AVIAN CONSERVATION
& ECOLOGY

VOLUME 13, ISSUE 1, ARTICLE 18

Scholer, M. N., M. Leu, and J. R. Belthoff. 2018. Patterns of co-occurrence in woodpeckers and nocturnal cavity-nesting owls within an Idaho forest. *Avian Conservation and Ecology* 13(1):18. https://doi.org/10.5751/ACE-01209-130118

Research Paper

Patterns of co-occurrence in woodpeckers and nocturnal cavity-nesting owls within an Idaho forest

Micah N. Scholer[1], *Matthias Leu*[2] and *James R. Belthoff*[1]
[1]Department of Biological Sciences and Raptor Research Center, Boise State University, Boise, Idaho, USA, [2]Biology Department, College of William and Mary, Williamsburg, Virginia, USA

ABSTRACT. Few studies have examined the patterns of co-occurrence between diurnal birds such as woodpeckers and nocturnal birds such as owls, which they may facilitate. Flammulated Owls (*Psiloscops flammeolus*) and Northern Saw-whet Owls (*Aegolius acadicus*) are nocturnal, secondary cavity-nesting birds that inhabit forests. For nesting and roosting, both species require natural cavities or, more commonly, those that woodpeckers create. Using day and nighttime broadcast surveys (n = 150 locations) in the Rocky Mountain biogeographic region of Idaho, USA, we surveyed for owls and woodpeckers to assess patterns of co-occurrence and evaluated the hypothesis that forest owls and woodpeckers co-occurred more frequently than expected by chance because of the facilitative nature of their biological interaction. We also examined co-occurrence patterns between owl species to understand their possible competitive interactions. Finally, to assess whether co-occurrence patterns arose because of species interactions or selection of similar habitat types, we used canonical correspondence analysis (CCA) to examine habitat associations within this cavity-nesting bird community. We found that Flammulated Owls co-occurred more with Hairy Woodpeckers (*Picoides villosus*), Northern Saw-whet Owls co-occurred with Northern Flickers (*Colaptes auratus*) and Red-naped Sapsuckers (*Sphyrapicus nuchalis*) and, when primary excavators were considered as a group, each species of owl was positively associated with the presence of woodpeckers. The owl species were distributed independently of one another suggesting a lack of competitive interactions. The CCA had relatively low explanatory power but suggested that habitat associations alone did not explain the patterns of positive co-occurrence we observed: Flammulated Owls and Hairy Woodpeckers associated with different habitats and Northern Saw-whet Owls, Northern Flickers, and Red-naped Sapsuckers appeared as habitat generalists. We interpret these patterns of co-occurrence and habitat use as evidence that woodpeckers facilitate presence of these species of owl and suggest management for forest owls could also include focus on the diurnal species with which they appear to associate.

Profils de cooccurrence des pics et des strigidés nocturnes nichant dans des cavités dans une forêt de l'Idaho

RÉSUMÉ. Peu d'études ont examiné la cooccurrence des oiseaux diurnes, comme les pics, et les oiseaux nocturnes, comme les strigidés. Les Petits-ducs nains (*Psiloscops flammeolus*) et les Petites Nyctales (*Aegolius acadicus*) sont des utilisateurs secondaires de cavités nocturnes nichant en forêt. Pour nicher et se reposer, ces deux espèces ont besoin de cavités naturelles ou, plus couramment, celles excavées par des pics. Au moyen de relevés diurnes et nocturnes accompagnés d'enregistrements sonores (n = 150 sites) réalisés dans la région biogéographique des Montagnes Rocheuses en Idaho, aux États-Unis, nous avons inventorié les strigidés et les pics afin d'évaluer leur tendance à cooccurrer et de valider l'hypothèse selon laquelle les pics et les strigidés forestiers cooccurrent plus souvent que le voudrait le hasard en raison de la nature facilitante de leur interaction biologique. Nous avons aussi examiné les profils de cooccurrence entre les espèces de strigidés afin d'essayer de comprendre leurs interactions compétitives possibles. Finalement, pour évaluer si les profils de cooccurrence découlaient d'interactions spécifiques ou de la sélection d'habitats similaires, nous avons réalisé une analyse de correspondance canonique afin d'examiner les associations avec l'habitat de cette communauté d'oiseaux nichant dans des cavités. Nous avons trouvé que les Petits-ducs nains cooccurraient plus souvent avec les Pics chevelus (*Picoides villosus*), tandis que les Petites Nyctales cooccurraient davantage avec les Pics flamboyants (*Colaptes auratus*) et les Pics à nuque rouge (*Sphyrapicus nuchalis*). Lorsque les excavateurs primaires étaient considérés en tant que groupe, chaque espèce de strigidés était associée positivement avec la présence de pics. Les espèces de strigidés étaient réparties indépendamment les unes des autres, laissant supposer l'absence d'interactions compétitives. L'analyse de correspondance canonique n'a pas vraiment montré de capacité explicative, mais indiquait que les associations avec l'habitat seules n'expliquaient pas les profils de cooccurrence positive que nous avons observés : les Petits-ducs nains et les Pics chevelus associés avec des habitats différents, et les Petites Nyctales, les Pics flamboyants et les Pics à nuque rouge s'avérant des espèces plus généralistes en termes d'habitat. Ces profils de cooccurrence et d'utilisation d'habitat sont sans doute des indications que les pics facilitent la présence de ces espèces de strigidés. Enfin, nous pensons que l'aménagement destiné aux strigidés forestiers devrait aussi inclure une attention particulière aux espèces diurnes avec lesquelles les strigidés semblent s'associer.

Key Words: *canonical correspondence analysis; cavity nesting; co-occurrence; facilitation; Idaho; owls; probabilistic model; woodpeckers*

Address of Correspondent: Micah N. Scholer, Department of Zoology and Biodiversity Research Centre , University of British Columbia, 2212 Main Mall, Vancouver, British Columbia, V6T 1Z4, micahscholer@gmail.com

INTRODUCTION

In forested ecosystems, obligate cavity-nesting birds form part of a distinct avian community that is useful for investigating patterns of structure and species co-occurrence, because their interactions revolve around the creation and availability of nest sites (Martin and Eadie 1999, Blanc and Walters 2008). For example, cavity-nesting birds may be part of facilitative interactions, where one species forms a nesting site another ultimately requires, or there may be competitive interactions in which members of the community require the same cavities. Primary cavity excavators such as woodpeckers create cavities for nesting and roosting and, once they vacate, the cavities become available for other species to use. Secondary cavity-nesting birds, including many passerines, waterfowl, and small owls cannot excavate their own nest sites so rely on those primary cavity nesters create. We were interested in secondary cavity-nesting forest owls and their potential relationships with cavity excavators (woodpeckers) because cavity-nesting owl species may be selecting habitat in part based upon the cavities available for nesting (Virkkala 2006). We focused our study on Boreal Owls (*Aegolius funereus*), Flammulated Owls (*Psiloscops flammeolus*), and Northern Saw-whet Owls (*Aegolius acadicus*). Although the geographic ranges of these obligate cavity-nesting forest species overlap, and they are sympatric at times, their interactions remain poorly understood (but see Hayward and Garton 1988); thus, if and how woodpeckers help structure their occurrence is of interest.

