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HILLS, SOUTH DAKOTA**

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ABSTRACT

We investigated the effects of stand size resulting from current logging practices on occurrence and species richness of song birds in the Black Hills. Richness of forest interior and forest interior/edge song birds was not related to stand area ($P \geq 0.40$) in stands of ponderosa pine (*Pinus ponderosa*) in the Black Hills. Brown creepers (*Certhia americana*) occurred only in stands of unmanaged forest >18 ha, but large diameter trees appeared to be more strongly associated with brown creepers than stand area. Ovenbirds (*Seiurus aurocapillus*) occurred in all size categories of stands but more frequently in stands 25-35 ha. Western tanagers (*Piranga ludoviciana*) did not occur in stands less 10 ha but do not appear to depend on dense late-seral forest in the Black Hills. These sizes of forest stands are within the normal range of stand sizes in the Black Hills National Forest. We offer an explanation why logging in the Black Hills might not fragment the forest for song birds.

Key words: song birds, fragmentation, species-area relations, logging.

INTRODUCTION

The Black Hills National Forest (BHNF) is an intensively managed forest dominated by ponderosa pine (*Pinus ponderosa*) in western South Dakota. Approximately 70 percent of the BHNF is managed primarily for timber production and harvest (Black Hills National Forest 1996). Logging in the BHNF alters the density and age (or average diameter-at-breast height, DBH) of forested stands, but only under special management objectives are forest stands converted to openings. Silvicultural techniques for logging in

the BHNF include seed-tree and three-step shelterwood. Logged stands must have 370 to 741 established seedlings/ha within five years after logging is completed (National Forest Management Act 1976). Thus, the context of forest fragmentation from logging in the BHNF differs from that described for eastern deciduous forests (e.g., Whitcomb *et al.* 1981, Ambuel and Temple 1983, Freemark and Merriam 1986, Faaborg *et al.* 1993). Nonetheless, some scientists maintain that logging and roads fragment the BHNF (Crompton 1994, Shinneman 1996) and are pushing the forest ecosystem farther from its range of natural variation (Shinneman and Baker 1997). In addition, fragmentation caused by logging has been a central theme in administrative appeals of timber sales in the BHNF by public organizations concerned with environmental protection. If logging activities fragment the forest in the Black Hills, it is important to understand the context and

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nature of the effects. The species-area relation for song birds is one aspect of forest fragmentation. In this paper, we investigate the species-area relations for song birds in the BHNF.

STUDY AREA AND METHODS

Forested stands, in the BHNF, are land units of relatively homogeneous forest vegetation 4-32 ha in size, but occasionally are larger. We described vegetation in stands as described in a hierarchical system using dominant vegetation types, DBH, and overstory canopy cover. Hereafter, we will refer to stand vegetation descriptions as forest vegetation structural stages. The boundaries of stands are delineated from topographic features such as ridges, drainages, and roads, and by changes in forest vegetation structural stage. Figure 1 depicts typical stands and boundaries in the BHNF.

We selected 40 stands of ponderosa pine; 20 stands were commercially logged within the previous 10 years (managed stands), and 20 stands had no timber management activity for >40 years (unmanaged stands). Because nearly all of the Black Hills have had some human intervention since nonnative settlement, we used this criterion to identify stands of dense mature timber as unmanaged stands. These stands represent the forest structure that is considered fragmented by logging in the BHNF. We digitized the area of each stand from aerial photographs. Stand area ranged from 4 to 50 ha. Managed stands averaged 16 m²/ha basal area, 23.4 cm DBH, and 43 percent overstory canopy cover; unmanaged stands averaged 28 m²/ha basal area, 22.2 cm DBH, and 68 percent overstory canopy cover (Dykstra *et al.* 1999). Lower average DBH in unmanaged stands resulted from the small trees beneath the primary forest canopy.

In each stand, we located two to five sites for variable-radius bird counts

(Reynolds *et al.* 1980). Generally, more sites for bird counts were located in larger stands than smaller stands. Sites for bird counts were >100 m from the stand boundary except in three small stands where size and configuration necessitated placing sites 50-70 m from the stand boundary. Bird counts began 1/2 hour before sunrise and were completed by 1100 hrs (Mills *et al.* 2000). We identified and recorded all birds seen or heard near the site while approaching the site (Hutto *et al.* 1986) and for eight minutes following arrival at each site. We conducted bird counts for two consecutive days, which constituted one count-session at each site. During 1993, we completed two count-sessions (beginning dates of 21 May and 9 June), and during 1994, we completed three count-sessions (beginning dates of 23 May, 7 June, and 20 June). We did not count birds during periods of moderate to heavy rain, when winds exceeded 10 km/h or if temperatures were <7 C or >24 C (Manuwal and Carey 1991).

Our analyses included birds ≤30 m from the bird count site that were perched in trees, on the ground, or in shrubs within the ponderosa pine forest. We selected 30 m as the furthest distance because observers begin to overlook birds at distances >30 m in forests (Emlen 1971, Verner and Ritter 1988). We assigned habitat affiliations of wide ranging, forest interior, interior/edge, or edge to birds based on Whitcomb *et al.* (1981), Blake (1991), and our understanding of species habitat requirements. Widely ranging species such as turkey vultures (*Cathartes aura*), hawks (Family *Accipitridae*), Merriam's turkeys (*Meleagris gallopavo merriami*), etc., were not included in these analyses. Species richness represents the sum of singing passerine and *Picidae* (e.g., Lescourret and Genard 1994) species occurring at sites or in stands, depending on the analysis. For example, analyses comparing species richness

