis of vegetation structure (tree density) and landscape context (surrounding vegetation). We found very few cavity nesters in fragments predominantly surrounded by forests. Fragments adjacent to meadows contained more species and a greater abundance of cavity nesters. Species richness and abundance were higher in sparsely than in densely treed meadow fragments. Because secondary cavity nesters are often limited by cavity availability, we aug-

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mented natural cavities with nest boxes. Although only five boxes contained bird nests, these were all in sparse aspen fragments predominantly surrounded by meadows. However, we found 25 northern flying squirrel (*Glaucomys sabrinus*) nests in boxes, none of which were in sparse meadow fragments. In addition to highlighting the importance of landscape context in avian and mammalian habitat relationships, our results suggest that predator or competitor interactions may help structure this cavity-nester community.

Key words: cavity-nesting birds, community composition, Glaucomys sabrinus, *habitat selection, landscape, northern flying squirrel, vegetation structure.*

Composición de las Comunidades de Aves que Nidifican en Cavidades en los Fragmentos de Bosque Montano de Álamo: El Papel del Contexto del Paisaje y la Estructura del Bosque

Resumen. Comparamos comunidades de aves que nidifican en cavidades en fragmentos de bosque de álamo (*Populus tremuloides*) clasificados en base a la estructura de la vegetación (densidad de árboles) y al contexto del paisaje (vegetación circundante). Encontramos muy pocas aves que nidifican en cavidades en los fragmentos rodeados predominantemente por bosque. Los fragmentos adyacentes a prados presentaron más especies y mayor abundancia de aves. La riqueza y la abundancia de especies fueron mayores en fragmentos con baja densidad de árboles que estuvieron rodeados por prados. Debido a que las aves que nidifican en cavidades secundarias están a menudo limitadas por la disponibilidad de cavidades, aumentamos las cavidades naturales con cajas de anidaje. Aunque solamente cinco cajas contuvieron nidos de aves, éstas estuvieron todas en los fragmentos con baja densidad de álamos rodeados predominantemente por prados. Sin embargo, encontramos 25 nidos de ardillas voladoras norteñas (*Glaucomys sabrinus*) en las cajas de anidaje, de las cuales ninguna estuvo en fragmentos con baja densidad de árboles rodeados por prado. Nuestros resultados destacan la importancia del contexto del paisaje en las relaciones entre el hábitat y las aves y mamíferos, y sugieren que las interacciones con depredadores o competidores pueden influenciar la estructura de la comunidades de aves que anidan en cavidades.

Of the many factors shaping avian communities, species-habitat associations form the coarsest filter of community assembly (Wiens 1989). Such associations define the pool of potential predators, prey, competitors, and facilitators that determine species composition and abundance. Traditionally, studies of avian habitat have been conducted at relatively fine spatial scales, linking foraging or nesting habitat with the composition and structure of vegetation (Cody 1985). More recently, birds have been found to be associated with patterns of vegetation at coarser spatial scales (Freemark et al. 1995, Saab 1999). For example, the abundance of birds in some environments has been linked to the shapes of habitat patches and the types of patch edges (Hawrot and Niemi 1996). Likewise, nesting success has been found to be associated with patch location (Wilcove 1985) and the distance to a patch edge (Flaspohler et al. 2001). Thus, community composition is potentially influenced by patterns of vegetation both within and surrounding forest stands or fragments.

Cavity-nesting birds are a major component of the aspen-forest (*Populus tremuloides*) bird community in the western United States (Salt 1957, Dobkin et al. 1995). At relatively fine spatial scales, the abundance, species richness, and nest-site locations of several species of cavity nesters are associated with sparse forests and open understories (Flack 1976, Brawn 1988), large trees (Harestad and Keisker 1989), high densities of snags (Raphael and White 1984), tall canopies (Gutzwiller and Anderson 1987), and trees with heart rot and fungal infections (Daily 1993). At coarser spatial scales, cavity nesters may be associated with landscape patterns. Northern Flickers (*Colaptes auratus*), Tree Swallows (*Tachycineta bicolor*), Mountain Bluebirds (*Sialia currucoides*), and House Wrens (*Troglodytes aedon*), for example, are edge-associated species (Conner and Adkisson 1977, Rendell and Robertson 1990).