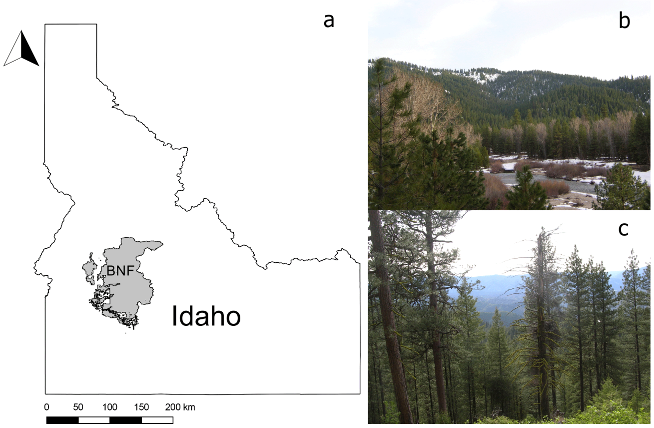
Our goal was to investigate the extent to which interspecific patterns of species co-occurrence existed within cavity nesting bird communities focused on owls and woodpeckers inhabiting coniferous forests of the Rocky Mountain biogeographic region of Idaho, USA. The literature reports that Flammulated Owls use cavities excavated by Hairy Woodpeckers (*Picoides villosus*), Northern Flickers (*Colaptes auratus*; hereafter Flickers), Pileated Woodpeckers (*Dryocopus pileatus*), Red-naped Sapsuckers (*Sphyrapicus nuchalis*), and others (McCallum and Gehlbach 1988, Bull et al. 1990, Arsenault 2004, Linkhart and McCallum 2013), while Boreal Owls and Northern Saw-whet Owls often use cavities excavated by Flickers and Pileated Woodpeckers (Hayward and Hayward 1993, Rasmussen et al. 2008). We therefore hypothesized that woodpeckers co-occur more frequently than expected by chance with cavity-nesting owls based on the potential facilitative nature of their interactions. We predicted that Flammulated Owls would be positively associated with the presence of any woodpecker regardless of species, while Boreal and Northern Saw-whet Owls would more frequently occur in sites where Flickers and Pileated Woodpeckers occurred. Similarly, we investigated patterns of co-occurrence among the cavity-nesting owls. Boreal Owls and Northern Saw-whet Owls breed earlier than Flammulated Owls (Powers et al. 1996, Rasmussen et al. 2008, Linkhart and McCallum 2013) and consequently are able to select available nesting cavities before migratory Flammulated Owls arrive in breeding areas. Boreal Owls and Northern Saw-whet Owls are also similar in size and may overlap in their use of nesting cavities (Hayward and Garton 1988, Hayward and Hayward 1993, Rasmussen et al. 2008). Thus, we evaluated the possibility of a negative relationship among owl species on the basis of competition over limited nest holes.

METHODS

Study area

We studied cavity-nesting owls and woodpeckers in and near the 10,260 km² Boise National Forest (BNF), located in southern Idaho, USA (Fig. 1). The mountainous terrain that characterizes most of the BNF developed through the uplifting, faulting, and stream cutting of the highly erodible Idaho Batholith (Steele et al. 1981). Elevation ranges from 870–3250 m, and forest cover is dominated by conifers. At low to mid elevations Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) predominate, while subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanii*), and lodgepole pine (*P. contorta*) help constitute the canopy at higher elevations. Shrubs such as ninebark (*Physocarpus malvaceus*), snowberry (*Symphoricarpos* sp.), serviceberry (*Amelanchier anlifolia*), rose (*Rosa* sp.), huckleberry (*Vaccinium* sp.), and chokecherry (*Prunus virginiana*) compose the forest understory, while ceanothus (*Ceanothus velutinus*), bitterbrush (*Purshia tridentata*), and sagebrush (*Artemesia tridentata*) inhabit drier, south-facing aspects. Deciduous trees, which compose only ~1% of forest landcover, and taller shrubs grow mainly in riparian and drainage areas and include aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*), willows (*Salix* sp.), dogwood (*Cornus sericea*), cascara (*Rhamnus purshiana*), thimbleberry (*Rubus parviflorus*), and others.

Fig. 1. Location of (a) the Boise National Forest (BNF) within Idaho, USA, and typical landcover (b and c) where surveys for nocturnal owls and diurnal woodpeckers were conducted during 2009–2010.



Sampling presence/absence of owls and woodpeckers

We established and characterized 150 point-count locations in areas with and near forested landcover in the Boise National Forest (Appendix 1) and surveyed each for owls and woodpeckers. As a potential control, we also recorded the occurrence of two passerine species, American Robin (*Turdus migratorius*) and Yellow Warbler (*Setophaga petechia*). Neither of these species inhabits tree cavities and therefore was not expected to have facilitative relationships with owls as was possible for woodpeckers. Point-count locations were within skiing, snowshoeing, or walking distance from a plowed road as necessary, because the earliest surveys occurred when snow cover obviated most other types of access. We stratified point-count locations by placing proportionately more in dominant forest habitats such as ponderosa pine and Douglas-fir (Appendix 1). To decrease chances of counting the same bird at multiple points, we spaced point-count locations ≥ 800 m apart and scored individuals of the focal species ≤ 400 m from survey points.

We conducted point-count surveys for the three species of cavity-nesting owls at night from February–May in 2009 and 2010. We timed these surveys to overlap with the breeding season of the cavity-nesting species of interest, although we anticipated few, if any, Flammulated Owl detections during that period because of their migratory habit and later arrival in breeding grounds (Powers et al. 1996, Barnes and Belthoff 2008, Linkhart and McCallum 2013). Therefore, we continued nighttime surveys focused on Flammulated Owls in June of both years. We surveyed woodpeckers and the two songbird species during the day in May–June 2009 and 2010, which overlapped their breeding seasons in the BNF (Dudley and Saab 2003). Because imperfect detection can bias estimates of site occupancy, i.e., the proportion of sites where a species is present, we used conspecific broadcasts of our target owl and woodpecker species and made repeat visits to point-count locations to maximize detection and minimize false-negative error rates (Takats et al. 2001). Presence of owls was typically recorded based on hearing their vocalizations and responses to broadcasts, whereas woodpeckers and the two songbird species were counted using a combination of visual/aural detections. We avoided surveys when average wind speeds were > 15 km/h or under persistent precipitation.

Nocturnal owl surveys

We visited each point-count location three times for Northern Saw-whet Owls and Boreal Owls, and one to three additional times for Flammulated Owls (median = 2). Surveys began at least 30 min after sunset, ended before 02:00 h, and consisted of an initial 3-min listening period followed by a series of broadcasts of territorial owl vocalizations (Stokes Field Guide to Bird Songs, Time Warner Audio Books, New York, NY). Using an NX3 Fox Pro Wildlife Caller (FOXPRO Inc., Lewiston, PA), we broadcasted Flammulated Owl and Boreal Owl vocalizations with audio output adjusted to 90–110 dB (Fuller and Mosher 1987) at 1 m. To avoid first attracting larger Boreal Owls and Northern Saw-whet Owls, we began broadcasts for the smaller Flammulated Owls first (Takats et al. 2001). Northern Saw-whet Owls routinely respond to calls of other species (Takats et al. 2001, Scholer et al. 2014); thus, we documented their vocal responses to the Boreal or Flammulated Owl calls rather than including broadcasts of Northern Saw-whet Owl calls. We broadcasted a recording of each species for 30 sec while rotating the Wildlife Caller 360°. A 1-min listening period followed each 30-sec broadcast. We repeated this broadcast-listening sequence twice for each owl species which, combined with the 3 min of silent listening, totaled 9 min at each point-count location during each survey. We detected no Boreal Owls so analyses of co-occurrence ultimately focused on Flammulated Owls and Northern Saw-whet Owls.

Diurnal woodpecker surveys

We surveyed each point-count location two to three (median = 2.5) times for Hairy Woodpeckers, Lewis's Woodpeckers (*Melanerpes lewis*), Northern Flickers, Pileated Woodpeckers, and Red-naped Sapsuckers between 30 min after sunrise and 10:00 h. During point counts focused on woodpeckers, we also scored presence of American Robins and Yellow Warblers. Point-counts began with 5 min of silent listening followed by broadcasts of woodpecker drums and vocalizations. We played 15 sec recordings of each species of woodpecker twice, each time followed by 30 sec of listening for a total of 12.5 min at each point during each survey. Because there was no concern for larger species of woodpecker preying on smaller species, as there was for owls, we randomly assigned the order of woodpecker species broadcasts prior to each survey. We did not detect any Lewis's Woodpeckers, so analyses included the other focal species.