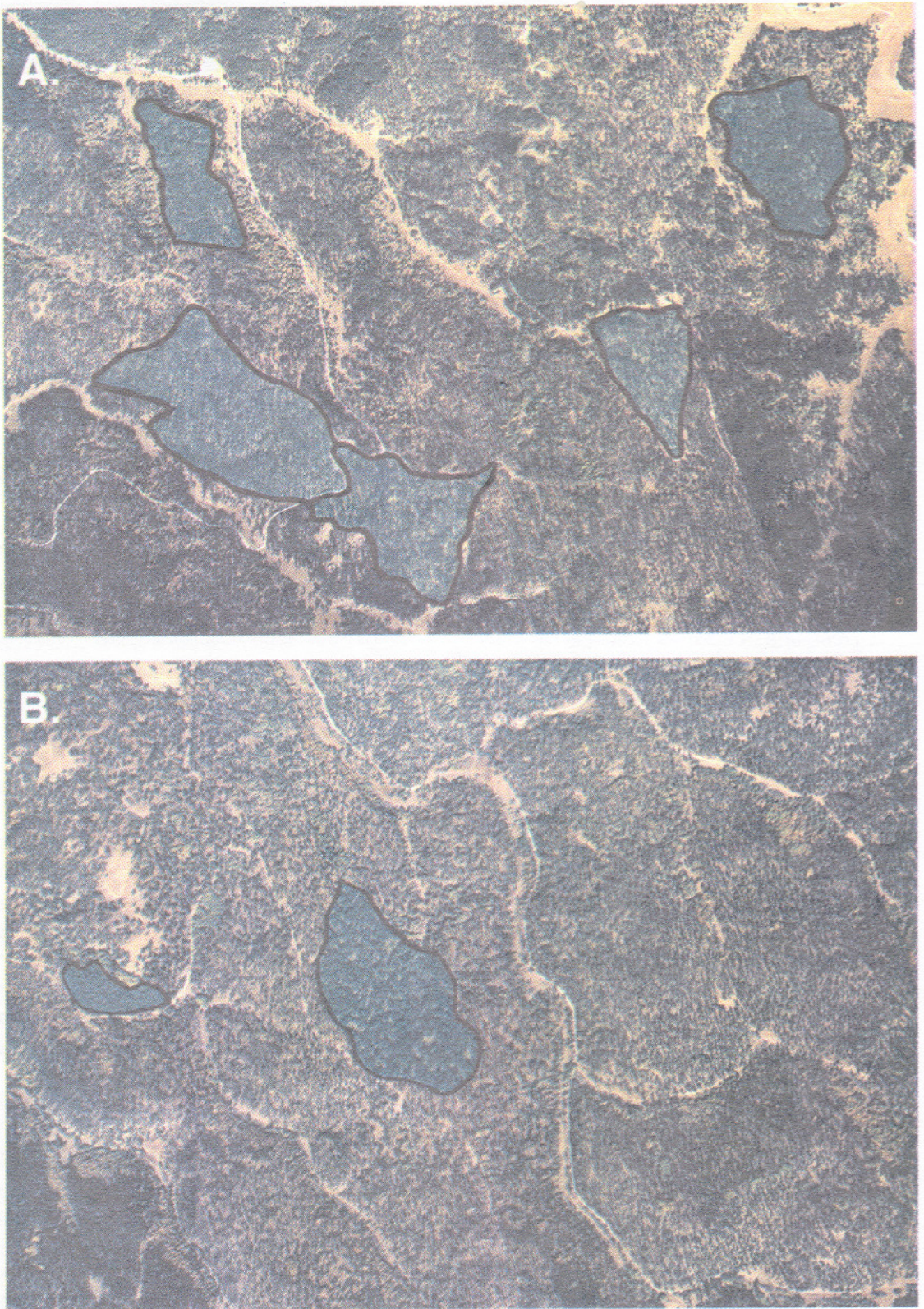


Figure 1. Aerial photographs (1:24000) depicting typical stands included in this study. A). Unmanaged ponderosa pine stands (upper right of photo) surrounded by lower density pine forest, meadows, and roads, and several managed stands (lower portion of photo) surrounded by roads and meadows. B). Two unmanaged stands surrounded by less dense forest meadows, and roads.

between years included the number of species occurring in each stand for each year. We used a paired *t*-test to compare species richness in stands between years. This test was not significant ($P = 0.78$); thus, species richness for subsequent analyses represents the sum of species occurring at sites or stands applicable to the analysis for both years.

We plotted species richness for successive count-sessions at sites in each stand to formulate species accumulation curves (Freemark and Merriam 1986, Blake and Karr 1987). These species accumulation curves were examined for evidence of asymptotes; an indication that the number of counts in the stand was adequate to estimate species richness. We tested the hypothesis "that occurrence of bird species was not related to the size of stands" using the following methods. We conducted linear regressions of species richness on stand area for 1) unmanaged stands, 2) managed stands, and 3) all stands (combined). For managed and unmanaged stands we conducted the regression analyses using: 1) all song birds (and *Picidae*) excluding wide ranging species, and 2) song birds and *Picidae* associated with forest interior or interior/edge conditions. Because placing more bird count sites in larger stands could result in detecting more species in those stands (Hutto *et al.* 1986), we also conducted linear regression analyses of species richness per count on stand area. We assessed the appropriateness of linear models by testing the residuals using the Shapiro-Wilk's test (Shapiro and Wilk 1965).

To estimate the pure effects that stand area has on occurrence of individual bird species, we compared the model chi square value of a logistic regression that predicted occurrence of species from vegetation characteristics with the model chi square of a logistic regression that predicted occurrence of species from vegetation characteristics and stand area (Lescourret and Genard

1994). The difference between the model chi square values tests the hypothesis "that the coefficient attributable to stand area is 0." We used both site-level and stand-level data to complete the logistic regression analyses. Site-level data are best for analyzing the effects of habitat characteristics on bird occurrence, but stand-level data better estimate effects of stand area on bird occurrence (Askins *et al.* 1987). To simplify vegetation characteristics for consideration in the logistic regression, we used principal components analysis (PCA) to develop a reduced number of variables that captured the vegetative features. Vegetation features data and sampling protocol are summarized in Dykstra *et al.* (1999). We completed the logistic regressions for a species only if that species occurred at more than five sites or in more than five stands for respective analyses because we felt there was little chance of obtaining meaningful results at lower rates of occurrence. We then used step-wise forward multiple regression including the PCA factor scores and stand area to determine if vegetation coupled with stand area showed a relation to species richness.

We calculated the average species observation frequency at sites within stands for six stand-size categories. Stand-size categories were selected as a post-hoc compromise between number of stands in each category and the range of area included in each category. The size-intervals and sample sizes (*n*) included 4-9 ha ($n = 4$), 10-14 ha ($n = 6$), 15-19 ha ($n = 10$), 20-24 ha ($n = 8$), 25-34 ha ($n = 5$), and 35-50 ha ($n = 7$). The average frequency of observation in stand size categories was plotted and these graphs were examined for a threshold in stand size, below which the species was absent or less common. This was a qualitative examination because all statistical evaluation of frequencies among uncommon species were not significant because of low and variable

occurrences.

Scientific names for birds follow the AOU (1983) checklist with supplements. We set statistical significance for all tests at $\alpha = 0.05$, marginal significance was determined at $\alpha = 0.10$. For $\alpha = 0.05$, this study had 92 percent chance of detecting $r \geq 0.5$ when all stands ($n = 40$) were considered and a 64 percent chance of detecting $r \geq 0.5$ when managed or unmanaged stands ($n = 20$) were considered separately. We considered $r \geq 0.5$ large enough to be biologically significant.

RESULTS

Cumulative species richness of count-sessions in stands indicated some small stands with only two sites did not demonstrate an asymptote (unpublished data, Rocky Mountain Research Station, Rapid City, SD), suggesting that we might have underestimated richness in these small stands. Most larger stands demonstrated an asymptote in species richness after counting three to four sites and several stands >20 ha showed an asymptote in species richness after counting only two sites. All stands >25 ha, except one, clearly exhibited an asymptote in species richness for the count efforts we completed. We included the small stands with only two sites in our analyses because any bias that might occur was not evident. If we underestimated species richness in small stands, the effect would have been to overestimate the strength of species-area relations (see below).

