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## THE INFLUENCE OF DWARF MISTLETOE ON BIRD COMMUNITIES IN COLORADO PONDEROSA PINE FORESTS<sup>1</sup>

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**Abstract.** Dwarf mistletoes (*Arceuthobium* spp.) are parasitic plants that are widely distributed in coniferous forests of the northern hemisphere. Because the effects of dwarf mistletoes on their host trees include stunted growth, reduced seed production, and death, these mistletoes may have a substantial influence on forest structure. Studies of the effects of dwarf mistletoe on forest communities have focused primarily on their influence on timber production. We studied the effects of southwestern ponderosa pine dwarf mistletoe (*A. vaginatum*) on the abundance and diversity of bird communities in central Colorado. Four stands, which ranged in level of mistletoe infestation from none to heavy, were selected at each of two locations. Each stand was surveyed approximately once per week during the avian breeding seasons of 1989 and 1990 by spot mapping. The number of bird registrations and bird species richness were positively correlated with the level of dwarf mistletoe, and this pattern was consistent among 24 of 28 avian species. No species had a significant negative correlation with the level of dwarf mistletoe. The relative abundance of bird species (i.e., evenness) did not differ among stands. The number of cavity-nesting birds detected also was positively correlated with both dwarf-mistletoe levels and number of snags. The number of snags and dwarf-mistletoe levels also were highly correlated. Most snags had been infected as live trees by dwarf mistletoe and the mistletoe probably contributed to their death.

While dwarf mistletoe has traditionally been viewed as a forest pest because of reductions in timber volume, we suggest that in areas where management goals are not strictly focused on timber production, control of dwarf mistletoe may not be justified, practical, or even desirable. Our data suggest that dwarf mistletoes may have positive influence on wildlife habitat. Consequently, we suggest that eradication efforts be reconsidered given that dwarf mistletoes have been a part of these forest ecosystems for thousands, and possibly millions, of years.

**Key words:** *Arceuthobium vaginatum*; bird abundance; bird communities; bird diversity; cavity-nesting birds; Colorado; dwarf mistletoe; forest pest; mistletoe infestation; ponderosa pine; snag; species richness.

### INTRODUCTION

Dwarf mistletoes (*Arceuthobium* spp.) are dicotyledonous parasitic plants of the family Viscaceae that occur throughout many parts of the northern hemi-

sphere (Hawksworth and Wiens 1972, 1995). Their host trees are conifers of the families Pinaceae and Cupressaceae (Hawksworth and Wiens 1972). Fossilized remains of *Arceuthobium* in packrat middens have been radiocarbon dated back as far as 21 500 ( $\pm 500$ ) yr ago (Spaulding 1981, Van Devender and Hawksworth 1986) and pollen grains have been dated back 10<sup>6</sup> yr (F. G. Hawksworth, *unpublished data*). Thus, dwarf mistletoes have coevolved with their coniferous host species as part of these forest communities (see also Gill 1935, Wicker 1984).

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The influence of dwarf mistletoes on host species includes a reduction of timber volume of commercial tree species (Johnson et al. 1984, Hawksworth et al. 1989, Maffei 1989). Southwestern pine dwarf mistletoe (*Arceuthobium vaginatum*) causes more damage to ponderosa pine in the southwest than any other "disease" agent (Hawksworth 1961a). Annual losses of timber volume due to dwarf mistletoes in Colorado alone may exceed half of the state's annual timber harvest, i.e.,  $>2.52 \times 10^4 \text{ m}^3$  (originally expressed as  $>9 \times 10^5 \text{ ft}^3$  by Johnson et al. 1984). This loss does not include additional indirect losses due to increased susceptibility to attack by other pathogens as a result of mistletoe infection (McCambridge et al. 1982, Maffei 1989). Annual timber losses in the southwest (i.e., Arizona, New Mexico, and Colorado) may exceed  $35 \times 10^4 \text{ m}^3$  (originally expressed as  $12.5 \times 10^5 \text{ ft}^3$  by Flake et al. 1972). Other influences of dwarf mistletoes on their host trees can include reduced growth (Korstian and Long 1922, Hawksworth 1961a, Hawksworth and Shaw 1984, Hawksworth et al. 1989, Maffei 1989), reduced seed production (Korstian and Long 1922, Schaffer et al. 1983, Hawksworth and Shaw 1984, Hawksworth et al. 1989), and reduced wood quality (Hawksworth 1961a, Piirto et al. 1974, Hawksworth and Shaw 1984, Hawksworth et al. 1989). In light of these effects on the annual timber harvest, it is not surprising that dwarf mistletoe traditionally has been viewed as a forest pest (e.g., numerous papers in Scharpf and Parmeter 1978, Wicker 1984).