Although habitat associations may provide the basic components for the assembly of cavity-nesting communities, the forces of facilitation of and competition for nest sites can have strong effects on community composition (van Balen et al. 1982). Primary cavity-nesting birds (those that excavate their own cavities) often play the essential role of creating cavities that are then used by secondary cavity nesters (nonexcavators, or cavity adopters). Competition for cavities can limit cavity-nester populations (von Haartman 1957). Some species, such as the House Wren (a bird that often fills several cavities with ''dummy nests'') can exert strong competitive forces (Brawn and Balda 1988). In addition, several nonavian species also play roles in structuring the cavity-nester community. Northern flying squirrels (*Glaucomys sabrinus*) have been found to be a component of cavity-nester communities in some western aspen forests (Peterson and Gauthier 1985). Because they nest in cavities and because squirrels are nest predators (Martin 1988), flying squirrels may be both competitors and predators of cavity-nesting birds.

We investigated the relationship between patterns of vegetation at two spatial scales and the composition and abundance of breeding cavity-nesting birds. At a relatively fine spatial scale, we asked whether community composition was related to tree density. At a coarser spatial scale, we investigated the relationship between bird community composition and landscape context (i.e., the type of vegetation surrounding an aspen woodland fragment). We used a 2 × 2 factorial design to classify aspen fragments into four groups: (1) densely treed and in a meadow context; (2) dense and in a forested context; (3) sparsely treed and in a meadow context; and (4) sparse and in a forested context. We located six fragments of each type and compared standard-sized plots within each in terms of the abundance and species composition of breeding cavity-nesting birds. Because nest-site selection by secondary cavity nesters can be limited by cavity availability, we augmented all fragments with nest boxes to determine if the four types of fragments were selected differentially by secondary cavity nesters.

METHODS

The study was conducted in the Wasatch National Forest on the north slope of the Uinta Mountains in northeastern Utah. This area is dominated by sagebrush (*Artemisia* spp.) steppe at lower elevations (to ~2500 m), lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), and quaking aspen at intermediate elevations (~2500 to 3050 m), and subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) at higher elevations (~3050 m to 3350 m). All of our study plots were between approximately 2750 m and 3050 m elevation. Although there are some extensive stands of aspen (>600 ha) along the north slope of the Uinta Mountains, much of the aspen forest consists of small fragments (<20 ha) surrounded by either sagebrush and grass meadows, or conifer forest.

We used a digital vegetation map in a geographic information system (GIS) to select aspen fragments in meadow and forest contexts. The map had 30-m resolution and was created from Landsat Thematic Mapper satellite imagery (Lawler and Edwards, in press). Because we were unable to find enough fragments that were completely surrounded by either meadow or conifer forest, we classified fragments into the two most distinct groups possible. We defined meadow fragments as those with >50% of their edge bordering a meadow and forested fragments as having <10% of their edge bordering a meadow. After choosing the aspen fragments with the GIS, we visited them and characterized them as sparsely or densely treed. Sparse fragments had <1250 stems ha^{-1} and dense fragments had >1250 stems ha^{-1}.

Although we standardized for tree density and the type of landscape directly surrounding the aspen fragments, we were unable to control for several other characteristics of the fragments that could influence nest-site selection. First, we could not totally control for the size of fragments. We addressed this issue in two ways. First, we used standard-sized plots (1–1.12 ha) within each fragment to assess the abundance and composition of breeding cavity nesters. Second, we compared the area of aspen within a fixed distance of the fragments. We used a GIS to measure the area of aspen contained within a 26-ha area centered on the plots placed in each fragment. With the exception of Tree Swallows that may range several kilometers when foraging (Robertson et al. 1992), a 26-ha plot should encompass the area used by most cavity-nesters in our study during the breeding season (Laudenslayer and Balda 1976, Evans and Conner 1979).

Because tree density is closely associated with tree size we compared the number of large trees (trees >23 cm in diameter at breast height [dbh]) in each of the four types of fragments. We chose 23 cm as a cutoff because we had observed that cavity nesters generally nested in trees at least this big on the north slope of the Uinta Mountains. We also measured six other fragment characteristics including canopy height, tree condition (the percentage of rotten wood in a tree core taken at breast height), distance to nearest stream, slope, aspect, and the number of snags in each plot. Finally, we measured and compared tree density and the area of meadow within a 26-ha area centered on the plot. These last two measures assessed the effectiveness of our classification of the stands as dense or sparse and in meadow or forested contexts. We used ten 0.04-ha plots per fragment to assess canopy height, tree condition, tree density, and the number of snags and large trees in each aspen fragment (Lawler 1999).