Linear regressions of bird species richness on stand area were not significant for analyses including all stands ($P = 0.18$, Fig. 2), unmanaged stands ($P = 0.23$), and managed stands ($P = 0.34$). Regressions of species richness of forest interior and interior/edge birds (combined) on stand area were also nonsignificant for all stands ($P = 0.40$), unmanaged stands ($P = 0.42$), and managed stands ($P = 0.65$). Residuals from these analyses were

normally distributed ($P \geq 0.11$), indicating linear models were appropriate for these data. Linear regressions of species per count on stand area indicated a negative slope that indicated species richness in large stands did not result from more counts (e.g., Hutto *et al.* 1986). These analyses did not change the interpretation of our results so are not presented here.

Eight principal components with eigenvalues greater than one accounted for 72 percent of the variation in the vegetation measurements. Including stand area in logistic regressions with PCA factor scores improved the logistic models at sites for red-naped sapsuckers (*Syphrapicus nuchalis*, $P = 0.04$), dark-eyed juncos (*Junco hyemalis*, $P = 0.03$), and chipping sparrows (*Spizella passerina*, $P = 0.07$). The associations of stand area and occurrence of these birds at sites were negative. Including area with stand-level PCA factor scores in logistic regressions improved logistic models for occurrence of yellow-bellied sapsuckers (*S. varius*, $P = 0.07$), white-breasted nuthatches (*Sitta carolinensis*, $P = 0.04$), and brown creepers (*Certhia americana*, $P < 0.01$). Of these species, only the occurrence of brown creepers in stands was positively associated with stand area. Nonetheless, adding stand area decreased the ability of the model to correctly classify stands with brown creepers from 80 percent, when only vegetation factors were considered, to 40 percent when stand area was added (the improvement in the logistic model was from improved classification of stands without brown creepers). To further evaluate the importance of stand area in predicting the occurrence of brown creepers in stands, we conducted a logistic regression with stand area as the only independent variable. This logistic regression was marginally significant ($P = 0.09$) with stand area positively associated with occurrence of brown

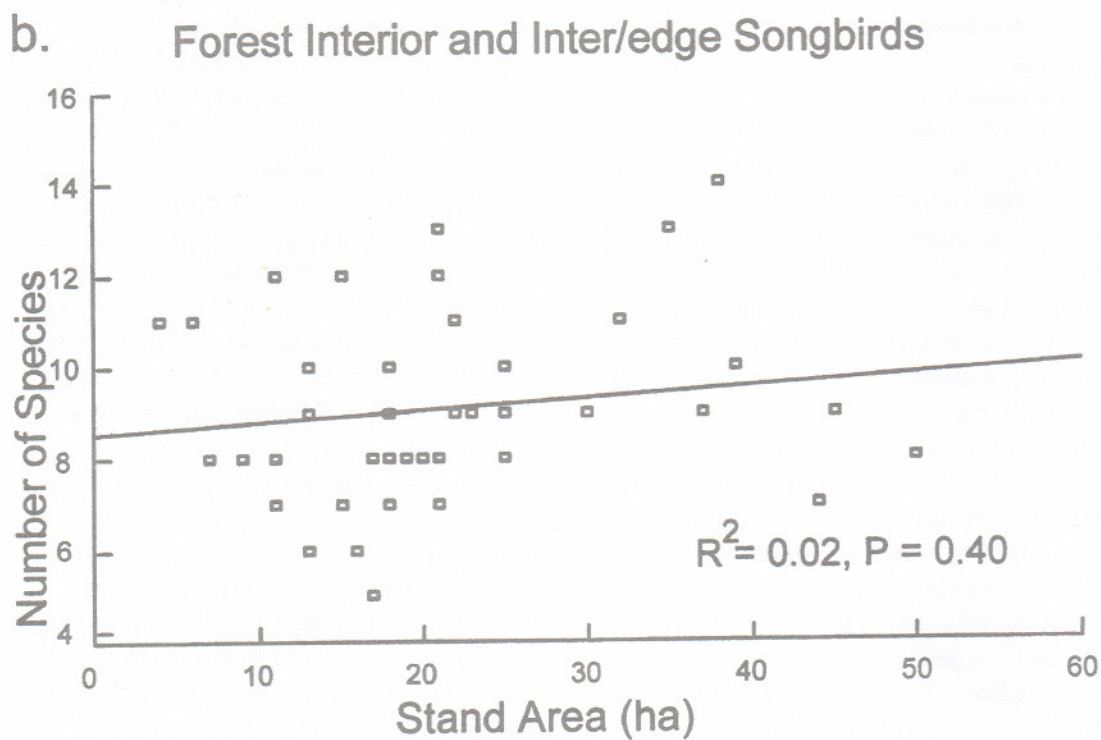
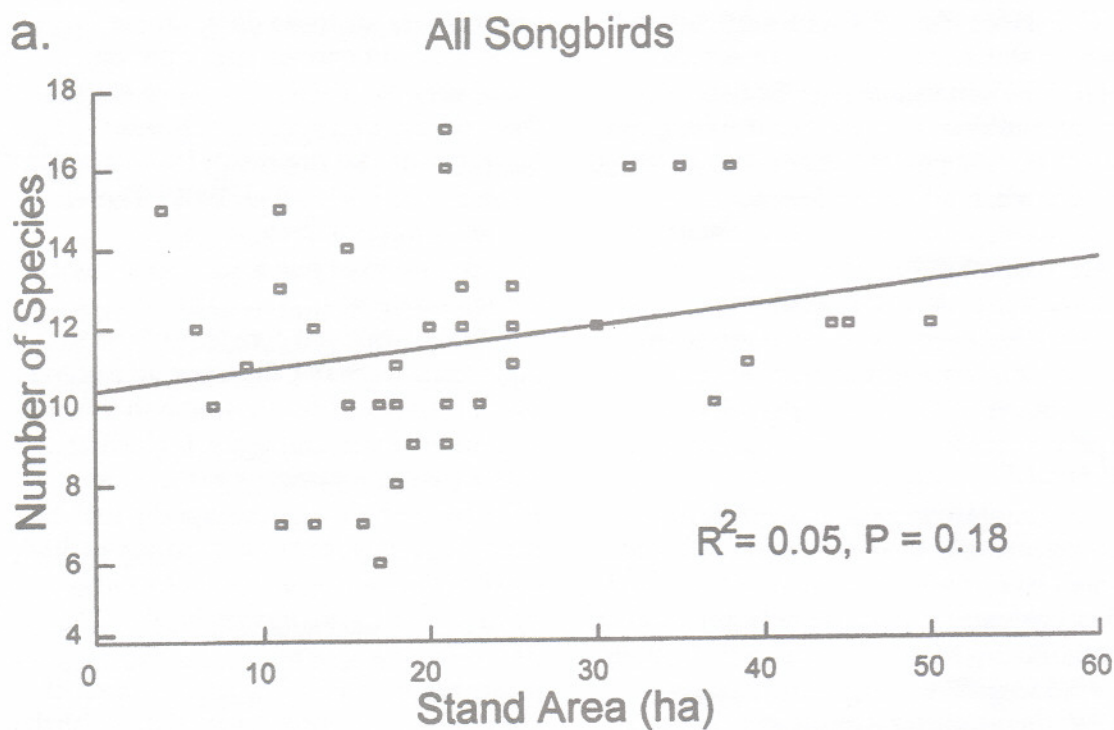