Associations between birds and mistletoes have long been recognized (e.g., Crouch 1943). Most previous studies, however, have focused on the leafy mistletoes, whose fruits are an attraction for frugivorous birds. In contrast, the seeds of dwarf mistletoes are rarely used as a food source for birds and the shoots are only a minor part of the diets of a few species, particularly grouse (e.g., Hawksworth and Wiens 1972, 1995, Zwickel et al. 1974, Nichols et al. 1984, Severson 1986). However, the presence of dwarf mistletoe may enhance insect populations that feed on or pollinate mistletoe or that take advantage of the weakened condition of trees infected by mistletoe (Stevens and Hawksworth 1970, Scharpf 1975).

Although dwarf mistletoes may influence food resources, its most substantial influence on bird communities is likely to be the result of changes in forest structure. Several species use the dense clumps (witches' brooms) that are formed by branches of the host tree for roost or nest sites (Reynolds et al. 1982, Nicholls et al. 1984, Bull et al. 1989, Bennetts 1991). Dwarf mistletoe infection also creates a mosaic of habitat structures within a given stand through its effects on tree growth and mortality (Hawksworth 1973, Parmeter 1978, Tinnin 1984).

Several studies have demonstrated the role of birds as animal vectors of dwarf mistletoe seeds (e.g., Hudler 1976, Nicholls et al. 1984); however, there has been

little other focus on the influence of dwarf mistletoe on bird communities. Here, we examine the relationships of southwestern ponderosa pine dwarf mistletoe (*A. vaginatum cryptopodum*) to abundance and diversity of birds in ponderosa pine (*Pinus ponderosa*) forests of the Rocky Mountain Front Range in central Colorado.

#### STUDY AREA AND METHODS

We studied the relationship between dwarf mistletoe and bird communities during 1989 and 1990 at two locations in central Colorado. Cheesman Reservoir is an area of contiguous stands of ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), or mixed conifers, located 60 km southwest of Denver, Jefferson County, at  $\approx 2200 \text{ m}$  elevation. Florissant Fossil Beds National Monument is an area of ponderosa pine and mixed conifer stands interspersed with open meadows located 80 km west of Colorado Springs, Park County, at  $\approx 2500 \text{ m}$  elevation. Both locations occur on Pikes Peak granite soils, and consist primarily of gently rolling slopes ( $<20\%$  [ $<20 \text{ m}$  change in altitude for each  $100 \text{ m}$  change in horizontal location]). Cheesman Reservoir is a municipal water supply for Denver, and consequently, is closed to public access except for limited shoreline fishing. Florissant Fossil Beds National Monument has considerable public access that is concentrated primarily on a system of trails through areas of fossil deposits and forest settings. Although some timber cutting has occurred in the past, primarily at the turn of the century, both sites have been protected from timber harvest for at least the past 20 yr. Thus, potential confounding effects from current timber harvest were minimized. These two locations were selected because they were protected from timber harvest, were close enough to enable a two-person crew to sample both locations, but were far enough apart ( $\approx 35 \text{ km}$ ) to include some geographic variability, allowing us to extend our scope of inference beyond a single location.

At each location, we selected four stands of ponderosa pine that varied in level of mistletoe from none to heavily infected, but were similar with respect to stand age, slope, aspect, elevation, and soil type. The selection of stands was based on a stratified (by property 3 in the following list) random sampling from a limited pool of available stands (usually from 2–4 stands in each mistletoe class) that met our criteria of (1)  $\geq 90\%$  ponderosa pine, (2) large enough area (stands ranged from 20 to 40 ha) to allow a 100-m buffer adjacent to the sampled area before encountering another vegetation type, and (3) visually appearing to have zero, moderate, or heavy levels of dwarf mistletoe. The four stands selected within each location were 1–5 km distant from each other. These stands were representative of ponderosa pine stands within the protected areas, but did not reflect the levels of timber harvest on surrounding forest lands. Within each stand, we surveyed a 10.2-ha area at 20-m intervals to form a grid

of 256 cells. The corner of each grid cell was marked with a 0.6-m wire flag with an X, Y coordinate for each grid cell enabling an observer to know their location within the plot.

