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Woodpeckers as reliable indicators of bird richness, forest health and harvest

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ABSTRACT

Woodpeckers (family Picidae) show promise as indicators of avian diversity in forests because their populations can be reliably monitored, and their foraging and nesting activities can positively influence the abundance and richness of other forest birds. A correlation between woodpecker richness and richness of forest birds is known to exist at the landscape scale, but uncertainty remains whether this correlation occurs at the smaller stand-level spatial scales where forest management activities take place. We used data collected under a diverse range of forest types, harvest treatments, and forest health conditions during a long-term study of bird communities in interior British Columbia, Canada, to examine two basic questions: (1) at the level of individual forest stands, is woodpecker richness correlated with bird richness (measured as richness of all other bird species)? and (2) do woodpecker richness and bird richness have similar habitat correlates? Bird richness was positively correlated with woodpecker richness ($\beta = 0.59$, SE = 0.22, 95% CI = [0.14 1.03]). Richness of both woodpeckers and all other birds were positively correlated with tree species richness and negatively correlated with density of pines, and the effect for forest harvest type was similar for both measures of avian richness (uncut < partial harvest < clearcut with reserves). The effect of density of lodgepole pines killed by mountain pine beetles differed between the two richness measures, being positive for woodpecker richness and negative for forest bird richness. We conclude that the richness of woodpeckers is indeed correlated with the richness of other birds at the stand-level, and can serve as a reliable indicator of overall bird richness in most forest stands and conditions, except during insect outbreaks when differential responses by woodpeckers and the rest of the avian community may decouple the relationship between bird richness and woodpecker richness.

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1. Introduction

Agencies charged with protecting biodiversity or ecological integrity often rely on indicator species, or suites of species, whose populations can be reliably quantified and monitored (Landres et al., 1988; Simberloff, 1998; Thomson et al., 2005).

Woodpeckers (family Picidae) in particular have many attributes that may make them, as a suite, good candidates as indicators of avian diversity in forests (Mikusiński and Angelstam, 1998; Scherzinger, 1998; Mikusiński et al., 2001; Aubry and Raley, 2002; Roberge and Angelstam, 2006; Virkkala, 2006). They are associated with forests, their drumming and

excavation activities make them readily detectable, and local richness tends to range between 5 to 10 species (Angelstam and Mikusiński, 1994; Mikusiński, 2006), such that field personnel may be easily trained in their species identification. In addition, the foraging and nesting activities of woodpeckers can positively influence the abundance and richness of other forest birds. Woodpeckers excavate cavities in trees for nesting which are then used by a variety of other forest species (known as the 'nest web', Martin and Eadie, 1999; Martin et al., 2004), although the importance of this role may vary by forest type (Aitken and Martin, 2007; Wesołowski, 2007). The foraging activities of woodpeckers often involve removing the bark of dead and dying trees, which exposes the underlying substrate for foraging by other birds (Bull and Jackson, 1995). Mikusiński et al. (2001) examined the Polish Ornithological Atlas and found a positive correlation between woodpecker richness and forest bird richness at the landscape scale. Similarly, Roberge and Angelstam (2006) found that woodpecker species were among the best indicators of avian richness in large forest plots. Uncertainty remains however whether this correlation occurs at the smaller spatial scales where the relevant forest management activities occur.

We used data from a long-term study of forest birds to examine two basic questions: (1) is the number of woodpecker species (hereafter, 'woodpecker richness') correlated with the number of other bird species (hereafter, 'bird richness') at the level of individual forest stands over a wide range of habitat conditions and forest harvest types? and (2) do woodpecker richness and bird richness have similar habitat correlates and responses to changes in habitat conditions? As a corollary to the first question, we also determined whether the correlation varied spatially, since spatial variation in this correlation would provide evidence that woodpecker richness may be an unreliable indicator. The answer to the second question may help untangle the mechanisms behind a correlation between woodpecker richness and bird richness because such a relationship may exist under two non-mutually exclusive hypotheses. Some forest features provide conditions for all bird species in general, of which woodpeckers are a component, and thus result in a positive correlation in richness of woodpeckers and other birds. We evaluated this possibility by comparing how bird richness and woodpecker richness varied with the same set of habitat variables. Alternatively, the nesting and foraging activities of woodpeckers may facilitate the existence of other bird species. We argue that if the relationship between woodpecker richness and bird richness remains after accounting for habitat correlates, then woodpeckers represent an additive effect to habitat, that is, woodpeckers themselves act as a forest feature contributing to avian biodiversity.

Our study may have particular relevance to forest management. Forests cover most of the landscape in the study region, of which approximately 70% has been modified by anthropogenic activities (Lee et al., 2003), and harvest is the dominant disturbance (Parminter, 1998). In addition, an outbreak of mountain pine beetle (Dendroctonus ponderosae) and other forest insects has resulted in wide-spread mortality of conifers, primarily lodgepole pine (Pinus contorta var. latifolia), affecting over 9.2 million ha in British Columbia in 2007 (BCMFR, 2007). This outbreak is the largest recorded in the province since 1910, and is thought to have occurred as a consequence of earlier forest management activities and low over-winter mortality of beetle larvae during a series of consecutive mild winters (Hughes and Drever, 2001; Wood and Unger, 1996). Thus assessing the relationship between woodpeckers and bird richness across a wide range of forest habitat conditions and forest harvest types will help determine the general applicability of woodpeckers as indicators.