Figure 2. Linear regressions of species richness with stand area for: a) all song birds, and b) song birds with habitat affiliations that are primarily forest interior or interior/edge.

creepers. However, this model failed to correctly predict the occurrence of any stands with brown creepers. Thus, adding stand area to the logistic model for brown creepers predicted stands that did not have brown creepers (which was most of the stands).

Brown creepers were not observed in stands <18 ha (Fig. 3) but occurred only in unmanaged stands. Stands with brown creepers had greater ($P < 0.01$, t -test) densities of large diameter (>38 cm DBH) ponderosa pine trees than stands without brown creepers. Within stands >18 ha, those that had brown creepers also had more ($P < 0.01$, t -test) large ponderosa pine trees than stands >18 ha without brown creepers.

Western tanagers did not occur in stands < 10 ha. Ovenbirds, which are forest interior birds in some portions of their range, occurred in all stand size categories but were more common in stands 25-34 ha.

PCA factor one accounted for a significant, but small, amount of the variation in species richness among stands for all species ($R^2 = 0.15$, $P = 0.01$) and richness of forest interior/edge species ($R^2 = 0.12$, $P = 0.03$). Stand area was not included in the regression model for forest interior/edge species richness ($P = 0.65$) or for richness of all species ($P = 0.19$) after the entrance of PCA factor one.

DISCUSSION

Our analyses found little evidence that stand size in the BHNF precludes occurrence of some bird species. There was a small chance we could have underestimated species richness in small stands (e.g., Freemark and Merriam 1986, Blake and Karr 1987) and overestimated species richness in large stands by placing more bird count sites in them (e.g., Hutto *et al.* 1986). However, if this were true, the effect would have been to bias our conclusion toward significant positive species-area relations. Our analyses did not support

this conclusion; large stands did not yield more bird species than small stands in either managed or unmanaged stands. Nor did large stands have more forest interior and interior/edge species than small stands. Species-area relations among song birds in conifer forests of the western United States and Europe tend to be weak (Rosenberg and Raphael 1987, Lehmkuhl *et al.* 1991, Lescourret and Genard 1994). In areas where forests surround logged stands that maintain some suitability for forest birds, species-area relations among birds may not occur (Estades and Temple 1999).

Although our study did not include stands that were extremely large, it did include the range of stand sizes for which species-area relations have been shown to occur elsewhere (Galli *et al.* 1976, Villard *et al.* 1993, Hinsley *et al.* 1996). These also represent the range of stand sizes for which opponents contend that logging fragments the forest in the Black Hills. Post-European settlement has greatly impacted forest vegetation in the Black Hills although most human impacts have resulted in greater tree densities than occurred historically (Parrish *et al.* 1996). Additionally, stands on the order of thousands of ha that are not broken by roads, natural meadows, or deciduous vegetation do not exist in the BHNF.

Evidence that brown creepers are sensitive to stand area was weak. They may require habitat blocks >18 ha, but brown creepers also require large snags or large trees with loose bark (Gilbert and Allwine 1991, Hansen *et al.* 1995). We observed brown creepers only in unmanaged stands of ponderosa pine with high densities of large diameter trees. Stands with brown creepers also had higher densities of large diameter ponderosa pine than stands of the same size categories. The weak logistic model in our study using stand area to predict occurrence of brown creepers and the strong differences in some habitat