We placed 120 nest boxes in 12 aspen fragments (10 boxes per fragment, three fragments per category) in 1997. Because sample sizes in 1997 were low, we added another 120 boxes in 12 additional fragments in 1998. Boxes were placed approximately 20 m apart, in grids that varied slightly in configuration depending on the shape of the fragment. We affixed boxes 2 m off the ground to randomly selected trees with the entrance facing east to standardize for entrance orientation. We used the area defined by the nest boxes as the plot, in which we searched for all nests and cavities. Plot areas for the four types of fragments are reported in Table 1.

We searched each of the plots for nests of cavity-nesting birds in natural cavities four times between 1 June and 15 August in 1997 and 1998. We followed birds to cavities and used adult behavior (e.g., frequency of visits, cavity occupancy, and food provisioning) or the presence of nestlings to assess whether the cavity contained an active nest. At the end of the breeding season, we measured several aspects of trees containing nests (tree height, dbh, percent rot, and live vs. dead).

We checked all boxes at least once per week from 1 June to 15 August in both years of the study. In addition, we checked the boxes two times during the summer of 1999 to determine whether box occupancy increased over a three-year period. We counted a pair of birds as nesting in a box only if eggs were laid. Although the study spanned two years, we analyzed data collected in only the first year that each plot was established, to exclude nests built by the same birds in consecutive years.

To assess the availability of natural cavities, we searched the plots for all cavities. The number of cavities in the plots changed only slightly over the two-year period (three new cavities were excavated in 1998, and no cavities were lost to fallen trees). Because we did not climb trees, we were unable to inspect cavities >2 m off the ground. Thus, it is possible that we overestimated the number of cavities in each plot by counting some holes that could not be used for nesting.

STATISTICAL ANALYSES

We used log-linear models (Fienberg 1980) to test for associations between landscape context and forest structure and both the number of nests in natural cavities and the number of cavities in each plot. We used analysis of variance (ANOVA; SAS Institute, Inc. 2001) to test for associations between our two variables of interest (landscape context and forest structure) and five of the additional 10 variables measured at each plot including plot size, slope, area of surrounding meadow, area of surrounding aspen forest, and the distance to the nearest stream. We used nested

TABLE 1. Characteristics of 24 aspen woodland fragments in the Uinta Mountains, Utah, classified by both forest structure (densely or sparsely treed) and the surrounding landscape composition (meadow or forest). Values are means ± SD of six replicate fragments. Values followed by the same lowercase letter were not significantly different ($P < 0.05$) in unplanned comparisons using Tukey's adjustment for multiple tests.

Fragment characteristics	Fragment type				ANOVA ($F_{3,20}$)
	Dense meadow	Sparse meadow	Dense forested	Sparse forested	
Tree density (trees ha^{-1})	2550 ± 1275 a	750 ± 550 b	3150 ± 1050 c	1000 ± 525 d	133.3[a]***
Slope (%)	9 ± 5 a	10 ± 6 a	24 ± 10 b	14 ± 8 a	11.2***
Meadow area (ha)	9.4 ± 3.7 a	11.6 ± 2.8 a	4.0 ± 1.7 b	2.7 ± 2.3 b	14.4***
Trees >23 cm dbh (trees ha^{-1})	109 ± 123 a	150 ± 143 ab	36 ± 42 c	195 ± 122 b	27.6[a]***
Snags ha^{-1}	82 ± 128 a	66 ± 86 a	63 ± 75 a	119 ± 87 b	8.7[a]***
Canopy height (m)	13 ± 4 a	13 ± 4 a	16 ± 4 b	19 ± 5 c	24.7[a]***

***$P < 0.001$.

[a] Nested analysis of variance was performed on subsamples taken within plots.

ANOVA to compare tree density, canopy height, tree condition, and the number of snags and large trees in each of the four types of aspen fragments. Because we performed 10 ANOVAs, we used a Bonferroni-adjusted alpha level of 0.005 to determine which variables differed significantly across stand types. We then performed unplanned comparisons with Tukey's adjustment for multiple comparisons for those variables with significant differences. All values reported are means ± SD.

RESULTS

Although we selected aspen fragments based on landscape context and tree density, the four types of fragments also differed with respect to a number of other characteristics (Table 1). Mean plot size (1.1 ± 0.1 ha) and the area of aspen forest within 26 ha (11.1 ± 4.4 ha) did not differ systematically among fragment types. Dense forest fragments were on steeper slopes and had fewer large trees than the other types of fragments. Although dense fragments in general had fewer large trees than sparse fragments, the number of large trees in sparse and dense meadow fragments did not differ. Sparse forested fragments had taller canopies and more snags than other types of fragments.