2. Methods

2.1. Study sites

We used data collected at 23 study sites in the Cariboo-Chilcotin region of British Columbia, all located within 50 km of the city of Williams Lake (52°08′30″N, 122°08′30″W). The sites varied between 15–35 ha in area, and were all mature forest stands (80–100 years old) prior to harvest, varying between sites of mixed deciduous/coniferous composition surrounded by grasslands, shallow ponds, and wetlands, to sites composed predominantly of dry coniferous forest with deciduous riparian zones bounded by small streams. The predominant coniferous species were Douglas-fir (Pseudotsuga menziesii), lodgepole pine, and hybrid white-Engelmann spruce (P. glauca x engelmannii), with occasional Rocky Mountain juniper (Juniperus scopulorum). The deciduous component of the forest was dominated by trembling aspen (Populus tremuloides), with occasional alder (Alnus spp.), paper birch (Betula papyrifera), and willow (Salix spp.).

These sites experienced a range of forestry operations during the study period (1997–2006) that were categorized into three basic treatments: 'uncut', which included sites of mature forests with no previous forest harvest activities, except for 2 sites that had selective cutting of Douglas-fir 20–40 years ago; 'partial harvest', which involved the removal of 15–30% of trees for small-scale commercial uses or hazard reduction resulting from the beetle outbreak; and 'clearcut with reserves', which involved removal of 50–90% of all trees, including all pine and spruce, with retention of most aspen and veteran Douglas-fir, either as reserves or spread throughout the cutblocks.

2.2. Richness and density of forest birds

We counted bird populations at study sites during May and June of each year, from 1997 to 2006, using point counts (Hutto et al., 1986) and playbacks (Johnson et al., 1981). Point count stations were spaced 100 m apart, and varied in number from 10 to 32 per site. Each point count station was sampled twice annually. From 0500–0930 h, point counts were completed at each station for 6 min during which every bird seen or heard within a 50-m-radius (0.79 ha) was recorded.

To survey woodpeckers, we used playbacks of woodpecker calls at every second point count station. After the initial 6 min observation period, the call of each woodpecker species known to be in the area was played twice, each call followed by 30 s of listening time, for a total of 13 min observation time. We noted the species and number of woodpeckers seen or heard calling, singing, or drumming during both the initial 6 min observation and the playback periods within the 50-m-radius.

Estimates of species richness vary strongly with sampling effort (Lande et al., 2003), so we used a sample-based rarefaction (Gotelli and Colwell, 2001) to standardize richness for sampling effort among sites and years. For each site/year combination, we estimated *bird richness* as the mean value of the number of bird species (excluding woodpeckers, raptors, and waterfowl) accumulated in 20 randomly selected point counts from 1000 random permutations of the data. The use of this averaging allowed us to simultaneously calculate richness measures using all the observation data for each site/year combination, and compare sites with different survey efforts. Data from site/year combinations with <20 point counts were not used; twenty (20) was arbitrarily selected as a round number comparable across sites. These calculations were done using the vegan package (Oksanen et al., 2007) in R (v. 2.5.0; R Development Core Team, 2007). Estimates of *woodpecker richness* were calculated in the same manner, using the number of species accumulated in 10 point counts with playbacks. Data from year/site combinations with <10 point counts with playbacks were not used. *Woodpecker density* was calculated as the total sum of woodpecker detections at each site/year, divided by the number of point counts, and converted into detections per ha by dividing by 0.79.

2.3. Vegetation and habitat measures

Vegetation and habitat data were collected yearly in 11.2 m radius vegetation plots (0.04 ha) around each point count station, with the point count station situated at the centre of the vegetation plot. We measured dbh ('diameter-at-breast height' [1.3 m]), and recorded tree species, decay class, and any signs of disease or animal use (e.g., feeding) for all trees with dbh ⩾ 12.5 cm. Decay class of trees ranged from 1 to 8, according to a classification system described in Backhouse and Louiser (1991), where 1 was a healthy tree, 2 was a live tree with evidence of disease or insect damage, and 3–8 were dead trees in increasing conditions of decay (see Martin et al., 2006 for more details). Decay classes 4–8 were rare in the data set, and were grouped into one decay class, 4+. In addition, trees in each plot were examined annually for evidence of disease, boring insects, such as mountain pine beetle, and fungal infections.

Using these data, we calculated for each site/year combination a series of habitat measures thought to be important to woodpeckers and birds in general. These measures were *density of Douglas-fir, lodgepole pine, hybrid spruce* (number of stems per ha for each conifer species), *density of deciduous trees* (number of stems per ha), *density of dead/dying aspen* (number of stems/ha), *mean dbh* (average dbh in cm for all stems measured at each site), *stand basal area* (in m^2/ha, calculated as the sum of the basal areas of all trees in vegetation plot and converted to per ha; $\sum \pi \times (dbh/200)^2/$[number of plots on site/0.04]), and *harvest type* ('uncut', 'partial harvest', 'clearcut with reserves'). We also calculated a number of habitat measures relevant to the mountain pine beetle outbreak, namely the density of beetle-attacked pines in decay classes 2, 3, and 4+, which corresponded to the *densities of 'green-attack' pines*, *'red-attack' pines*, and *'grey-attack' pines*, respectively. These names corresponded to the sequence of needle colour changes that occurred when lodgepole pines were attacked

and killed by the mountain pine beetle (Safranyik et al., 1974). 'Green-attack' pines were pines with evidence of beetle attack (pitch tubes), but whose needles were green and appeared healthy. 'Red-attack' pines were pines whose needles had turned red, which typically occurred 1 year after the initial beetle attack and indicated the tree was dying. Beetle larval densities under the bark can reach high densities in the summer prior to the foliage turning red (Safranyik and Wilson, 2006). 'Grey-attack' pines were those whose needles were falling off, which typically occurred 1 year following the red-attack stage, and indicated the tree was dead. Last, we calculated two stand-level tree diversity measures, *tree species richness* (mean number of tree species in 10 vegetation plots, using the same rarefaction approach described above), and *number of size classes* (the mean number of size classes in 10 vegetation plots, using the rarefaction approach described above, and where tree stems were classified into separate size classes of 12.5–14.9 cm, 15.0–24.9 cm, 25.0–34.9 cm, continuing to 115.0–124.9 cm).