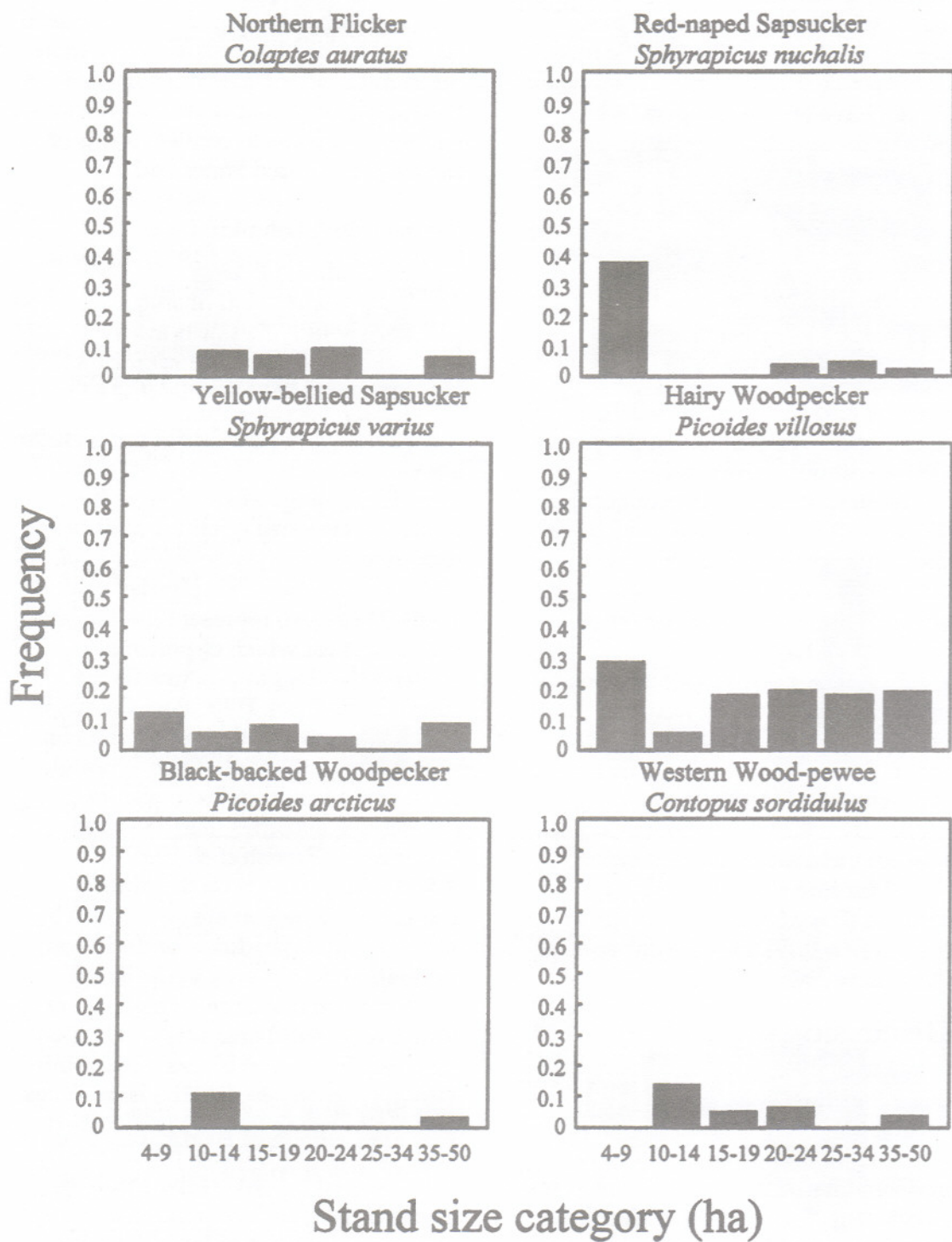


Figure 3. Average frequency of birds at sites for six stand-size categories in the Black Hills, SD in 1993 and 1994.