Measuring landcover, topographic and snag characteristics

We characterized landcover around point-count locations for a suite of variables with putative importance for cavity-nesting owls and woodpeckers (Scholer et al. 2014). Briefly, using ArcGIS 9.3 (Environmental Systems Research Institute Inc., Redlands, California, USA) we derived percent cover of canopy, proportion of Douglas-fir, nonforest, and ponderosa, as well as aspect (cosine transformed degrees) and terrain ruggedness (topographic heterogeneity expressed as the average elevational difference between adjacent cells in a digital elevation model; Riley et al. 1999) within 0.4-, 1-, and 3-km radius circular plots centered on each point-count location from a national landcover dataset (LANDFIRE 2013) and a digital elevation model (USGS 2013), respectively. We also developed and analyzed a variable that captured landcover diversity (hereafter diversity) for each of the three spatial scales using the Shannon Diversity Index (Shannon and Weaver 1949) calculated using 11 of the most common landcover classes and the proportion of each. We considered the 0.4-km buffer distance to encompass features owls (Hayward and Garton 1988, Barnes and Belthoff 2008, Rasmussen et al. 2008, Linkhart and McCallum 2013) and woodpeckers (Dudley and Saab 2003, Wiebe and Moore 2017, Bull and Jackson 2011) may experience within their individual home-range sizes. We assumed that measurements at the 1- and 3-km buffers reflected scales at which dispersal of cavity-nesting species may occur or over which predators, such as Great Horned Owls (*Bubo virginianus*), Northern Goshawks (*Accipiter gentilis*), and others potentially operated (Scholer et al. 2014). We also estimated the abundance and mean diameter at breast height (DBH) of snags within four 10-m wide transects of 100 m, 200 m, 300 m, and 400 m in length and averaged over each point-count location (Bate et al. 1999). Transects emanated in random directions from point-count locations with the constraint that each occurred in a separate quadrant defined by the four cardinal directions. We measured all snags that were > 15 cm DBH and > 2 m tall, with the stipulations that the snag had no excessive deterioration, no fracturing from crown to base, could stand without support from surrounding trees, and was visually judged as capable of serving as a nest tree for an owl or woodpecker.

Statistical analyses

Species co-occurrence

We used estimates of presence/absence derived from point-count surveys to test for nonrandom associations among owls and woodpeckers, owls and songbirds, and between Flammulated Owls and Northern Saw-whet Owls. We chose to use a probabilistic model (Veech 2013) in the package *cooccur 1.2* (Griffith et al. 2016) in R (R Development Core Team 2014) from which species associations are judged as positive, negative, or random. This probabilistic model compares the observed number of times two species co-occur relative to an expected number of times based on the joint probability of two species occurring together (Pitta et al. 2012, Veech 2013). One advantage of the probability-based model is that it is strictly analytical and does not require data randomization to generate the null-distribution for a test statistic, which is necessary in any matrix-level approach. Thus, it eliminates an important source of Type I and II errors, i.e., violations of assumptions about the distribution of a test statistic (Veech 2013). Furthermore, the probabilistic model is conceptually intuitive because results are interpreted as the probability that two species would co-occur at a greater (P_{gt}) or lower (P_{lt}) number of sites than that which would be expected if they were distributed independently of one another. These probabilities can also be interpreted as *P*-values (Veech 2013); thus, the probabilistic model can also be used as a statistical test for significant patterns of correlation in species co-occurrence. Another advantage of this approach is that it requires fewer parameters to be estimated compared to, for instance, two-species occupancy models (Veech 2013, MacKenzie et al. 2004). Finally, the procedure maintains error rates at alpha even when conducting all pairwise comparisons (Veech 2013). We tested for all pairwise associations between owls and individual woodpecker species and between Flammulated Owls and Northern Saw-whet Owls. We also considered whether occurrence of woodpeckers, regardless of species, was positively associated with each species of owl. Lastly, we examined American Robins and Yellow Warblers to validate the assumption that they occurred independently of cavity-nesting owls, which would strengthen evidence for facilitative relationships between woodpeckers and owls if the latter were detected. We considered a pairwise association significant when $P < 0.05$.

Relationships between species occurrence and habitat characteristics

Because positive or negative associations between species may arise from species selecting or avoiding similar habitat characteristics, we used a multivariate approach in addition to the probabilistic model to explore habitat characteristics underlying observed associations. We examined relationships among landcover, topographic, and snag characteristics and woodpecker and owl occurrence using canonical correspondence analysis (CCA, R package *vegan,* Oksanen et al. 2018) after standardizing variables to z-scores. We used a backward selection procedure based on Akaike's Information Criteria with all variables at all three scales as the starting point to help select a subset of predictor variables. When the same variable appeared at multiple scales in the final set, we examined variance inflation factors (VIF) and dropped the scale with the higher value. We used Monte Carlo permutation tests (n = 999) to test for significance of the final model and remaining predictor variables. Because we were interested in explaining habitat characteristics that potentially drive co-occurrence patterns, point-count locations where no woodpeckers or owls were detected were excluded from the CCA analysis.

RESULTS

Point-count surveys

We conducted 720 nighttime surveys at the 150 point-count locations and detected Flammulated Owls and Northern Saw-whet Owls at 18% and 30% of locations, respectively (Table 1), with at least one species detected at 64 locations (43%). The point-count surveys that focused on Flammulated Owls during June of each year yielded no new Northern Saw-whet Owl detections.

Table 1. Co-occurrence of sympatric cavity-nesting owls and (1) woodpeckers and (2) two passerines species used as controls in the Boise National Forest, Idaho, USA. Number of point-count locations (of 150) where species were detected is shown in parentheses. Table values represent the percentage of point-count locations occupied by Flammulated Owls (*Psiloscops flammeolus*) and Northern Saw-whet Owls (*Aegolius acadicus*) that were also occupied by sympatric cavity-nesting owls, woodpeckers, or passerines.

Co-occurring species	Flammulated Owl	Northern Saw-whet Owl
	% of occupied	% of occupied
Flammulated Owl (27)	-	11
Northern Saw-whet Owl (45)	19	-
Hairy Woodpecker *Picoides villosus* (29)	41	27
Northern Flicker *Colaptes auratus* (43)	48	40
Pileated Woodpecker *Dryocopus pileatus* (14)	11	13
Red-naped Sapsucker *Sphyrapicus nuchalis* (27)	26	29
All Woodpeckers† (79)	75	66
American Robin *Turdus migratorius* (79)	55	53
Yellow Warbler *Setophaga petechia* (132)	92	93

†Number of point-counts where any one of the four woodpecker species occurred.

We conducted 373 daytime surveys for woodpeckers and the two songbird species at the same 150 point-count locations surveyed for owls. Woodpeckers occurred at 52%, with more than one species of woodpecker at 27 (18%) of occupied sites. Flickers occurred at the largest percentage of point-count locations (29%), followed by Hairy Woodpeckers (19%), Red-naped Sapsuckers (18%), and Pileated Woodpeckers (Table 1). American Robins and Yellow Warblers were more common than owls or woodpeckers and occurred at 53% and 88% of sites, respectively (Table 1).

Pairwise patterns of species co-occurrence

At least one species of woodpecker was present at the majority of sites occupied by each species of owl and, as a group, woodpeckers co-occurred slightly more with Flammulated Owls (Table 1). Both species of owl co-occurred most frequently with

Table 2. Number of observed and expected instances of co-occurrence among owls and woodpeckers, owls and passerines, and between cavity-nesting owl species based on survey of 150 point-count locations in the Boise National Forest, Idaho, USA. P_{lt} and P_{gt} represent the probability that each species pair co-occurs less than or greater than expected by chance, respectively.

Owl species	Co-occuring species	Observed	Expected	P_{lt}	P_{gt}
Flammulated Owl *Psiloscops flammeolus*	Northern Flicker *Colaptes auratus*	11	7.6	0.97	0.08
	Hairy Woodpecker *Picoides villosus*	11	5.2	0.99	<0.01[‡]
	Pileated Woodpecker *Dryocopus pileatus*	3	2.5	0.77	0.479
	Red-naped Sapsucker *Sphyrapicus nuchalis*	7	4.9	0.92	0.180
	All Woodpeckers[†]	20	14.2	0.99	< 0.01[‡]
	American Robin *Turdus migratorius*	15	14.2	0.70	0.45
	Yellow Warbler *Setophaga petechia*	25	23.8	0.87	0.33
Northern Saw-whet Owl *Aegolius acadicus*	Flammulated Owl	8	8.1	0.58	0.60
	Northern Flicker	18	12.6	0.99	0.03[‡]
	Hairy Woodpecker	12	8.7	0.95	0.10
	Pileated Woodpecker	6	4.2	0.92	0.21
	Red-naped Sapsucker	13	8.1	0.99	0.02[‡]
	All Woodpeckers[†]	30	23.7	0.99	0.02[‡]
	American Robin	24	23.7	0.61	0.53
	Yellow Warbler	42	39.6	0.95	0.15

[†] Occurrence of any of the four woodpecker species at a point-count location.
[‡] Significance at $P < 0.05$.