While several of these habitat variables were inter-correlated and some variables were included in more than one model, all correlations among independent variables were less than 0.75, that is, below values that might cause collinearity problems (i.e., Pearson's correlation coefficient > 0.9; Burnham and Anderson, 2002).

2.4. Data analyses: is bird richness correlated with woodpecker richness?

We used a mixed-effects modeling approach (Pinheiro and Bates, 2000) to gauge the strength of the correlation of bird richness with woodpecker richness and density. Mixed-effects models incorporate both fixed effects, which explain variation in the response variable, and random effects, which serve as additional error terms to account for correlations among observations within the same group. The use of mixed models allowed us to assess the effects of woodpecker richness on bird richness as a population-level effect over all sites, to treat the site/year combinations as individual replicates, and to account for the repeated sampling of sites over time. Using the maximum likelihood method in package nlme in R (R Development Core Team, 2007), we fit a model with bird richness as the response variable, woodpecker richness as a fixed effect and site as a random effect. The slope parameter for woodpecker richness served as a measure of the average effect of woodpecker richness on forest bird richness over all sites. The variance of the random effect of site provided a measure of the contribution of site-level differences to the total variation in bird richness. Further, we reasoned that the extent to which the relationship between bird richness and woodpecker richness was invariant across a range of sites provided evidence that woodpecker richness could be viewed as a reliable indicator. This first model assumed a common relationship between bird richness and woodpecker richness for all sites. Therefore, we fit a second model that included random effects for woodpecker richness and site, which allowed the relationship between bird richness and woodpecker richness to vary by site, and compared the two models using a likelihood ratio test.

2.5. Data analyses: do bird richness and woodpecker richness have the same habitat correlates?

To examine whether and how richness of woodpeckers and other birds varied with forest habitat correlates, we grouped the explanatory variables into a suite of general linear mixed models, each representative of a biological hypothesis (Table 1), and then ranked the models using an information-theoretic approach (Burnham and Anderson, 2002). Each model had site as a random effect, but a different set of fixed effects. Model 1 was termed the 'stand composition' model, and included densities of conifer species, density of deciduous trees, density of dead/dying aspen, and tree species richness. Model 2 was the 'stand structure' model, which included variables related to the structural characteristics of the forest: mean dbh, basal area, and number of size classes. Model 3, the 'mountain pine beetle' model, included density of green-attack pines, density of red-attack pines, and density of grey-attack pines. Model 4 was termed the 'forest harvest' model, and included only harvest type as an explanatory variable. Model 5 was the 'all habitat correlates' model, which included all the above habitat features. In addition, when considering bird richness we evaluated two further models. Model 6, the 'woodpecker' model, included only woodpecker richness. Model 7, the 'all habitat correlates and woodpecker richness' model, included all habitat correlates and woodpecker richness as explanatory variables.

We evaluated the strength of evidence by calculating the value of Akaike's Information Criterion corrected for small sample sizes (AICc), and Akaike weight (w_i) for each model (Burnham and Anderson, 2002). The Akaike weight is a measure of the probability that a particular model is the most parsimonious of the suite, and can be used to calculate evidence ratios to compare pairs of models (Burnham and Anderson, 2002). In particular, we calculated the evidence ratio of model 7 (all habitat correlates and woodpecker richness) to model 5 (all habitat correlates) to assess the weight of evidence for

an additive effect of woodpecker richness on bird richness. In addition, we calculated model-averaged parameter estimates and their standard errors as weighted averages of the parameter estimates from all models, using Akaike weights as weighting factors normalized to 1 for the subset of models where that parameter appeared (Burnham and Anderson, 2002). The proportion of total variance in the response variable explained by each model was calculated as $r^2 = 1 - (\sigma^2 / \sigma_0^2)$, where σ^2 is the variance of the residuals for each model, and σ_0^2 is the total variance in the response variable (Xu, 2003). We also fit models 1–5 using woodpecker density as an response variable in the place of woodpecker richness. However, results for the two woodpecker measures were similar because of the strong correlation between woodpecker richness and density (see Section 3). For the sake of brevity, only the results for woodpecker richness are presented here.

3. Results

3.1. Is bird richness correlated with woodpecker richness?

The final data set consisted of 8286 point counts conducted between 1997 to 2006, during which 7 woodpecker species and 76 other bird species were observed (see Appendix 1), from which measures of woodpecker richness, bird richness, and habitat attributes were calculated for 206 site/year combinations. The mean number of bird species observed during 20 point counts ranged between 7.3 and 24.8 species (mean = 14.8 species, variance = 9.66 species). The mean number of woodpecker species observed during 10 point counts with playbacks ranged between 0 and 3.6 species (mean = 1.2 species, variance = 0.60), and densities of woodpeckers ranged between 0 and 0.9 individuals per ha (mean = 0.2 individuals per ha, variance = 0.03). Woodpecker density and richness were strongly correlated over the 206 site/year combinations (Pearson's correlation coefficient = 0.94), such that site/years with high densities had high woodpecker richness.