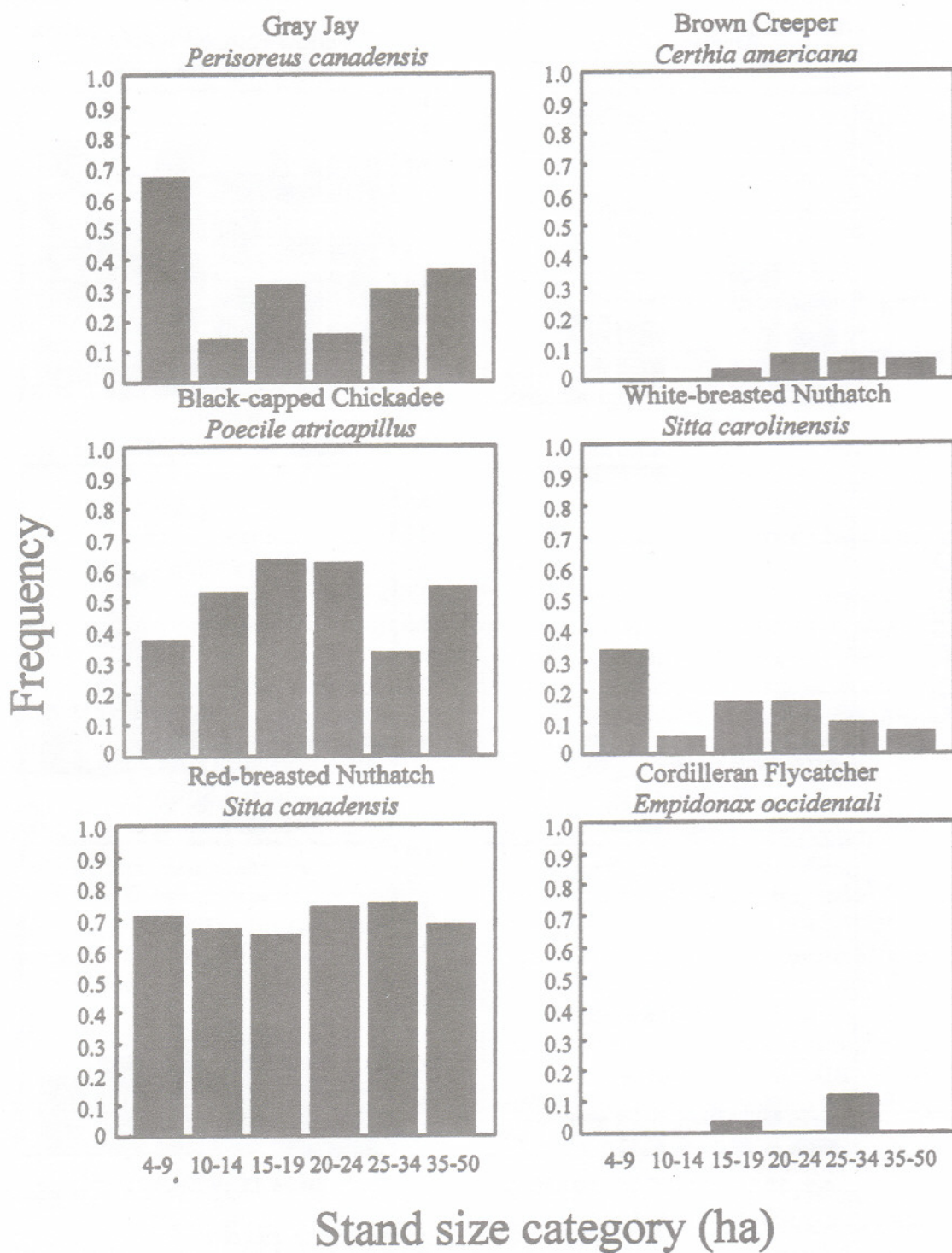


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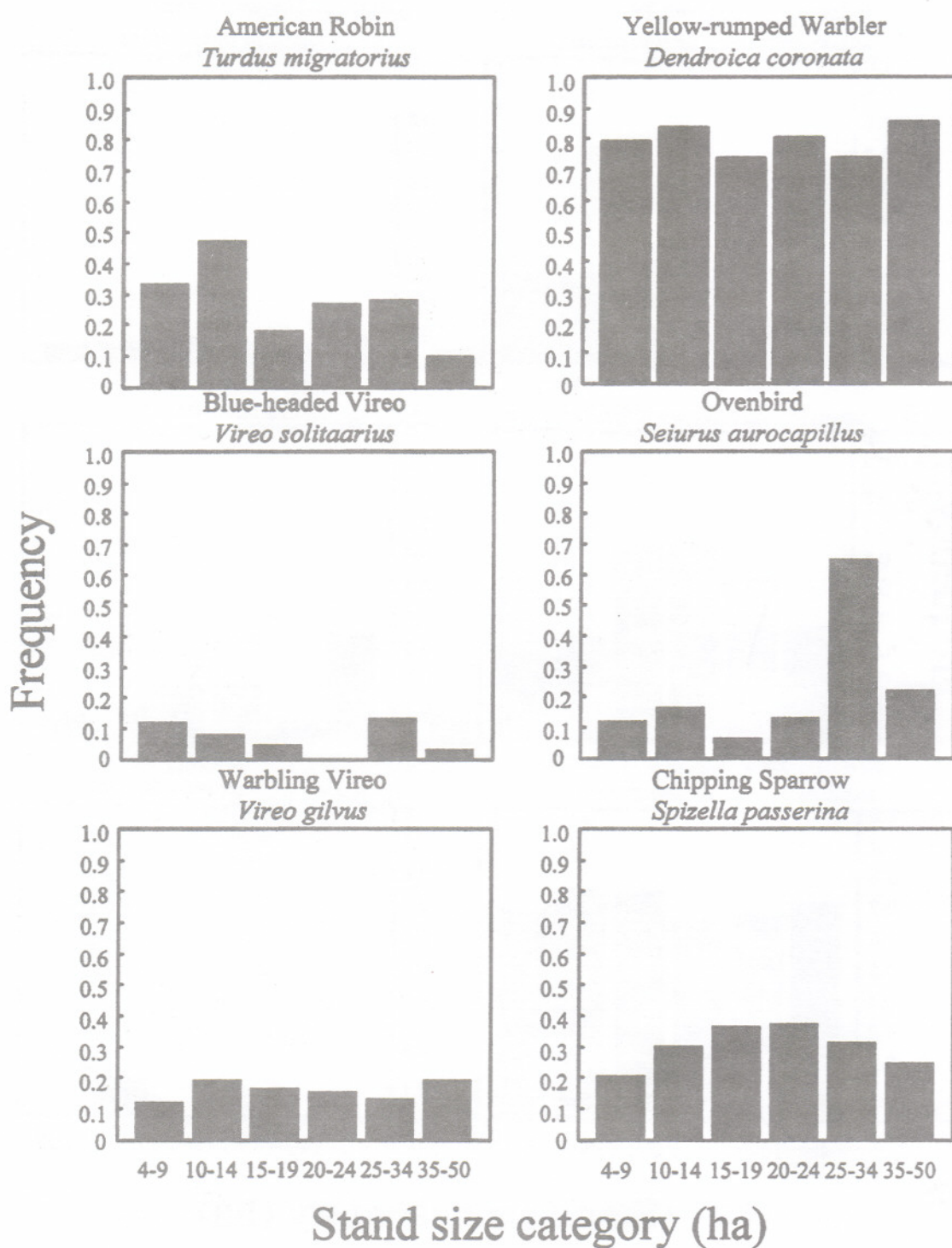


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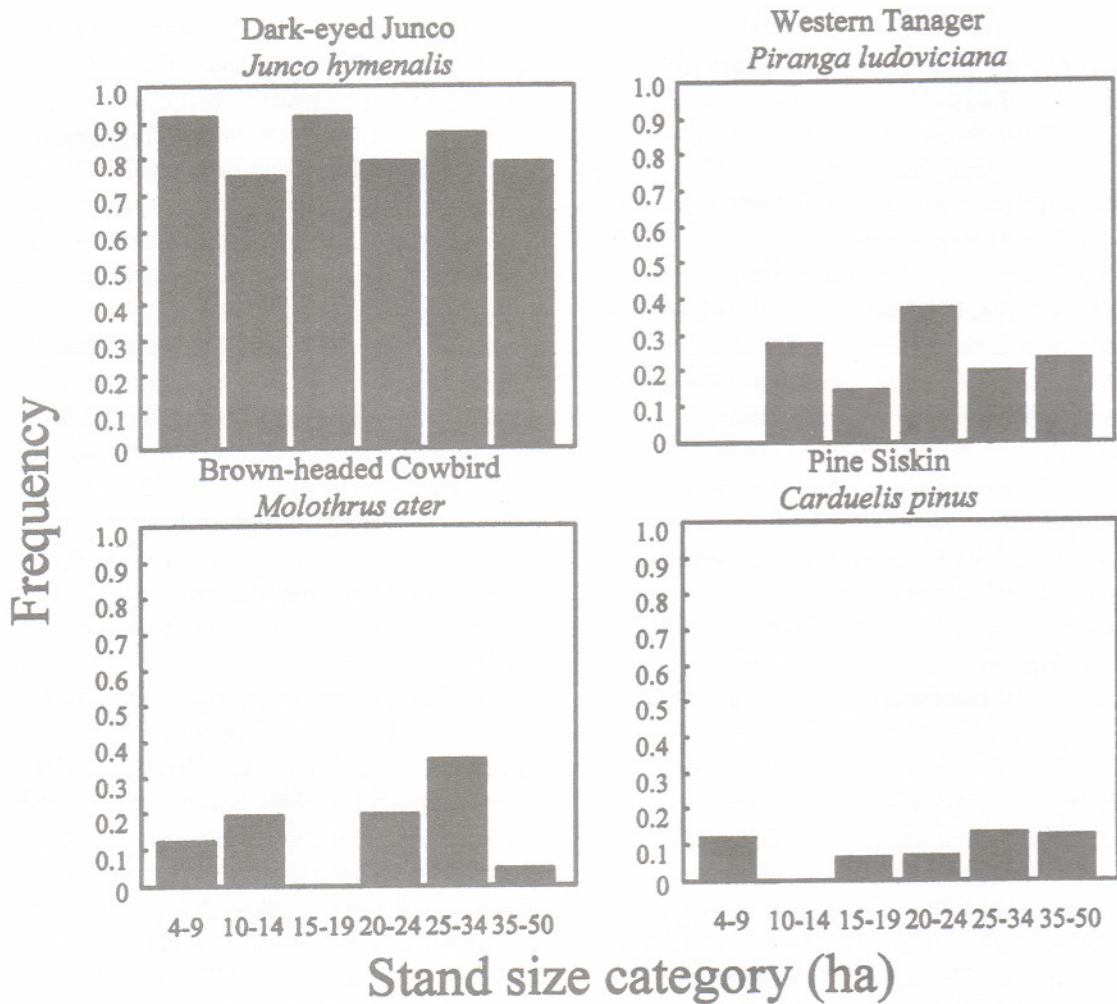


Figure 3. (Continued)

features suggest that large trees were more important than stand area in determining suitable habitat for brown creepers in the Black Hills. Brown creepers are dependent on late-seral forests but are not considered sensitive to fragmentation (Lehmkuhl and Ruggiero 1991). In Wyoming, (Keller and Anderson 1992) concluded that small stand sizes from logging reduced the abundance of brown creepers, but did not eliminate them from forests. The minimum stand size for brown creepers in Alaska was estimated at 1.7 ha (Hansen *et al.* 1996). Logging in the BHNH has a negative effect on brown creepers (Dykstra *et al.* 1999, Mills *et al.* in press), but that effect is more likely due to the alteration of forest structure

than to alteration of stand size.

Even though ovenbirds occurred in all stand size categories, their increased frequency in stands 25-34 ha might indicate greater mating success (Villard *et al.* 1993). Ovenbirds require interior forest conditions in eastern forests (Whitcomb *et al.* 1981) and are aspen (*Populus tremuloides*) obligates in the Rocky Mountain region (Holthausen 1984, Finch and Reynolds 1987). In the Black Hills, we found ovenbirds in ponderosa pine if deciduous trees were present in the understory or in small patches. Unmanaged stands of ponderosa pine had more deciduous understory and greater abundance of ovenbirds than managed stands (Dykstra *et al.* 1999). Nesting, pairing,

and population productivity of ovenbirds in relation to habitats of the Black Hills need further research.