We found a total of 40 nests belonging to eight species of cavity-nesting birds in natural cavities in the 24 plots (Fig. 1). Primary cavity nesters included Red-naped Sapsuckers (*Sphyrapicus nuchalis*), Northern Flickers, and Red-breasted Nuthatches (*Sitta canadensis*). Secondary cavity nesters included Mountain Chickadees (*Poecile gambeli*), Tree Swallows, Mountain Bluebirds, House Wrens, and Northern Saw-whet Owls (*Aegolius acadicus*). The sparse meadow fragments contained the most birds (26 nesting pairs) and the highest species richness (six species). By contrast, dense forested fragments contained only one nesting pair.

Overall, more birds nested in meadow (37 pairs) than forested fragments (3 pairs; scaled deviance $D = 34.1$, df = 1, $P < 0.001$). Only three species (Northern Saw-whet Owls, Red-breasted Nuthatches, and Mountain Chickadees) were found in the forested fragments. In meadow fragments, more nests were found in sparse than in dense fragments ($D = 6.6$, df = 1, $P = 0.01$). This difference was driven largely by the nesting patterns of Mountain Bluebirds, Tree Swallows, and Northern Flickers, which all nested in higher abundances in the sparser fragments (Fig. 1).

In general, birds that nested in natural cavities selected nest trees that were greater than 23 cm dbh (25 ± 5 cm) and showed some sign of rot (74% ± 24%). Although only 22% of all nests were built in snags (five chickadees, two sapsuckers, one bluebird, and one nuthatch), birds selected snags more often than predicted by relative snag abundance ($\chi^2_1 = 21.6$, $P < 0.001$). Nest-tree heights ranged from 3.7 to 24.8 m (12.5 ± 4.9 m).

We found a total of 271 cavities in the 24 plots. The majority of these cavities (238) were in meadow fragments, with sparse meadow fragments containing the most cavities overall (135). Sparse forested fragments had 25 cavities, and dense forested fragments had eight. The abundance of cavities was associated with

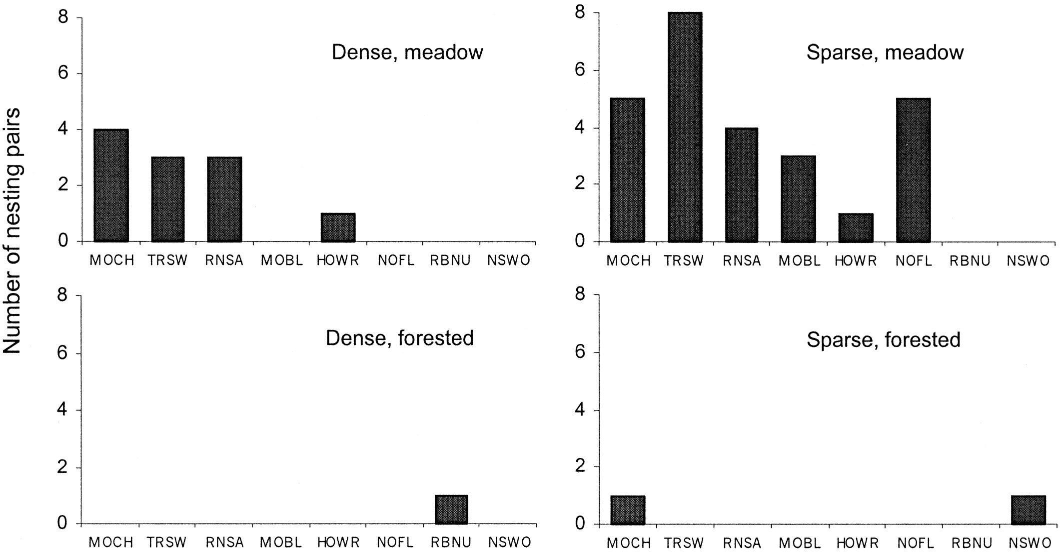

FIGURE 1. Numbers of nests of all species of cavity-nesting birds nesting in natural cavities in each of four types of aspen fragments in the Uinta Mountains of Utah. Species are Mountain Chickadee (MOCH), Tree Swallow (TRSW), Red-naped Sapsucker (RNSA), Mountain Bluebird (MOBL), House Wren (HOWR), Northern Flicker (NOFL), Red-breasted Nuthatch (RBNU), and Northern Saw-whet Owl (NSWO).

the four types of aspen fragments, evidenced by a significant interaction between landscape context and tree density in the log-linear model ($D = 4.6$, df = 1, $P = 0.03$). The number of nests of both primary and secondary cavity-nesting birds in each plot was positively correlated with the number of cavities in each plot ($r_s = 0.74$, $P < 0.001$; $r_s = 0.48$, $P < 0.02$, respectively). Furthermore, secondary cavity-nester abundance did not differ from the numbers predicted by the availability of cavities ($\chi^2_1 = 2.3$, $P = 0.13$).