Table 1 – Ranking of models relating bird richness and woodpecker richness to forest habitat variables in the Cariboo-Chilcotin region, British Columbia, Canada, 1997–2006

#	Model name	n	K	$-2*LL$	ΔAICc	w	r^2
Forest bird richness							
4	Forest Harvest	206	5	946.4	0.0	0.49	0.58
1	Stand Composition	206	9	938.3	0.6	0.37	0.57
6	Woodpecker richness	206	4	952.5	4.0	0.07	0.56
5	All habitat correlates	206	17	924.7	5.3	0.03	0.60
7	All habitat correlates + woodpecker richness	206	18	923.3	6.3	0.02	0.61
2	Stand Structure	206	6	951.2	7.0	0.01	0.57
3	Mountain Pine Beetle	206	6	952.8	8.6	0.01	0.56
Woodpecker richness							
5	All habitat correlates	206	17	369.8	0.0	0.85	0.41
4	Forest Harvest	206	5	397.9	3.5	0.15	0.39
1	Stand Composition	206	9	398.5	12.7	0.00	0.42
2	Stand Structure	206	6	411.0	18.8	0.00	0.42
3	Mountain Pine Beetle	206	6	442.1	49.8	0.00	0.35

= Model number, model name (see text for explanation of variables); n = sample size; K = number of parameters; $-2*LL = -2*$ log likelihood; ΔAICc = the difference in Akaike's Information Criterion corrected for small sample sizes (AICc), between each model and the model with the minimum AICc; w = Akaike weight; r^2 = proportion of total variation in response variable explained by each model. Models are ranked in ascending order by ΔAICc.

We found that bird richness was weakly but positively correlated with woodpecker richness, and that this relationship did not vary among sites. Bird richness varied widely among sites, and the slope parameter for the effect of woodpecker richness was $\beta = 0.59$ (SE = 0.22, 95% CI = [0.14 1.03]), indicating that, as an average effect over all sites, bird richness was positively correlated with woodpecker richness (Fig. 1). The standard deviation of the site random effect was 2.08 species, roughly comparable to the standard deviation of the residuals of 2.15 species, indicating that bird richness varied among sites with approximately the same magnitude as the annual variation within sites. While the relationship between bird richness and woodpecker richness appeared to vary somewhat among sites (Fig. 1), the model that allowed the relationship between bird richness and woodpecker richness to vary among sites did not have significantly improved model fit over the model in which the relationship was invariant across sites (difference in log likelihood = 0.20, df = 2, P = 0.90). Thus, the simpler model provided a better representation of the data, and indicated that the relationship between bird richness and woodpecker richness did not vary across sites.

3.2. Do bird richness and woodpecker richness have the same habitat correlates?

Bird richness in forest plots was affected by several habitat attributes, particularly those related to forest harvest, stand composition, and woodpecker richness. The best model explaining variation in bird richness was the forest harvest model (Table 1). This model had a value of $w = 0.49$, suggesting that support for this model relative to others in the suite was not strong. The next best models were the stand composition model and the woodpecker richness model ($w = 0.37$ and 0.07, respectively). The evidence ratio for model 7 relative to model 5 was 0.7 ($w_7/w_5 = 0.02/0.03$), indicating these two models had similar support, such that model fit did not improve with the addition of woodpecker richness. The data thus provided weak evidence for an additive effect of woodpecker richness on richness of birds above that provided by the habitat variables.

Model-averaged parameters also supported the correlation of multiple habitat attributes with bird richness (Table 2). In particular, we found evidence of negative correlations
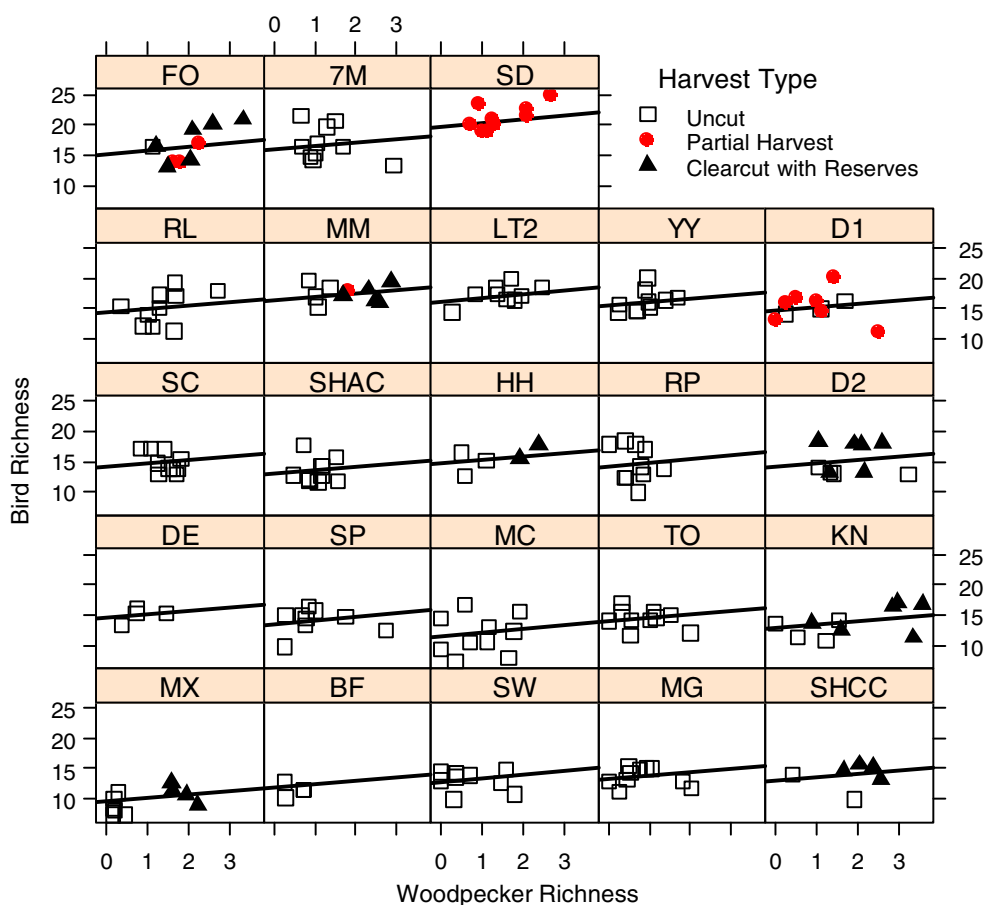