Western tanagers are long-distance migrants with low abundance that depend on late-succession forest in the west and are sensitive to fragmentation (Lehmkuhl and Ruggiero 1991). In the Black Hills, the habitat requirements of western tanagers appear to be less restrictive. Western tanagers occur in managed and unmanaged stands of ponderosa pine in the northern Black Hills (Dykstra *et al.* 1999) but were absent from stands < 10 ha. In the central Black Hills western tanagers were most common in multi-storied stands, but also were common in sapling-pole and mature ponderosa pine and in all overstory canopy cover categories (Mills *et al.* *in press*).

The size of stands that brown creepers, western tanagers, and ovenbirds occurred were in the mid- to upper-range of forest stand sizes managed by the BHNF. Managing for the full array of forest structural stages in stands >25 ha, including stands with larger diameter trees and >70 percent overstory canopy cover, would ensure that habitat requirements for these species occur across the forest. Rosenberg and Raphael (1986) recommended managing old-growth forests in stands >20 ha in California.

We offer explanations why logging, as currently practiced in the BHNF, might not affect song birds as in eastern deciduous forests. Despite the fact that 70 percent of the BHNF is managed for timber production (Black Hills National Forest 1996), the managed forest does not result in abrupt edges between forested and nonforested stands. Predominant logging methods affect the vegetation structure of the forest, but do not eliminate the forest. National Forests are required to re-establish or regenerate the forest after logging (National Forest Management Act 1976). Although most of the BHNF has been logged in the

past, 81 percent (SE $\pm 1\%$) of the area surrounding the stands we studied were forested. Fragmentation effects are minimal until <60 percent of the forest remains (Franklin and Forman 1987, Andr  n 1994). When surrounding habitat continues to support forest vegetation, species-area relations of song birds might become negative (Estades and Temple 1999). In forests where >60 percent of forest cover remains, bird species richness increases after logging because generalist birds are added to the community (Franklin and Forman 1987, Lehmkuhl *et al.* 1991). Proximity or connectedness to forest, even of different vegetation types, increases bird abundance (Lescourret and Genard 1994).

Before nonnative people settled in the Black Hills, open forest conditions dominated the landscape (Wright 1978, Brown and Sieg 1996, Parrish *et al.* 1996). Fewer, more widely spaced, and larger ponderosa pine trees resulted from recurring creeping ground fires that occurred 100-600 years ago (Fisher *et al.* 1987, Brown and Sieg 1996, Parrish *et al.* 1996). Large stands of dense forest common in the Black Hills today resulted from fire suppression (Covington and Moore 1994) and probably occurred historically only at higher elevations of the northwestern Black Hills (Parrish *et al.* 1996). Present vegetation patterns in the Black Hills might have developed only during the last few thousand years (FAUNMAP Working Group 1996) because of variation in climate and vegetation over the past 20,000 years (Graham 1990, Weedon and Wolken 1990, Pielou 1991). Ponderosa pine did not occur in the southern Black Hills ca. 26,000 years ago (Mead *et al.* 1990). This variation in climate and vegetation may not have provided adequate time for birds to develop small exclusive niches (e.g., Orians and Wilson 1964, Slobodkin and Sanders 1969, Gilbert and Allwine 1991). Thus, historical forest conditions in the

Black Hills, were probably more conducive to generalist birds that are not sensitive to stand area. The effects of forest fragmentation on song birds on naturally patchy western landscapes are seemingly different than those observed in eastern deciduous forests (Tewksbury *et al.* 1998).

CONCLUSIONS

Although our results are not dramatic, they are important because of the biological, economic, and political consequences if we had demonstrated that logging fragmented the BHNF for song birds. Our data should not be construed to suggest that logging does not affect the bird community in the Black Hills. Changes that logging induces to the forest alters species composition and abundance of birds in the BHNF (Mills *et al.* in press, Dykstra *et al.* 1999). We did not address reproductive success, survival, or densities of song birds in this study. However, effects of logging on these population parameters of song birds in western forests differ from those shown for midwestern or eastern forests (Franklin and Forman 1987, Lehmkuhl *et al.* 1991, Tewksbury *et al.* 1998). Within the context of species richness area relations for song birds, our findings do not support an argument that logging fragments the BHNF to an extent that adversely affects species richness of song birds.

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LITERATURE CITED

- Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64:1057-1068.
- Andr  n, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71:355-366.
- A.O.U. 1983. Checklist of North American birds. American Ornithologists Union. Allen Press, Inc. Lawrence, KS.
- Askins, R. A., M. J. Philbrick, and D. S. Sugeno. 1987. Relationships between regional abundance of forest and the composition of forest bird communities. *Biol. Conserv.* 39:129-152.
- Black Hills National Forest. 1996. Land and resource management plan. U. S. Dept. Agric., Black Hills National Forest, Custer, SD.
- Blake, J. G. 1991. Nested subsets and the distribution of birds on isolated woodlots. *Conserv. Biol.* 5:58-66.
- Blake, J. G., and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. *Ecology* 68:1724-1734.
- Brown, P. M., and C. H. Sieg. 1996. Fire history in interior ponderosa pine communities of the Black Hills, South Dakota, USA. *Internat'l. J. Wildland Fire* 6:97-105.
- Covington, W. W., and M. M. Moore. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. For.* 92:39-47.
- Crompton, B. J. 1994. Songbird and small mammal diversity in relation to timber management practices in the northwestern Black Hills. M.S. thesis. University of Wyoming, Laramie, WY. 202pp.