All trees >10 cm dbh (diameter at breast height) in each grid cell were assigned to one of 7 classes (including a class for uninfected) of dwarf mistletoe infection following the rating procedure described by Hawksworth (1977). All dwarf mistletoe rating was conducted by a trained pathology crew who had extensive experience in rating trees in this area for mistletoe. The Hawksworth (1977) procedure divides each tree canopy vertically into thirds and assigns a value to each third depending on whether it is uninfected (0),  $\leq 50\%$  of the branches infected (1), or  $>50\%$  of the branches infected (2). The sum of the thirds is then used for the final tree rating. We used the average dwarf mistletoe rating (DMR) of the 256 cells for each stand as a stand average, rather than using the average among individual trees. We think that this more accurately reflects the spatial distribution of mistletoe infections over the entire stand because scattered dense pockets of infected trees can heavily influence the stand average. This approach does not, however, influence our conclusions and is more conservative because dense pockets of infected trees could inflate the overall mistletoe ratings.

In each stand we censused all snags >12 cm dbh (the smallest diameter in which we observed use by cavity-nesting birds [CNB]). We recorded the dbh, height, top condition (i.e., intact, broken above mid-height, or broken below mid-height), the presence or absence of needles, the percentage class of bark remaining on the tree (i.e., 0–25, 25–50, 50–75, and 75–100), and the presence or absence of excavated cavities for each snag. Needle presence and bark retention were used to indicate the relative time since death of the tree.

#### *Bird surveys*

We surveyed each stand approximately once per week from 15 May to 4 July 1989 (7 surveys/stand) and from 12 May to 4 July 1990 (8 surveys/stand). Two observers surveyed one stand each at the same location (i.e., Cheesman or Florissant) on the same day. The remaining two stands at that location were then surveyed the following day. The observers walked every third grid line and recorded location and species of each bird observed, using a spot-mapping protocol (Anonymous 1970, Verner 1985). The distance between adjacent grid lines was 20 m. Birds detected in the same location on consecutive grid lines were not recorded twice. The observer's pace was timed (through practice) so that it took  $\approx 2.5$  h to complete each survey. Observers alternated between consecutive surveys of each stand to minimize observer bias. We used the mapping procedure because it enabled a simultaneous survey of dwarf mistletoe levels of each stand. We did

not, however, use clusters of locations to delineate breeding pairs because: (1) most of the 47 bird species that we observed had too few sightings to delineate clusters, (2) birds were not marked, which reduced our ability to assess territory boundaries, and (3) delineating pairs based on clusters may be highly subjective (Svensson 1974, Best 1975). Because of these problems and because our questions required relative rather than absolute abundance of each species, we used the number of registrations during each survey as a measure of bird abundance. This approach resulted in completing fewer than the 8–10 surveys usually recommended for spot mapping (Anonymous 1970); however, we believed that increasing the number of stands surveyed was of greater concern than number of repeated visits to each stand, especially since we were not making inferences about the actual number of territories on each stand.

#### *Analyses*

We tested whether the size distributions of snags were equal among the stands at each location using a Multi-Response Permutation Procedure (MRPP) (Mielke 1984, Zimmerman et al. 1985, Biondini et al. 1988). We used MRPP rather than ANOVA (or some analogous statistic) because we were interested in differences in distribution rather than differences only among the means. MRPP provides a more powerful test of these differences than more traditionally used non-parametric tests (e.g., Kolmogorov-Smirnov) without the inherent assumptions about the underlying distribution or variance structure of their parametric counterparts (Biondini et al. 1988). We used dbh rather than height as a measure of snag size for this analysis because height may be influenced by the age of the snag if the top is no longer intact.

We used a simple linear multiple regression model to initially explore the relative contribution of several variables in explaining variation in number of birds detected. We began with a univariate analysis of each independent variable. Because the effects of some variables may be masked (e.g., important only in an interaction term), we relaxed our level of protection against rejection of a true null hypothesis at this stage to  $\alpha = 0.25$  (Bendel and Afifi 1977, Hosmer and Lemeshow 1989). We simultaneously tested a fully saturated model including the effects of each independent variable and all interaction terms. We then refined our model by including only those terms where  $\alpha < 0.25$  from either the univariate or the fully saturated models. We did not discard any main effects if the effect was significant in an interaction term. Because this analysis was used in an exploratory, rather than a hypothesis testing or prediction context, we also maintained the two-way interaction terms. Based on a visual inspection of the standardized residuals we used a  $\log(x + 1)$  transformation on the bird counts for all analyses to better approximate normality.