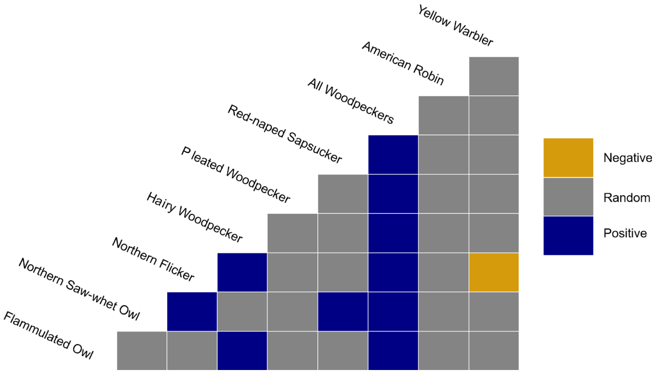
Flickers, which were also the most common woodpecker detected, and least frequently with Pileated Woodpecker, which was the least commonly detected woodpecker species (Table 1). Flammulated Owls and Northern Saw-whet Owls co-occurred at eight point-count locations (5% of locations; Table 2).

Of the 17 pairwise relationships we investigated between owls and woodpeckers, between owls and songbirds, and between owl species, there were five significant positive associations and no significant negative relationships (Fig. 2, Table 2). Flammulated Owls occurred more than expected with Hairy Woodpeckers and with woodpeckers as a group. Northern Saw-whet Owls were more likely to occur at point-count locations where a woodpecker was also detected, regardless of species, and they had a higher probability of occurrence with Flickers and Red-naped Sapsuckers. There was no evidence of species association, negative or positive, between Flammulated Owls and Northern Saw-whet Owls or between cavity-nesting owls and American Robins or Yellow Warblers (Table 2).

Relationships between habitat characteristics and woodpecker/owl occurrence

Snag abundance, aspect, canopy cover, and nonforest were removed from further modeling after the backward variable selection procedure. Terrain ruggedness index (TRI) and ponderosa appeared in the candidate variable set at two scales: 0.4 and 1 km. For ponderosa the VIF was high at the 1-km scale (17.45), so we removed this variable. The final model included the habitat variables snag DBH, ponderosa and TRI (0.4-km scale), diversity and TRI (1-km scale), and Douglas-fir (3-km scale).

Fig. 2. Species co-occurrence matrix for all possible pairwise comparisons between cavity nesting forest owls and woodpeckers in the Boise National Forest, Idaho, USA. Species co-occurrence was also investigated between owls and two passerines and was random. Yellow Warbler (*Setophaga petechia*); American Robin (*Turdus migratorius*); Red-naped Sapsucker (*Sphyrapicus nuchalis*); Pileated Woodpecker (*Dryocopus pileatus*); Hairy Woodpecker (*Picoides villosus*); Northern Flicker (*Colaptes auratus*); Northern Saw-whet Owl (*Aegolius acadicus*); Flammulated Owl (*Psiloscops flammeolus*).



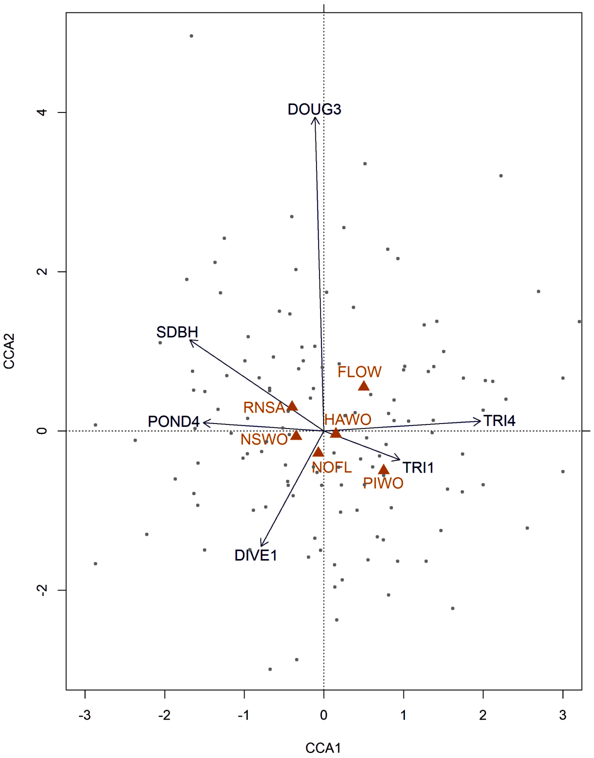
The CCA ordination of landcover variables explained only 14% of the total variation in cavity-nester occurrence, 72% of which was accounted for by the first two principal axes (Fig. 3). The first axis largely represented a gradient in heterogeneity of terrain with

Table 3. Summary of Monte-Carlo tests conducted on the canonical correspondence analysis for the ordination of cavity-nesting woodpeckers and owls and the habitat characteristics with which they associated. Results for predictor variables chosen based on the backward variable selection procedure are shown. Subscripts indicate the extent at which each variable was selected. Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*).

Variable	Chi-square value	Degrees of freedom	*P*-value
Douglas-fir $_{3km}$	0.08	1	0.03[‡]
Ponderosa $_{0.4km}$	0.06	1	< 0.01[‡]
TRI[†] $_{1km}$	0.07	1	< 0.01[‡]
TRI[†] $_{0.4km}$	0.04	1	0.04[‡]
Snag DBH	0.04	1	0.08
Diversity $_{1km}$	0.03	1	0.18

[†] Terrain ruggedness index derived from digital elevation model.
[‡] Significance at $P < 0.05$.

Fig. 3. Distribution of cavity-nesting forest owl and woodpecker occurrence (triangles) along the first two axes of a canonical correspondence analysis (CCA) and the landcover, topographic, and snag characteristic variables with which they associated. Bird species are: (FLOW) Flammulated Owls, *Psiloscops flammeolus*; (NSWO) Northern Saw-whet Owl, *Aegolius acadicus*; (HAWO) Hairy Woodpecker, *Picoides villosus*; (NOFL) Northern Flicker, *Colaptes auratus*; (PIWO) Pileated Woodpecker, *Dryocopus pileatus*; and (RNSA) Red-naped Sapsucker, *Sphyrapicus nuchalis*. Variables used to assess habitat associations were: (SDBH) diameter at breast height of snags, (POND4) ponderosa pine 0.4 km-scale, (TRI4, TRI1) terrain ruggedness index 0.4 and 1 km-scale, respectively, (DIVE1) landcover diversity 1 km-scale, and (DOUG3) Douglas-fir 3 km-scale, which combined explained 14% of the variation in the occurrence of this avian community.



more rugged sites having positive values and sites where the topography was flatter negative values. Flatter sites also tended to have more ponderosa pine and snags with a higher DBH. Sites along the second axis with positive values comprised primarily Douglas-fir forest and snags with larger DBH while sites with negative values had higher diversity of landcover types, which often consisted of mixed stands of grand and subalpine fir, Douglas-fir, and ponderosa pine, and grassland and shrubland. Monte-Carlo permutation test of the joint effect of constraining variables showed that Douglas-fir, ponderosa, and TRI were significant predictors of the cavity-nesting community structure (Table 3).

Hairy Woodpeckers, Flickers, and Northern Saw-whet Owls plotted near the intersection of two principal axes (Fig. 3). The latter two species had slightly negative scores along both axes and thus were in areas with lower topographic relief and smaller proportions of Douglas-fir at the 3-km scale, while Northern Saw-whet Owls tended to have a higher proportion of ponderosa pine. No one landcover variable appeared best at explaining Hairy Woodpecker occurrence. Flammulated Owls and Pileated Woodpeckers were in areas with more rugged terrain (Fig. 3) as indicated by higher values along axis 2. These species differed in their use of habitat, however; Flammulated Owls tended to occur in areas with a greater proportion of Douglas-fir whereas Pileated Woodpeckers were in forests with a more diverse assemblage of landcover types. Red-naped Sapsucker occurrence was best characterized by sites with larger DBH snags and a mix of both ponderosa at the 0.4-km scale and Douglas-fir at the 3-km scale (Fig. 3).