Fig. 1 – Correlation between bird richness and woodpecker richness at 23 sites in the Cariboo-Chilcotin region, British Columbia, Canada, 1997–2006. Bird richness was calculated as the mean value of the number of bird species (excluding woodpeckers, raptors, and waterfowl) accumulated in 20 randomly selected point counts. Woodpecker richness was calculated as the number of woodpecker species accumulated in 10 point counts with playbacks. Alphanumeric codes indicate site names, and sites are arranged in order of mean bird richness per site. Lines are predicted values of mean relationship between bird richness and woodpecker richness across all sites, and the point symbols indicate forest harvest type.

Table 2 – Model-averaged parameter estimates for models explaining variation in forest bird richness and woodpecker richness to forest habitat and harvest variables (defined in text) in the Cariboo-Chilcotin region, British Columbia, Canada, 1997–2006

Parameter	Bird richness			Woodpecker richness		
	Estimate	SE	t	Estimate	SE	t
Intercept	13.20	1.75	**7.55**	0.9955	1.1232	0.89
Density of dead/dying aspen	0.0337	0.0387	0.87	−0.0043	0.0068	−0.63
Density of deciduous trees	0.0031	0.0109	0.28	−0.0002	0.0021	−0.12
Density of Douglas-fir	−0.0017	0.0035	−0.48	−0.0025	0.0015	−1.61
Density of lodgepole pine	−0.0068	0.0024	**−2.88**	−0.0030	0.0013	**−2.26**
Density of hybrid spruce	−0.0037	0.0062	−0.59	−0.0028	0.0017	−1.64
Number of tree species	1.60	0.66	**2.42**	0.32	0.11	**2.89**
Basal area	0.135	0.120	1.13	0.0385	0.026	1.48
Mean dbh	0.004	0.251	0.02	0.0478	0.053	0.90
Number of size classes	−0.170	0.486	−0.35	−0.2136	0.079	**−2.72**
Density of 'green-attack' pines	0.0070	0.0048	1.47	0.0006	0.0013	0.42
Density of 'red-attack' pines	−0.0061	0.0031	**−1.97**	0.0018	0.0008	**2.20**
Density of 'grey-attack' pines	0.0037	0.0390	0.09	−0.0058	0.0066	−0.88
Forest harvest ('uncut' vs. 'clearcut with reserves')	−1.87	0.58	**−3.22**	−0.86	0.16	**−5.26**
Forest harvest ('partial cut' vs. 'clearcut with reserves')	−0.62	0.92	−0.67	−0.59	0.21	**−2.81**
Number of woodpecker species	0.52	0.23	**2.21**			

Parameters for forest harvest were calculated as mean differences in relation to harvest type 'clearcut with reserves'. For example, a negative estimate for forest bird richness in forest harvest ('uncut'–'clearcut with reserves') indicates that forest bird richness was lower in 'Uncut' sites than on 'clearcut with reserves' sites. t = estimate/SE. Parameters where $|t| > 1.96$ have 95% confidence intervals that do not include 0 (in bold).

between bird richness and densities of lodgepole pines and red-attack pines, and positive correlations with number of tree species and woodpecker richness (Table 2). The parameters for forest harvest indicated that sites with partial harvest and clearcuts with reserves had similar bird richness, whereas uncut sites had on average 1.87 fewer species than clearcuts with reserves (Table 2, Fig. 2). Predicted population margins from the forest harvest model (which provide a measure of mean value when controlling for other factors in the model) indicated that bird richness across the three levels of forest harvest varied along the spectrum of harvest intensity where uncut < partial harvest < clearcut with reserves (Fig. 2).

Woodpecker richness was similarly correlated with multiple habitat features, as indicated by the strong support found for the 'all habitat correlates' model, which had $w = 0.85$ (Table 1). Model-averaged parameter values for woodpecker richness indicated negative correlations with density of lodgepole pines and number of size classes, and positive correlations with the density of red-attack pines and number of tree species (Table 2). The parameters for forest harvest indicated that highest values of woodpecker richness were found in clearcuts with reserves, which had on average 0.59 more woodpecker species than sites with partial harvest, and 0.86 more woodpecker species than uncut sites (Fig. 2). Predicted population margins from the 'all habitat correlates' model for woodpecker richness indicated that woodpecker richness varied across the three levels of forest harvest in a similar manner to bird richness, such that uncut < partial harvest < clearcut with reserves (Fig. 2).