- Dykstra, B. L., M. A. Rumble, and L. D. Flake. 1999. Effects of harvesting ponderosa pine on birds in the Black Hills of South Dakota and Wyoming. *Biannual N. Amer. For. Ecol. Workshop* 1:16-26.
- Emlen, J. T. 1971. Population densities of birds derived from transect counts. *Auk* 88:323-342.
- Estades, C. F., and S. A. Temple. 1999. Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. *Ecol. Appl.* 9:573-585.
- Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. 1993. Habitat fragmentation in the temperate zone: a perspective for managers. Pp. 331-338 in D. M. Finch and P. W. Stangel, eds. *Status and management of neotropical migratory birds*. U.S. Dept. Agric., For. Serv., Gen. Tech. Rep. RM-229. 422pp.
- FAUNMAP Working Group. 1996. Spatial response of mammals to late quaternary environmental fluctuations. *Science* 272:1601-1606.
- Finch, D. M., and R. T. Reynolds. 1987. Bird response to understory variation and conifer succession in aspen forests. Pp. 87-96 in J. Emmerick, *et al.*, eds. *Proceedings of issues and technology in the management of impacted wildlife*. Thorne Ecological Inst., Colorado Springs, CO. 177pp.
- Fisher, R. F., M. J. Jenkins, and W. F. Fisher. 1987. Fire and the prairie-forest mosaic of Devils Tower National Monument. *Am. Midl. Nat.* 117:250-257.
- Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecol.* 1:5-18.
- Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biol. Conserv.* 36:115-141.
- Galli, A. E., C. F. Leck, and R. T. T. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. *Auk* 93:356-364.
- Gilbert, F. F., and R. Allwine. 1991. Spring bird communities in the Oregon Cascade Range. Pp. 145-158 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coord. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Dept. Agric., For. Serv. Gen. Tech. Rep. PNW-285. 533pp.
- Graham, R. W. 1990. Evolution of new ecosystems at the end of the Pleistocene. Pp. 54-60 in L. D. Agenbroad, J. I. Mead, and L. W. Nelson, eds. *Megafauna and man: discovery of America's heartland*. Sci. Pap. Vol. 1. Mammoth Site of Hot Springs, Inc., Hot Springs, SD. 143pp.
- Hansen, A. J., W. C. McComb, R. Vega, M. G. Raphael, and M. Hunter. 1995. Bird habitat relationships in natural and managed forests in the western Cascades of Oregon. *Ecol. Appl.* 5:555-569.
- _____, R. Patten, E. DeGayner, and B. L. Marks. 1996. Simulating forest and habitat changes in south-east Alaska with the landscape model PAYSAGE. *Trans. GIS* 1:119-136.
- Hinsley, S. A., P. E. Bellamy, I. Newton, and T. H. Sparks. 1996. Influences of population size and woodland area on bird species distributions in small woods. *Oecologia* 105:100-106.
- Holthausen, R. 1984. Coordinated aspen-wildlife management. Pp. 25-37 in J. Capp and L. Gadt, eds. *Proceedings of aspen symposium*. U.S. Dept. Agric., For. Serv. Rocky Mtn. Reg., Colorado Springs, CO. 126pp.

- Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed-plot point count methods for nonbreeding and breeding season use. *Auk* 103:593-602.
- Keller, M. E., and S. H. Anderson. 1992. Avian use of habitat configurations created by forest cutting in southeastern Wyoming. *Condor* 94:55-65.
- Lehmkuhl, J. F., and L. F. Ruggiero. 1991. Forest fragmentation in the Pacific Northwest and its potential effects on wildlife. Pp. 145-158 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coord. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Dept. Agric., For. Serv. Gen. Tech. Rep. PNW-285. 533pp.
- _____, and _____, and P. A. Hall. 1991. Landscape-scale patterns of forest fragmentation and wildlife richness and abundance in the southern Washington Cascade Range. Pages 425-442 in L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coord. *Wildlife and vegetation of unmanaged Douglas-fir forests*. U.S. Dept. Agric., For. Serv. Gen. Tech. Rep. PNW-285. 533pp.
- Lescourret, F., and M. Genard. 1994. Habitat, landscape and bird composition in mountain forest fragments. *J. Environ. Manage.* 40:319-328.
- Manuwal, D. A., and A. B. Carey. 1991. Methods for measuring populations of small diurnal forest birds. U.S. Dept. Agric., For. Serv., Gen. Tech. Rep. PNW-278. 23pp.
- Mead, J. I., R. H. Hevly, and L. D. Agenbroad. 1990. Late Pleistocene invertebrates and plant remains, Mammoth Site, Black Hills, South Dakota. Pp. 9-10 in L. D. Agenbroad, J. I. Mead, and L. W. Nelson, eds. *Megafauna and man: discovery of America's heartland*. Sci. Pap. Vol. 1. Mammoth Site of Hot Springs, Inc., Hot Springs, SD. 143pp.
- Mills, T. R., M. A. Rumble, and L. D. Flake. 2000. Optimum timeframes for detecting songbird vocalizations in the Black Hills. U. S. Dept. Agric., For. Serv., Res. Pap. RMRS-RP-21. 6pp.
- _____, _____, and _____. 2000. Habitat of birds in ponderosa pine and aspen/birch forest in the Black Hills, South Dakota. *J. Field Ornith.* 71:187-206.
- National Forest Management Act. 1976. Public Law 94-588. 94th Congress, S. 3091. 43 pp.
- Orians, G. H., and M. F. Wilson. 1964. Interspecific territories of birds. *Ecology* 45:736-745.
- Parrish, J. B., D. J. Herman, and D. J. Reyher. 1996. A century of change in the Black Hills forest and riparian ecosystems. U.S. Dept. Agric., For. Serv. and Agric. Exp. Stn., South Dakota State University, Brookings. 20pp.
- Pielou, E. C. 1991. *After the ice age: return of life to glaciated North America*. Univ. of Chicago Press, Chicago, IL.
- Reynolds, R. T., J. M. Scott, and R. A. Nussbaum. 1980. A variable circular-plot method for estimating bird numbers. *Condor* 82:309-313.
- Rosenberg, K. V., and M. G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pp. 263-272 in J. Verner, M. L. Morrison, and C. J. Ralph, eds. *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. Univ. Wisconsin Press, Madison.
- Shapiro, S. S., and M. B. Wilk. 1965. An analysis-of-variance test for normality (complete samples). *Biometrika* 52:591-611.

- Shinneman, D. J. 1996. An analysis of range of natural variability, roads, and timber harvesting in a Black Hills ponderosa pine landscape. M.S. thesis. University of Wyoming, Laramie. 99pp.
- _____, and W. L. Baker. 1997. Essay: nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. *Conserv. Biol.* 12:1276-1288.
- Slobodkin, L. B., and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. *Brookhaven Symp. Biol.* 22:88-95.
- Tewksbury, J. J., S. J. Heijl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890-2903.
- Verner, J., and L. V. Ritter. 1988. A comparison of transects and spot mapping in oak-pine woodlands of California. *Condor* 90:401-419.
- Villard, M., P. R. Martin, and C. G. Drummond. 1993. Habitat fragmentation and pairing success in the ovenbird (*Seiurus aurocapillus*). *Auk* 110:759-768.
- Weedon, R. R., and P. M. Wolken. 1990. The Black Hills environment. Pp. 123-135 in L. D. Agenbroad, J.I. Mead, and L.W. Nelson, eds., *Megafauna and man: discovery of America's heartland*. Sci. Pap. Vol. 1. Mammoth Site of Hot Springs, Inc., Hot Springs, SD. 143pp.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125-206 in R. L. Burgess and D. M. Sharpe, eds., *Forest dynamics in man-dominated landscapes*. Springer-Verlag, New York, NY.
- Wright, H. A. 1978. The effects of fire on vegetation in ponderosa pine forest: a state-of-the-art review. *Range and Wildl. Info. Ser.* 2. Texas Tech University, Lubbock. 21pp.