DISCUSSION

There was no evidence of avoidance between owl species. However, there was strong indication that cavity-nesting owls associated with woodpeckers because Flammulated Owls co-occurred with Hairy Woodpeckers, and Northern Saw-whet Owls co-occurred with Northern Flickers and Red-naped Sapsuckers more often than expected. For both species of owl, we also found a significant positive association with the presence of woodpeckers as a group. Evidence for a facilitative relationship between woodpeckers and owls was strengthened by the lack of an observed relationship between owls and the two passerine control species that do not rely on cavities.

The patterns we observed agreed with predictions of a facilitative relationship between woodpeckers and cavity-nesting owls

(Martin et al. 2004). This positive association is perhaps a function of a lack of suitable, naturally occurring cavities, e.g., those created through decay or by broken tree limbs, in which owls could breed and, consequently, a reliance on cavities that woodpeckers create (Martin and Eadie 1999). For managed forest landscapes like those in the BNF, this may be especially true because standing dead wood, the most likely place for naturally occurring cavities, is frequently removed as part of forestry practices (Newton 1994, Kroll et al. 2012). Studies reporting cavity use by Flammulated Owls do suggest this species almost exclusively uses cavities excavated by woodpeckers (Linkhart and McCallum 2013), rather than those that exist through decay or other natural processes. Northern Saw-whet Owls readily breed in nest boxes, but they too use cavities excavated by woodpeckers (Rasmussen et al. 2008). Consistent with our prediction, we found that both species of owl co-occurred significantly more than expected with woodpeckers as a group. Often, the number of cavities becomes a limiting factor for populations of cavity-nesting species (Newton 1994), and occurrence of woodpeckers likely represents a higher availability of cavities for nesting and roosting by other species compared to locations in which woodpeckers do not occur. However, even when the number of available cavities is high, the proportion of high quality cavities may limit occupancy (Cockle et al. 2008). Although cavities can indeed be an important limiting factor for forest dwelling birds (Cockle et al. 2008, Aitken and Martin 2012), sometimes there is also no clear relationship between the number of cavities and the density of breeding birds (Bonar 2000, Wiebe 2011).

Flickers were the most common woodpecker and occurred at almost 30% of point-count locations. Our results concur with others and suggest that Northern Saw-whet Owls are more likely to occur in areas also occupied by Flickers. Northern Saw-whet Owls (Groce and Morrison 2010, Scholer et al. 2014) and Flickers (Wiebe and Moore 2017) may be more habitat generalists than some of the other species we studied. Both were clustered around the center of the CCA triplot (Fig. 3), which suggests lack of specificity to any one habitat variable. In contrast, Flammulated Owls appeared to be associated with different elements of the habitat compared to Northern Saw-whet Owls and Flickers. The first axis of the CCA indicated that Flammulated Owls occurred in more rugged areas with lower percentage of ponderosa pine at the 0.4-km scale, while the second axis indicated that they were associated with stands of Douglas-fir at the 3-km scale. Thus, the observed lack of co-occurrence between Flammulated Owls and Flickers may be a result of differences in their habitat use. The relative size of cavities that Flickers create may be an additional factor explaining any lack of a positive association with Flammulated Owls. Body size is one of the most important components in determining the degree of resource overlap in cavity use (Martin et al. 2004), with Flickers creating cavities that are most similar in dimensions to those Northern Saw-whet Owls use. Flammulated Owls may rely on cavity dimensions that are slightly smaller than those used by Northern Saw-whet Owls, for example, those Hairy Woodpeckers create. The lack of relationship with Flickers and a positive relationship with Hairy Woodpeckers seems best explained by the cumulative result of Flammulated Owls likely using cavities of slightly smaller dimensions and located in more rugged habitats in which Hairy Woodpeckers also occur.

Northern Saw-whet Owls and Red-naped Sapsuckers also had a significant positive association. This is curious because we found no suggestion in the literature about Northern Saw-whet Owls using cavities created by *Sphyrapicus* spp. Northern Saw-whet Owls generally require cavity openings of > 75 mm in diameter, which is roughly 1.5 times larger than those Red-naped Sapsuckers typically create (Martin et al. 2004, Rasmussen et al 2008). Moreover, in a 14-year study of cavity-nesting vertebrates in central British Columbia, Cockle and Martin (2015) found no instances of Northern Saw-whet Owls nesting or roosting in cavities excavated by Red-naped Sapsuckers, despite relatively high abundance of both species. One possibility is that Northern Saw-whet Owls use cavities excavated by Red-naped Sapsuckers if those cavities are enlarged by decomposition or squirrels. Tarver (2003) documented one such case where a cavity excavated by a Hairy Woodpecker was enlarged and subsequently inhabited by the Northern Saw-whet Owl subspecies *A. a. brookski*. Whether incidences such as these exist with sufficient frequency to drive the positive co-occurrence pattern we observed is questionable, however. More likely these species co-occurred because of similar habitat associations. Both Red-naped Sapsuckers and Northern Saw-whet Owls did appear to occur in areas characterized by a higher proportion of ponderosa pine and, although less important, larger DBH snags in the BNF (Fig. 3).

Flammulated Owls and Northern Saw-whet Owls may frequently use cavities Pileated Woodpeckers excavated, which suggests potential for a positive association between these species (Cannings 1987, Bull et al. 1990, Rasmussen et al. 2008). Contrary to these expectations, however, we did not find evidence of such a relationship in the BNF. One potential reason is that there was relatively low occurrence (*n* = 14 occupied point-count locations) of Pileated Woodpeckers in our study area. In the Western United States, Pileated Woodpeckers reach the southern extent of their range in montane regions of Western Montana and Northern Idaho (Bull and Jackson 2011). The role of Pileated Woodpeckers in providing nest holes for cavity-nesting owls in the BNF may therefore be of less importance than those reported for regions where this woodpecker species is more abundant, i.e., Ontario, Canada (Peck and James 1983, Bull et al. 1990). For our study, we most commonly detected Pileated Woodpeckers in the northern portion of the BNF, which is characterized by fewer monotypic stands of Douglas-fir and ponderosa and higher landcover diversity. The CCA results appeared to support this and suggest that where they did occur, Pileated Woodpeckers used different habitat characteristics than those used by other members of the cavity nesting community: more diverse landcover in more rugged terrain.

There was no evidence that Northern Saw-whet Owls excluded the smaller Flammulated Owls through competition. These results contrast with studies of owls in which large- and medium-sized species appear to out-compete small species for space or resources in forest systems (Hakkarainen and Korpimaki 1996, Vrezec 2003, Vrezec and Tome 2004). Our prediction was based on studies reporting that similar primary cavity excavators (Flickers and Pileated Woodpeckers) were preferred cavity creators for Flammulated Owls (McCallum and Gelbach 1988, Bull et al. 1990, Arsenault 2004, Linkhart and McCallum 2013) and Northern Saw-whet owls (Rasmussen et al. 2008). However, Flammulated Owls and Northern Saw-whet Owls differ in their physical size, i.e., mass, wingspan, and length, and in the size of cavities they typically use for nesting. As such, the much smaller Flammulated Owl may tend to occupy cavities created by smaller primary cavity nesters, such as Hairy Woodpeckers. Alternatively, if there is a surplus of available cavities, as indicated by Bonar (2000) for example, then competition over nest sites may occur only rarely between these species. It is also almost certain that competition over food resources does not occur because Northern Saw-whet Owls consume primarily woodland mice (*Peromyscus* spp.), voles (*Microtus* sp.), and small passerines (Grove 1985, Cannings 1987, Marks and Dormeus 1988), whereas Flammulated Owls are insectivorous (Linkhart and McCallum 2013). Although our findings suggest no competitive exclusion between Flammulated Owls and Northern Saw-whet Owls, they also provide no evidence of a positive relationship between the two species; instead, their occurrence was independent of one another.