The opposing effects of red-attack pines on bird richness and woodpecker richness (see Section 4) pointed out the possibility that the relationship between bird richness and woodpecker richness may have varied with the density of beetle-attacked pines. We conducted one post hoc test for this possibility by fitting a model of bird richness as a function of

the relevant habitat variables from Table 2, woodpecker richness, and the interaction between woodpecker richness and density of red-attack pines, with site as a random effect. The 95% confidence interval for the interaction effect was [−0.032 −0.005], which did not encompass 0. This negative interaction between woodpecker richness and density of red-attack pines suggested that the positive relationship between bird richness and woodpecker richness decreased in magnitude as density of 'red-attack' pines increased, such that the correlation between bird richness and woodpecker richness was nearly 0 at high densities of red-attack pines (Fig. 3).

4. Discussion

Bird richness at our study sites was positively correlated with woodpecker richness, and this correlation was consistent among sites with different forest composition and management histories. This stand-level correlation is consistent with correlations seen at the landscape level (10 km × 10 km plots, Mikusiński et al., 2001; 1 km × 1 km plots, Roberge and Angelstam, 2006), and suggests that woodpecker richness can also serve as a reliable indicator of bird richness at smaller landscape units. We also found that bird richness and woodpecker richness had several habitat correlates in common (negative correlations with density of lodgepole pine, positive correlation with number of tree species), and importantly had similar effects of forest harvest, which add to the general reliability of woodpecker richness as an indicator. However, we identified one habitat condition that had an effect that differed in direction between bird richness and woodpecker richness. The density of red-attack pines had a negative effect on bird richness, and positive effect on woodpecker richness. These opposing correlations suggest that following trends in woodpecker richness during outbreaks of bark beetles may

Bird Richness

Woodpecker Richness

Fig. 2 – Forest management and avian richness in the Cariboo-Chilcotin region, British Columbia, 1997–2006. Bird richness was calculated as the mean value of the number of bird species (excluding woodpeckers, raptors, and waterfowl) accumulated in 20 randomly selected point counts. Woodpecker richness was calculated as the number of woodpecker species accumulated in 10 point counts with playbacks. Values represent predicted population margins (which provide a measure of mean value when controlling for other factors in the model) from the best model for each richness measure (see text for details). Bar categories indicate type of forest management. 'Uncut' refers to sites of mature forests with no previous forest harvest activities; 'Partial', refers to 'partial harvest', which involved the removal of 15–30% of trees; and 'C. Cut' refers to 'clearcuts with reserves', which involved removal of 50–90% of all trees, with retention of most aspen and veteran Douglas-fir. Lines on bars indicate standard errors, and bars with different letters indicate groups where the 95% confidence interval of the difference between groups did not included 0.

provide misleading information about trends in bird richness in forests. Therefore, we conclude that woodpecker richness can generally serve as an indicator of forest bird richness,

but it must be used with caution during outbreaks of forest insects.

The weak evidence of an additive effect of woodpecker richness on bird richness and the number of shared habitat correlates suggest that the observed correlation between bird richness and woodpecker richness resulted from similar responses to changes in habitat, rather than due to the facilitative role that woodpeckers may play within the entire avian community. Alternatively, it may be that complex interactions within the avian community dampen the keystone effect of woodpeckers. With a reduced data set from the same study area, Martin and Eadie (1999) examined correlations in abundances of birds in different compartments of the nest web (cavity excavators (e.g., woodpeckers), weak excavators, secondary cavity nesters, and non-cavity nesters), and demonstrated that the abundance of secondary cavity nesters was strongly and positively correlated with the abundance of excavators, and negatively correlated with the abundance of non-cavity nesters. Following Bock et al. (1992), the authors speculated that this negative correlation between secondary cavity nesters and non-cavity nesters may have resulted from competition for invertebrate prey. If this is the case, then the correlation between woodpecker richness and bird richness may thus represent the balance between the facilitative role of woodpeckers for secondary cavity nesters and the possibly competitive relationship between secondary cavity nesters and rest of the avian community.

Forest harvest type had a strong and similar effect on bird richness and woodpecker richness, with richness varying across management types such that clearcut with reserves > partial harvest > uncut stands. Martin and Eadie (1999) predicted that forest harvesting that retained most mature aspen and large Douglas-fir trees, as was done in our clearcuts with reserves and partial harvest sites, would meet the requirements of most cavity-nesting guilds, and we speculate that the parkland conditions created by the harvesting may have allowed the incursion of several species from the surrounding grasslands in which many of our study sites are enmeshed as well as retaining most species from the original avian community (Appendix 1). A detailed species by species breakdown to test this idea is beyond the scope of this paper, and we note only that the similar effects of forest harvest on woodpecker and bird richness provides support for the use of woodpecker richness as an indicator for the effect of forest management on birds.