Four Tree Swallow pairs and one Mountain Bluebird pair laid eggs in five nest boxes in three aspen fragments (all were sparse meadow fragments). Box occupancy did not increase over the three years that the boxes were available. Northern Flying Squirrels nested in three nest boxes (all in dense forested fragments) the first year that the boxes were available. In the second year, squirrels nested in a total of 22 boxes, and there was no further increase the third year. Twelve of the 22 nests (from the second year) were in dense forested fragments, and no squirrels nested in sparse meadow fragments. Six squirrel nests were in dense meadow fragments and four were in sparse forested fragments.

DISCUSSION

The most striking result of the present study was the overall lack of cavity-nesting birds in aspen fragments predominantly surrounded by conifer forest. The most parsimonious explanation for the selection of aspen fragments in meadow contexts centers on the use of multiple habitat types by several species of cavity nester. Tree Swallows are aerial insectivores that often forage over open meadows and riparian areas, and Northern Flickers and Mountain Bluebirds forage predominantly in meadows. Red-naped Sapsuckers use a variety of food resources including willow bark, insects, and tree sap. These birds might nest on or near meadow edges to reduce commute time between nesting and feeding habitat (Dobkin et al. 1995). Although access to multiple resources is likely to play a significant role in shaping the composition of cavity-nester communities in the Uinta Mountains, this hypothesis does little to explain the distribution of Mountain Chickadees (arboreal leaf and bark gleaners) among the four types of fragments in our study.

The conspicuous difference in the types of aspen fragments used by flying squirrels and the majority of the cavity-nesting birds in our study suggests at least one additional hypothesis for the selection of fragments in meadow contexts. Although northern flying squirrels have been found to nest or den in cavities in aspen trees (Peterson and Gauthier 1985), they are usually associated with conifer forests, particularly with dense vegetation (Cotton and Parker 2000). These general associations may help explain the tendency for the squirrels in our study to nest in dense stands and stands predominantly surrounded by coniferous forest. Thus the apparent divergence in habitat use by the birds and the squirrels may reflect unrelated responses to different proximate habitat cues. However, because squirrels are known predators of cavity nests (Martin 1988, Purcell and Verner 1999), and because flying squirrels nest in cavities, these squirrels may play the dual role of predator and competitor of some cavity-nesting birds. Determining if competitive exclusion or predator avoidance plays a role in structuring these cavity-nester communities clearly requires further investigation.

Although we classified aspen fragments by tree density and landscape context, the four types of fragments differed with respect to other structural and landscape-related characteristics as well. Most notably, some dense forested fragments tended to be in ‘‘snowpockets,’’ areas high on protected slopes that tend to retain snow. Dobkin et al. (1995) showed that cavity nesters tended to avoid aspen snowpocket woodlands, potentially due to the lack of large trees and cooler, moister microclimates. Although cavity nesters in our study may have avoided some dense forested fragments for these reasons, the absence of most birds from sparse forested fragments cannot be explained by tree sizes or microclimates.

In the Uinta Mountains, Red-naped Sapsuckers and Northern Flickers are the most abundant woodpeckers and, as primary cavity nesters, likely produce the bulk of the nesting cavities available to secondary cavity-nesting birds (Raphael and White 1984, Dobkin and Wilcox 1986). The fact that abundance of secondary cavity nesters was correlated with cavity availability implies that the composition of the community may largely reflect the habitat associations of sapsuckers and flickers. We noted that Mountain Bluebirds tended to nest more frequently in cavities created by Northern Flickers, and Tree Swallows in cavities created by Red-naped Sapsuckers. These observations agree with those made by Dobkin et al. (1995), who studied a similar bird community in aspen forests of southeastern Oregon.

Studies of avian habitat have only recently begun to include patterns and processes at relatively coarse spatial scales. Our results stress the importance of considering landscape context in the study of both avian and mammalian habitat selection and community composition. Furthermore, the differential use of habitat by the birds and squirrels in our study highlights the need to consider the influence of competition and predation on these and other landscape correlates of community composition.

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