CONCLUSION

In addition to increasing our knowledge of how species interactions help shape avian communities, understanding co-occurrence patterns informs species and land management (MacKenzie et al. 2004, Halme et al. 2009). If woodpeckers ultimately facilitate nesting opportunities for secondary cavity-nesting owls, then single species approaches to management and monitoring may not be as effective as those focused on biological communities. By elucidating biological interactions such as those we studied, land managers can better adapt actions to suit the conservation needs of a particular group of plants or animals. This is especially important in cases where one species, e.g., cavity-nesting owls, relies on the occurrence of another species, i.e., woodpeckers, to successfully reproduce. Although we observed that secondary cavity-nesting owls co-occurred more than expected with woodpeckers, clear and unambiguous cases of interspecific interactions are difficult to produce (Connell 1983) and require a level of experimental control, e.g., removal or common garden experiments, beyond the scope of most field studies, including this one. Because our statistical approach was correlational, reasons for species co-occurrence could have been multifaceted. For instance, our results do not rule out that co-occurrence patterns could have emerged from species selection or avoidance of similar habitat features. Nevertheless, the two-species probabilistic model that we used, while correlational in nature, had the advantage that interpretation was straightforward with lower rates of both Type I and Type II statistical errors. If the nocturnal owl community indeed co-occurs with woodpeckers more than expected, which our data suggest, forest managers may be able to use results from surveys focused on diurnal bird distributions to help understand and manage for the nocturnal owl community. However, although we found cavity-nesting owls were positively associated with some members of the woodpecker community, we do not advocate the use of woodpecker surveys as a substitute for cavity-nesting owl monitoring. Rather, if the goal is conservation of cavity-nesting owls, we recommend that land managers explore the degree of association between owls and woodpeckers specific to their management areas and incorporate habitat needs of both species into conservation planning. For many secondary cavity nesters, including owls, the long-term viability of populations may depend on how well the woodpecker community is managed (Cockle and Martin 2015).

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1209

Acknowledgments:

We are grateful to L. Nutt (USDA Forest Service) for providing logistical support, help with project planning, and funding for work within the Boise National Forest. Project funding was also provided by the Department of Biological Sciences and the Raptor Research Center at Boise State University. We thank R. Miller, I. Seferovich, A. Sherwood, and L. Vanderlugt for assistance in data collection and L. Bond and J. Heath for earlier discussions of this manuscript.

LITERATURE CITED

Aitken, K. E. H., and K. Martin. 2012. Experimental test of nest-site limitation in mature mixed forests of central British Columbia, Canada. *Journal of Wildlife Management* 76:557-565. http://dx.doi.org/10.1002/jwmg.286

Arsenault, D. P. 2004. Differentiating nest-sites of primary and secondary cavity-nesting birds in New Mexico. *Journal of Field Ornithology* 75:257-265. http://dx.doi.org/10.1648/0273-8570-75.3.257

Barnes, K. P., and J. R. Belthoff. 2008. Probability of detection of Flammulated Owls using nocturnal broadcast surveys. *Journal of Field Ornithology* 79:321-328. http://dx.doi.org/10.1111/j.1557-9263.2008.00166.x

Bate, L. J., E. O. Garton, and M. J. Wisdom. 1999. *Estimating snag and large tree densities and distributions on a landscape for wildlife management.* General Technical Report GTR-425. U.S. Forest Service Pacific Northwest Research Station, Portland, Oregon, USA. http://dx.doi.org/10.2737/PNW-GTR-425

Blanc, L. A., and J. R. Walters. 2008. Cavity excavation and enlargement as mechanisms for indirect interactions in an avian community. *Ecology* 89:506-514. http://dx.doi.org/10.1890/07-0219.1

Bonar, R. L. 2000. Availability of Pileated Woodpecker cavities and use by other species. *Journal of Wildlife Management* 64:52-59. http://dx.doi.org/10.2307/3802974

Bull, E. L., and J. A. Jackson. 2011. Pileated Woodpecker (*Dryocopus pileatus*). *In* A. F. Poole, editor. *The birds of North America online.* Cornell Lab of Ornithology, Ithaca, New York, USA. http://dx.doi.org/10.2173/bna.148

Bull, E. L., A. L. Wright, and M. G. Henjum. 1990. Nesting habitat of Flammulated Owls in Oregon. *Journal of Raptor Research* 24:52-55.

Cannings, R. J. 1987. The breeding biology of Northern Saw-whet Owls in southern British Columbia. Pages 193-198 *in* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, editors. *Biology and conservation of northern forest owls: symposium proceedings.* General Technical Report RM-142. U.S. Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Cockle, K. L., and K. Martin. 2015. Temporal dynamics of a commensal network of cavity-nesting vertebrates: increased diversity during an insect outbreak. *Ecology* 96:1093-1104. http://dx.doi.org/10.1890/14-1256.1

Cockle, K. L., K. Martin, and K. Wiebe. 2008. Availability of cavities for nesting birds in the Atlantic Forest, Argentina. *Ornitología Neotropical* 19:269-278.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661-696. http://dx.doi.org/10.1086/284165

Dudley, J., and V. Saab. 2003. *A field protocol to monitor cavity nesting birds.* Research Paper RMRS-RP-44. U.S. Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA. http://dx.doi.org/10.2737/RMRS-RP-44

Fuller, M. R., and J. A. Mosher. 1987. Raptor survey techniques. Pages 37-65 *in* B. A. Giron-Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird, editors. *Raptor research management techniques manual.* National Wildlife Federation, Washington, D.C., USA.

Griffith, D. M., J. A. Veech, and C. J. Marsh. 2016. Cooccur: probabilistic species co-occurrence analysis in R. *Journal of Statistical Software* 69:1-17. http://dx.doi.org/10.18637/jss.v069.c02

Groce, J. E., and M. L. Morrison. 2010. Habitat use by Saw-whet Owls in the Sierra Nevadas. *Journal of Wildlife Management* 74:1523-1532. http://dx.doi.org/10.1111/j.1937-2817.2010.tb01280.x

Grove, R. A. 1985. Northern Saw-whet Owl winter food and roosting habits in north-central Washington. *Murrelet* 66:21-24. http://dx.doi.org/10.2307/3535463

Hakkarainen, H., and E. Korpimaki. 1996. Competitive and predatory interactions among raptors: and observational and experimental study. *Ecology* 77:1134-1142. http://dx.doi.org/10.2307/2265582

Halme, P., M. Mönkkönen, J. S. Kotiaho, A. Ylisirniö, and A. Markkanen. 2009. Quantifying the indicator power of an indicator species. *Conservation Biology* 23:1008-1016. http://dx.doi.org/10.1111/j.1523-1739.2009.01206.x

Hayward, G. D., and E. O. Garton. 1988. Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. *Oecologia* 75:253-265. http://dx.doi.org/10.1007/BF00378606

Hayward, G. D., and P. H. Hayward. 1993. Boreal Owl (*Aegolius funereus*). *In* A. F. Poole and F. B. Gill, editors. *The birds of North America online.* Cornell Lab of Ornithology, Ithaca, New York, USA. http://dx.doi.org/10.2173/bna.63

Kroll, A. J., M. J. Lacki, and E. B. Arnett. 2012. Research needs to support management and conservation of cavity-dependent birds and bats on forested landscapes in the Pacific Northwest. *Western Journal of Applied Forestry* 27:128-136. http://dx.doi.org/10.5849/wjaf.10-021

LANDFIRE. 2013. *Vegetation.* LANDFIRE Project, U.S. Forest Service, USA. [online] URL: https://www.landfire.gov/vegetation.php

Linkhart, B. D., and D. A. McCallum. 2013. Flammulated Owl (*Psiloscops flammeolus*). *In* A. F. Poole, editor. *The birds of North America online.* Cornell Lab of Ornithology, Ithaca, New York, USA. http://dx.doi.org/10.2173/bna.93

MacKenzie, D. I., L. B. Larissa, and J. D. Nichols. 2004. Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* 73:546-555. http://dx.doi.org/10.1111/j.0021-8790.2004.00828.x

Marks, J. S., and J. H. Doremus. 1988. Breeding season diet of Northern Saw-whet Owls in southwestern Idaho. *Wilson Bulletin* 100:690-694.