We found that both woodpecker richness and bird richness were positively correlated with tree species richness and negatively correlated with density of lodgepole pine. These results concur with other studies comparing avian diversity across forest stands that have found that avian richness varies with stand composition in descending order from mixed stands, to deciduous stands, to coniferous stands (James and Wamer, 1982; Turchi et al., 1995; Willson and Comet, 1996; Hobson and Bayne, 2000). This pattern is thought to result from the greater availability of invertebrate prey in deciduous forests relative to coniferous forests (Willson and Comet, 1996; Niemelä, 1997), and presumably sites with high richness of tree species provide a diversity of habitat conditions that facilitate the co-existence of multiple bird species (MacArthur and MacArthur, 1961).
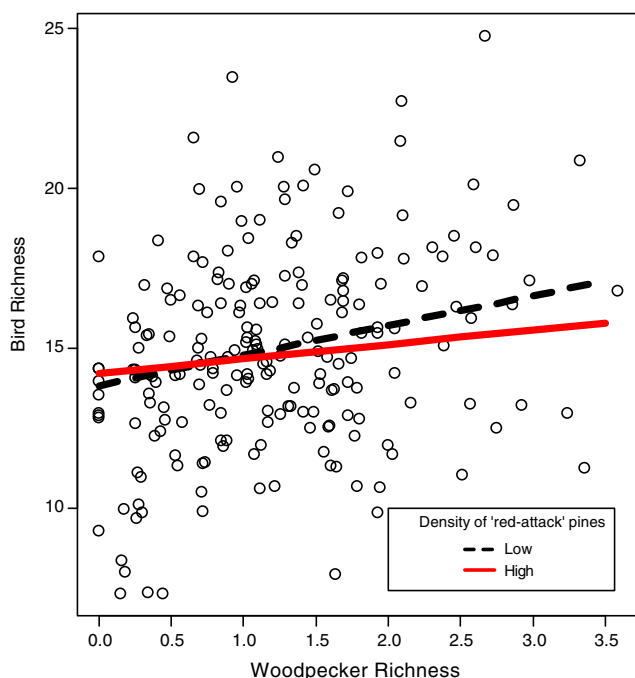
Fig. 3 – Variation in the relationship between bird richness and woodpecker richness with density of lodgepole pines killed by mountain pine beetles in the Cariboo-Chilcotin region, British Columbia, 1997–2006. Lines indicate predicted values from a mixed-effects model of bird richness as a function of density of 'red-attack' pines, woodpecker richness, and their interaction. High and low densities of 'red-attack' pines refer to 0.25 and 0.75 quantiles. Parameters values (with SE) were intercept, 13.8 (0.56); density of 'red-attack' pines, 0.014 (0.009); woodpecker richness, 1.02 (0.26); and density of red-attack pines∗woodpecker richness, −0.018 (0.007). Standard deviations for random effects were site: 2.07, and residual: 2.08.

In contrast to the consistent effect of pine density and tree species diversity, the effect of beetle-killed trees differed between bird richness and woodpecker richness, and this differential response may partly account for the weak correlation we observed between the two richness measures. Similar patterns of reduced bird richness in forests following outbreaks of *Dendroctonus* beetles were observed in Oregon and Alaska (Bull, 1983; Lance and Howell, 2000). The negative correlation between bird richness and density of red-attack pines at our study sites was largely driven by a decrease in the richness of foliage gleaning species as the conifers lost their needles (Martin, unpublished data), similar to the decline in numbers of foliage gleaning species following a mountain pine beetle outbreak in Oregon (Bull, 1983). Woodpeckers have been shown to increase in abundance and diversity immediately following bark beetle outbreaks (Yeager, 1955; Bull, 1983; Stone, 1995; Lance and Howell, 2000; Conner et al., 2001; Scherzinger, 2006), largely due to the increase in abundance of woodpecker species that forage predominantly on dead and dying conifers, such as the three-toed woodpecker and black-backed woodpecker, whose populations have increased throughout the study period at

our study sites (Drever and Martin, 2007). The association with red-attack pines however suggests this increase is temporary, as pines only remain in this state for 1–2 years (Safranyik et al., 1974). As such, woodpeckers may expect to experience 'boom and bust' trends, where the initial increases are followed by declines in abundance (Conner et al., 2001; Scherzinger, 2006; Martin et al., 2006). Such a decline would mean woodpecker richness would again match bird richness, but the lag introduced by the differential response by woodpeckers and other birds reduces the reliability of woodpeckers as indicators of bird richness during the peak phase of bark beetle outbreaks.

The use of indicator species provides an appealing shortcut to monitoring biodiversity because it can enable efficient use of limited resources available for monitoring. This efficiency however must be balanced against the increased uncertainty about the underlying process or community being monitored (e.g., Field et al., 2005). In our case, the bulk of the survey effort is spent in accessing sites, and information on woodpeckers can be collected simultaneously with information on composition of the entire community. Therefore, monitoring only woodpeckers may not warrant the increased uncertainty. However, if the intent is to survey extensive land areas, rather than to intensively survey smaller plots as in our study, then surveying woodpeckers will provide a valuable increase in efficiency allowing for more sites to be surveyed. In addition, our results are valuable from the perspective of conservation planning for ecological integrity (Parks Canada, 2000; Favreau et al., 2006), because they suggest that maintaining habitats that allow for a diversity of woodpeckers will also aid in the maintenance of overall avian diversity. Furthermore, our results are consistent with the general finding that subsets of species can be good predictors of the full suite of species (Vellend et al., 2007), which can shed some light into processes that govern biodiversity of the entire community (e.g., we found that both woodpecker richness and bird richness were strongly correlated with the number of tree species).