Martin, K. K., E. H. Aitken, and K. L. Wiebe. 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* 106:5-19. http://dx.doi.org/10.1650/7482

Martin, K., and J. M. Eadie. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. *Forest Ecology and Management* 115:243-257. http://dx.doi.org/10.1016/S0378-1127(98)00403-4

McCallum, D. A., and F. R. Gehlbach. 1988. Nest-site preference of Flammulated Owls in western New Mexico. *Condor* 90:653-661. http://dx.doi.org/10.2307/1368355

Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* 70:265-276. http://dx.doi.org/10.1016/0006-3207(94)90172-4

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2018. *Vegan: community ecology package.* R package version 2.5-1. [online] URL: http://cran.r-project.org/package=vegan

Peck, G. K., and R. D. James. 1983. *Breeding birds of Ontario: nidiology and distribution. Volume 1: nonpasserines.* Royal Ontario Museum, Toronto, Ontario, Canada. http://dx.doi.org/10.5962/bhl.title.60694

Pitta, E., S. Giokas, and S. Sfenthourakis. 2012. Significant pairwise co-occurrence patterns are not the rule in the majority of biotic communities. *Diversity* 4:179-193. http://dx.doi.org/10.3390/d4020179

Powers, L. R., A. Dale, P. A. Gaede, C. Rodes, L. Nelson, J. J. Dean, and J. D. May. 1996. Nesting food habits of the Flammulated Owl (*Otus flammeolus*) in south central Idaho. *Journal of Raptor Research* 30:15-20.

R Development Core Team. 2014. *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Rasmussen, J. L., S. G. Sealy, and R. J. Cannings. 2008. Northern Saw-whet Owl (*Aegolius acadicus*). *In* A. F. Poole, editor. *The birds of North America online.* Cornell Lab of Ornithology, Ithaca, New York, USA. http://dx.doi.org/10.2173/bna.42

Riley, S. J., S. D. Degloria, and R. Elliot. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Science* 5:23-27.

Scholer, M. N., L. Matthias, and J. R. Belthoff. 2014. Factors associated with Flammulated Owl and Northern Saw-whet Owl occupancy in southern Idaho. *Journal of Raptor Research* 48:128-141. http://dx.doi.org/10.3356/JRR-13-00049.1

Shannon, C. E., and W. Weaver. 1949. *The mathematical theory of communication*. University of Illinois Press, Urbana, Illinois, USA.

Steele, R., R. D. Pfister, R. A. Ryker, and J. A. Kittams. 1981. *Forest habitat types of central Idaho.* General Technical Report INT-114. U.S. Forest Service Intermountain Forest and Range Experiment Station, Ogden, Utah, USA. http://dx.doi.org/10.2737/INT-GTR-114

Takats, D. L., C. M. Francis, G. L. Holroyd, J. R. Duncan, K. M. Mazur, R. J. Cannings, W. Harris, and D. Holt. 2001. *Guidelines for nocturnal owl monitoring in North America.* Beaver-Hill Bird Observatory and Bird Studies Canada, Edmonton, Alberta, Canada.

Tarver, C. 2003. *Northern Saw-whet Owl nest on East Limestone Island.* Laskeek Bay Research, Laskeek Bay Conservation Society, Queen Charlotte City, British Columbia, Canada.

U.S. Geological Survey (USGS). 2013. *The national map viewer.* U.S. Geological Survey, USA. [online] URL: http://www.nationalmap.gov/viewer.html

Veech, J. A. 2013. A probabilistic model for analyzing species co-occurrence. *Global Ecology and Biogeography* 22:252-260. http://dx.doi.org/10.1111/j.1466-8238.2012.00789.x

Virkkala, R. 2006. Why study woodpeckers? The significance of woodpeckers in forest ecosystems. *Annales Zoologici Fennici* 43:82-85.

Vrezec, A. 2003. Breeding density and altitudinal distribution of the Ural, Tawny, and Boreal Owls in North Dinaric Alps (Central Slovenia). *Journal of Raptor Research* 37:55-62.

Vrezec, A., and D. Tome. 2004. Altitudinal segregation between Ural Owl, *Strix uralensis*, and Tawny Owl, *Strix aluco*: evidence for competitive exclusion in raptorial birds. *Bird Study* 52:2-7.

Wiebe, K. L. 2011. Nest sites as limiting resources for cavity-nesting birds in mature forest ecosystems: a review of the evidence. *Journal of Field Ornithology* 82:239-284. http://dx.doi.org/10.1111/j.1557-9263.2011.00327.x

Wiebe, K. L., and W. S. Moore. 2017. Northern Flicker (*Colaptes auratus*). *In* P. G. Rodewald, editor. *The birds of North America online.* Cornell Lab of Ornithology, Ithaca, New York, USA. http://dx.doi.org/10.2173/bna.norfli.02.1

Editor-in-Chief: Keith A.Hobson
Subject Editor: Philip D.Taylor

Sponsored by the Society of Canadian Ornithologists and Bird Studies Canada
Parrainée par la Société des ornithologistes du Canada et Études d`oiseaux Canada

SCO - SOC

BIRD STUDIES ÉTUDES D'OISEAUX CANADA

Table A1.1. Elevation and aspect of point-count locations (n = 150) within the Boise National Forest, Idaho, USA surveyed for owls and woodpeckers during 2009-2010. Data derived from a 30-m resolution digital elevation model (The National Map 2013).

	Mean	SD	Median	Min	Max
Elevation (m)	1489	289	1428	957	2376
Aspect (degrees)[1]	222	104	225	2	353

[1] Mean vector (*u*), circular standard deviation, and median calculated using circular statistics. Min and Max are linear values.

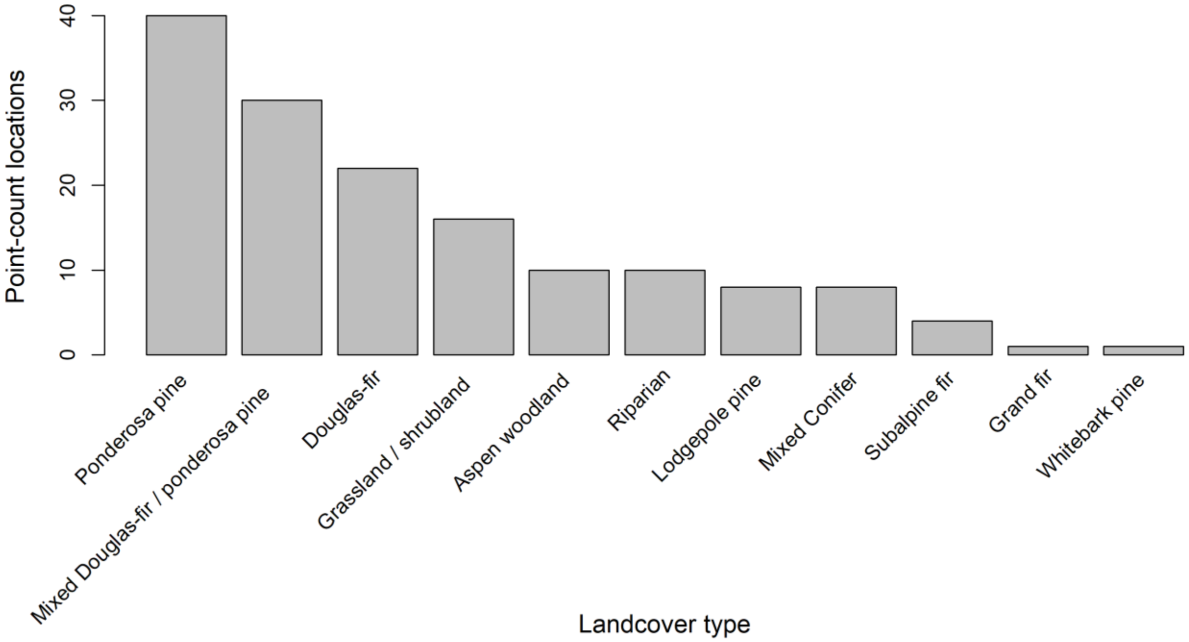


Figure A1.1. Landcover type at point-count locations (n = 150) within the Boise National Forest, Idaho, U.S.A. described using the southwest LANDFIRE (2013) database.

Table A1.2. Landcover and topographic variables ($\bar{x}$ ± SE) within 0.4-, 1- and 3-km radius circular plots surrounding point-count locations (n = 150) where cavity nesting owls were present and where they were absent in the Boise National Forest, Idaho, USA during 2009-2010. Proportion of canopy cover, Douglas-fir, non-forest, and ponderosa as well as landcover diversity, which was calculated as the Shannon Diversity Index, were derived from the LANDFIRE (2013) dataset. The topographic variable aspect was transformed using a cosine transformation and TRI (terrain ruggedness index) was expressed as the average elevational difference between adjacent cells in a digital elevation model (The National Map 2013). Snag characteristics were only measured at the 0.4 km-scale using 10m-wide belt transects centered on the point-count location and totaling 1km in length.

Variable	Flammulated Owl		Northern Saw-whet Owl	
	Present (27)	Absent (123)	Present (45)	Absent (105)
Aspect $_{\text{0.4km}}$	0.03±0.01	0.04±0.01	0.03±0.01	0.05±0.01
Canopy $_{\text{0.4km}}$	0.42±0.17	0.36±0.15	0.35±0.16	0.38±0.15
Diversity $_{\text{0.4km}}$	1.15±0.31	1.35±0.29	1.27±0.31	1.34±0.3
Douglas-fir $_{\text{0.4km}}$	0.23±0.22	0.13±0.14	0.18±0.21	0.14±0.13
Non-forest $_{\text{0.4km}}$	0.11±0.14	0.16±0.15	0.16±0.15	0.15±0.15
Ponderosa $_{\text{0.4km}}$	0.28±0.24	0.27±0.2	0.29±0.21	0.26±0.21
TRI $_{\text{0.4km}}$	8.07±2.37	8.34±2.9	7.36±2.83	8.69±2.72
Aspect $_{\text{1km}}$	0.03±0	0.05±0.03	0.02±0.03	0.06±0.03
Canopy $_{\text{1km}}$	0.4±0.08	0.37±0.08	0.35±0.07	0.38±0.09
Diversity $_{\text{1km}}$	1.38±0.18	1.57±0.2	1.51±0.2	1.55±0.2
Douglas-fir $_{\text{1km}}$	0.19±0.11	0.13±0.08	0.13±0.09	0.14±0.09
Non-forest $_{\text{1km}}$	0.13±0.12	0.17±0.1	0.2±0.1	0.15±0.11
Ponderosa $_{\text{1km}}$	0.3±0.21	0.26±0.16	0.29±0.18	0.26±0.17
TRI $_{\text{1km}}$	8.47±2.09	8.87±2.3	8.54±2.35	8.91±2.23
Aspect $_{\text{3km}}$	0.03±0	0.1±0.03	0.09±0.03	0.09±0.03
Canopy $_{\text{3km}}$	0.38±0.08	0.38±0.08	0.37±0.07	0.38±0.09
Diversity $_{\text{3km}}$	1.03±0.18	1.15±0.2	1.08±0.20	1.15±0.20
Douglas-fir $_{\text{3km}}$	0.17±0.11	0.14±0.08	0.14±0.09	0.15±0.09
Non-forest $_{\text{3km}}$	0.20±0.12	0.18±0.1	0.21±0.10	0.18±0.11
Ponderosa $_{\text{3km}}$	0.29±0.21	0.23±0.16	0.27±0.18	0.23±0.17
TRI $_{\text{3km}}$	8.69±2.09	9.11±2.3	9.25±2.35	8.95±2.23
# of Snags	11.4±8.03	12.7±26.00	8.6±7.14	14.1±27.90
Avg. DBH Snags	36.3±8.40	34.9±12.05	37.9±11.49	34.0±11.31

Table A1.3. Landcover and topographic variables ($\bar{x}$ ± SE) within 0.4-, 1- and 3-km radius circular plots surrounding point-count locations where woodpeckers were present versus absent in the Boise National Forest, Idaho, USA during 2009-2010. Proportion of canopy cover, Douglas-fir, non-forest, and ponderosa as well as landcover diversity, which was calculated as the Shannon Diversity Index, were derived from the LANDFIRE (2013) dataset. The topographic variable aspect was transformed using a cosine transformation and TRI (terrain ruggedness index) was expressed as the average elevational difference between adjacent cells in a digital elevation model (The National Map 2013). Snag characteristics were only measured at the 0.4 km-scale using 10m-wide belt transects centered on the point-count location and totaling 1km in length.

Variable	Hairy Woodpecker		Northern Flicker		Pileated Woodpecker		Red-naped Sapsucker	
	Present (29)	Absent (121)	Present (42)	Absent (108)	Present (14)	Absent (136)	Present (27)	Absent (123)
Aspect $_{0.4km}$	0.02±0.01	0.03±0.01	0.02±0.01	0.05±0.01	0.02±0.01	0.04±0.01	0.05±0.01	0.04±0.01
Canopy $_{0.4km}$	0.36±0.15	0.42±0.16	0.33±0.15	0.39±0.15	0.43±0.15	0.36±0.15	0.37±0.17	0.37±0.15
Diversity $_{0.4km}$	1.22±0.39	1.15±0.27	1.22±0.38	1.35±0.26	1.32±0.19	1.31±0.31	1.2±0.33	1.34±0.29
Douglas-fir $_{0.4km}$	0.21±0.23	0.23±0.13	0.16±0.19	0.15±0.15	0.13±0.14	0.15±0.16	0.2±0.2	0.14±0.15
Non-forest $_{0.4km}$	0.12±0.13	0.11±0.15	0.16±0.18	0.15±0.13	0.09±0.13	0.16±0.15	0.15±0.17	0.15±0.14
Ponderosa $_{0.4km}$	0.31±0.25	0.28±0.19	0.35±0.26	0.24±0.18	0.18±0.12	0.28±0.21	0.32±0.28	0.26±0.19
TRI $_{0.4km}$	7.21±2.56	8.07±2.81	7.22±2.76	8.7±2.74	8.66±2.45	8.25±2.85	7.12±2.48	8.55±2.82
Aspect $_{1km}$	0.04±0.01	0.05±0.03	0.07±0.04	0.04±0.02	0.07±0.05	0.05±0.02	0.05±0.04	0.05±0.02
Canopy $_{1km}$	0.36±0.07	0.38±0.08	0.35±0.08	0.39±0.08	0.41±0.08	0.37±0.08	0.37±0.1	0.37±0.08
Diversity $_{1km}$	1.45±0.22	1.56±0.19	1.44±0.22	1.58±0.18	1.57±0.14	1.54±0.2	1.5±0.21	1.55±0.19
Douglas-fir $_{1km}$	0.16±0.08	0.13±0.09	0.13±0.08	0.14±0.09	0.11±0.06	0.14±0.09	0.18±0.1	0.13±0.09
Non-forest $_{1km}$	0.14±0.11	0.17±0.11	0.16±0.1	0.17±0.11	0.2±0.13	0.16±0.1	0.15±0.1	0.17±0.11
Ponderosa $_{1km}$	0.34±0.22	0.25±0.16	0.34±0.22	0.24±0.14	0.18±0.08	0.28±0.18	0.3±0.21	0.26±0.16
TRI $_{1km}$	7.92±2.47	9.01±2.2	7.84±2.62	9.17±2.01	8.87±2.38	8.79±2.26	7.48±2.18	9.09±2.25
Aspect $_{3km}$	0.07±0.01	0.1±0.03	0.15±0.04	0.06±0.02	0.22±0.05	0.08±0.02	0.15±0.04	0.08±0.02
Canopy $_{3km}$	0.35±0.07	0.38±0.08	0.35±0.08	0.39±0.08	0.38±0.08	0.38±0.08	0.39±0.1	0.37±0.08
Diversity $_{3km}$	1.03±0.22	1.15±0.19	1.03±0.22	1.16±0.18	1.14±0.14	1.12±0.2	1.04±0.21	1.14±0.19
Douglas-fir $_{3km}$	0.14±0.08	0.14±0.09	0.11±0.08	0.16±0.09	0.12±0.06	0.15±0.09	0.17±0.1	0.14±0.09

Non-forest $_{\text{3km}}$	0.18±0.11	0.19±0.11	0.17±0.1	0.19±0.11	0.23±0.13	0.18±0.1	0.17±0.1	0.19±0.11
Ponderosa $_{\text{3km}}$	0.31±0.22	0.22±0.16	0.32±0.22	0.21±0.14	0.17±0.08	0.25±0.18	0.27±0.21	0.23±0.16
TRI $_{\text{3km}}$	8.46±2.47	9.18±2.2	8.21±2.62	9.39±2.01	0.02±0.01	9.04±2.26	8.25±2.18	9.21±2.25
# of Snags	19.4±48.48	10.8±11.78	17.6±42.07	10.6±10.55	15.9±18.82	12.1±24.25	10.3±8.4	12.9±25.96
Avg. DBH Snags	32.6±10.79	35.8±11.59	34.7±10.81	35.2±11.67	34.7±12.92	35.2±11.36	39.2±12.44	34.3±11.11