In evaluating the utility of woodpecker richness as an indicator of bird richness at our study sites, the positive correlation between the two measures and the similar effects of forest harvest and habitat variables must be balanced against the uncertainties introduced by the disparate effects on richness during the mountain pine beetle outbreak. Combined with the known role of woodpeckers as excavators of nesting sites used by other species (Martin and Eadie, 1999; Aitken and Martin, 2007), which merit their specific monitoring efforts as keystone or facilitator species (Simberloff, 1999), our results suggest that woodpeckers are useful indicators of bird richness across a wide range of forest types and conditions. We add the caveat that the use of woodpeckers as indicators must be viewed with caution during insect outbreaks.

Acknowledgements

Appendix 1

List of bird species recorded during point count surveys in 23 forest stands in the Cariboo-Chilcotin region, British Columbia, 1997–2006

Species
Ruffed grouse (*Bonasa umbellus*)
Sharp-tailed grouse (*Tympanuchus phasianellus*)
Common snipe (*Gallinago gallinago*)
Common nighthawk (*Chordeiles minor*)
Rufous hummingbird (*Selasphorus rufus*)
Olive-sided flycatcher (*Contopus cooperi*)
Western wood-pewee (*Contopus sordidulus*)
Alder flycatcher (*Empidonax alnorum*)
Dusky/Hammond's flycatcher (*Empidonax oberholseri/ hammondii*)
Least flycatcher (*Empidonax minimus*)
Pacific-slope flycatcher (*Empidonax difficilis*)
Willow flycatcher (*Empidonax traillii*)
Eastern kingbird (*Tyrannus tyrannus*)
Cassin's vireo (*Vireo cassinii*)
Red-eyed vireo (*Vireo olivaceus*)
Warbling vireo (*Vireo gilvus*)
Red-naped sapsucker (*Sphyrapicus nuchalis*)
American three-toed woodpecker (*Picoides dorsalis*)
Black-backed woodpecker (*Picoides arcticus*)
Downy woodpecker (*Picoides pubescens*)
Hairy woodpecker (*Picoides villosus*)
Northern flicker (*Colaptes auratus*)
Pileated woodpecker (*Dryocopus pileatus*)
American crow (*Corvus brachyrhynchos*)
Black-billed magpie (*Pica hudsonia*)
Common raven (*Corvus corax*)
Gray jay (*Perisoreus canadensis*)
Barn swallow (*Hirundo rustica*)
Northern rough-winged swallow (*Stelgidopteryx serripennis*)
Tree swallow (*Tachycineta bicolor*)
Violet-green swallow (*Tachycineta thalassina*)
Black-capped chickadee (*Poecile atricapillus*)
Boreal chickadee (*Poecile hudsonica*)
Mountain chickadee (*Poecile gambeli*)
Red-breasted nuthatch (*Sitta canadensis*)
Brown creeper (*Certhia americana*)
Marsh wren (*Cistothorus palustris*)
Winter wren (*Troglodytes troglodytes*)

Appendix 1 – (continued)

Species
Golden-crowned kinglet (*Regulus satrapa*)
Ruby-crowned kinglet (*Regulus calendula*)
Mountain bluebird (*Sialia currucoides*)
Townsend's solitaire (*Myadestes townsendi*)
Hermit thrush (*Catharus guttatus*)
Swainson's thrush (*Catharus ustulatus*)
Veery (*Catharus fuscescens*)
Evening grosbeak (*Coccothraustes vespertinus*)
American robin (*Turdus migratorius*)
Varied thrush (*Ixoreus naevius*)
European starling (*Sturnus vulgaris*)
American pipit (*Anthus rubescens*)
Bohemian waxwing (*Bombycilla garrulus*)
Cedar waxwing (*Bombycilla cedrorum*)
Common yellowthroat (*Geothlypis trichas*)
Magnolia warbler (*Dendroica magnolia*)
MacGillivray's warbler (*Oporornis tolmiei*)
Northern waterthrush (*Seiurus noveboracensis*)
Orange-crowned warbler (*Vermivora celata*)
Townsend's warbler (*Dendroica townsendi*)
Wilson's warbler (*Wilsonia pusilla*)
Yellow-rumped warbler (*Dendroica coronata*)
Yellow warbler (*Dendroica petechia*)
Blackpoll warbler (*Dendroica striata*)
Western tanager (*Piranga ludoviciana*)
Clay-colored sparrow (*Spizella pallida*)
Chipping sparrow (*Spizella passerina*)
Vesper sparrow (*Pooecetes gramineus*)
Savannah sparrow (*Passerculus sandwichensis*)
Lincoln's sparrow (*Melospiza lincolnii*)
Song sparrow (*Melospiza melodia*)
Golden-crowned sparrow (*Zonotrichia atricapilla*)
White-crowned sparrow (*Zonotrichia leucophrys*)
Dark-eyed junco (*Junco hyemalis*)
Red-winged blackbird (*Agelaius phoeniceus*)
Western meadowlark (*Sturnella neglecta*)
Yellow-headed blackbird (*Xanthocephalus xanthocephalus*)
Brewer's blackbird (*Euphagus cyanocephalus*)
Rusty blackbird (*Euphagus carolinus*)
Brown-headed cowbird (*Molothrus ater*)
Cassin's finch (*Carpodacus cassinii*)
Purple finch (*Carpodacus purpureus*)
Red crossbill (*Loxia curvirostra*)
White-winged crossbill (*Loxia leucoptera*)
Pine siskin (*Carduelis pinus*)

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