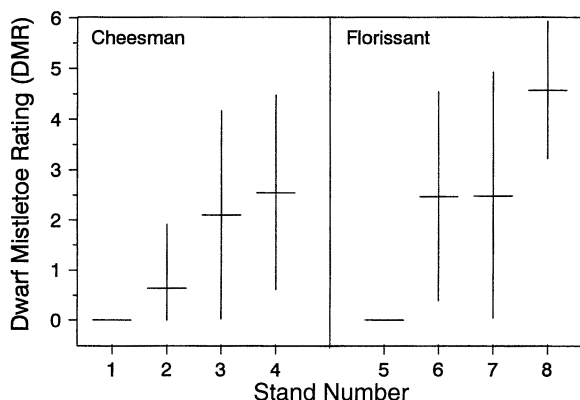


FIG. 1. Average dwarf mistletoe rating (DMR; mean  $\pm$  1 SD) for each stand at Cheesman and Florissant. Because all trees were rated within each stand, the standard deviation represents actual variation among stands, rather than sampling variation.

To refine our assessment of relationships between mistletoe level and number of bird detections and to account better for the error term used to test these relationships, we used a separate regression model of mistletoe level and number of bird detections for each individual survey at each location. This resulted in 30 separate regression models (seven surveys in 1989 and eight surveys in 1990, at each of two locations). We then used a  $t$  test to determine if the mean slope from these regression models differed from zero. We avoided the pseudoreplication (Hurlbert 1984) from using each individual survey (i.e., a repeated measure) by basing this test only on the means from each location (1 df), year (1 df), and the interaction between location and year (1 df).

The power of the  $t$  test above was estimated as  $1 - \beta$ , where  $\beta$  is the probability that a random variable with a noncentral  $t$  distribution falls below the critical  $t$  value given a specified  $\alpha$  level (Pearson and Hartley 1951, Desu and Raghavarao 1990). The noncentrality parameter ( $\hat{\lambda}$ ) was approximated using the test statistic derived where the observed slope was the alternative to the hypothesized slope of zero.

Because the relationship of cavity-nesting birds (CNBs) and snag densities or characteristics have been well documented (e.g., Raphael and White 1984, Sedgwick and Knopf 1990), we also repeated our analysis for only CNBs. In order to assess whether any observed effects from either our general analysis or our analysis of CNBs were associated with individual species, we also repeated the above analysis for each individual species. The mean values from the slopes of our regression analyses include only those surveys with sufficient data points to enable parameter estimation. Species with insufficient data to enable a regression analysis for any survey were excluded from this procedure.

Size of the areas sampled and amount of effort were equal among stands. Consequently, we compared spe-

cies richness among stands using the actual number of species observed. We also used the model selection procedure of the program CAPTURE (Otis et al. 1978) to suggest an appropriate mathematical estimator for which variance estimates could be derived. The program CAPTURE bases selection of an appropriate estimator on the sources of variation in the data rather than an arbitrary choice of the numerous available estimators. To accomplish this we constructed an  $X$ -matrix (Otis et al. 1978) of species detections for each survey. We assigned a "1" to all surveys in which the  $i$ th species was observed and a "0" otherwise. The program CAPTURE then uses a combination of likelihood-ratio and goodness-of-fit tests to select an appropriate estimator. The philosophy of their model selection procedure as well as the estimators are discussed by Otis et al. (1978) (see also Burnham and Overton 1979 for an application to species richness), but the goal is to find the most parsimonious model that adequately accounts for variation in the data due to time (i.e., among surveys), behavior (i.e., that the detection of species  $i$  on a given survey does not influence detection of that species on another survey), and differences among species in detectability (i.e., species heterogeneity).

Although a number of indices are available to examine species evenness (reviewed by Ludwig and Reynolds 1988, Magurran 1988), we used a direct comparison of the cumulative proportions of individuals in each species (Taille 1979, James and Rathbun 1981). We tested differences among the stands at each location using a Kolmogorov-Smirnov  $k$ -sample test (SAS Institute 1988).

## RESULTS

Average dwarf mistletoe rating (DMR) for each stand ranged from 0 to 4.55 (Fig. 1). The overall infestation levels at Florissant were higher than at Cheesman. The DMR of the most heavily infested stand at Cheesman was similar to the DMR of moderate levels at Florissant.

## Snags

We counted 806 snags on the study plots. Of these, 91% ( $n = 729$  snags) were ponderosa pine. The remaining were a mix of Douglas-fir (*Pseudotsuga menziesii*; 7%) and quaking aspen (*Populus tremuloides*; 2%). Because *Arceuthobium vaginatum* does not parasitize Douglas-fir or aspen and because of the small percentage of the total number of snags accounted for by these species, we restricted our analyses to ponderosa pine snags.

Evidence from witches' brooms, swollen branches, and basal cups of fallen mistletoe shoots (Hawksworth 1961b, Baranyay et al. 1971) indicated that  $\geq 78\%$  of the snags on infected stands had been infected as live trees by dwarf mistletoe. This is a minimal estimate of

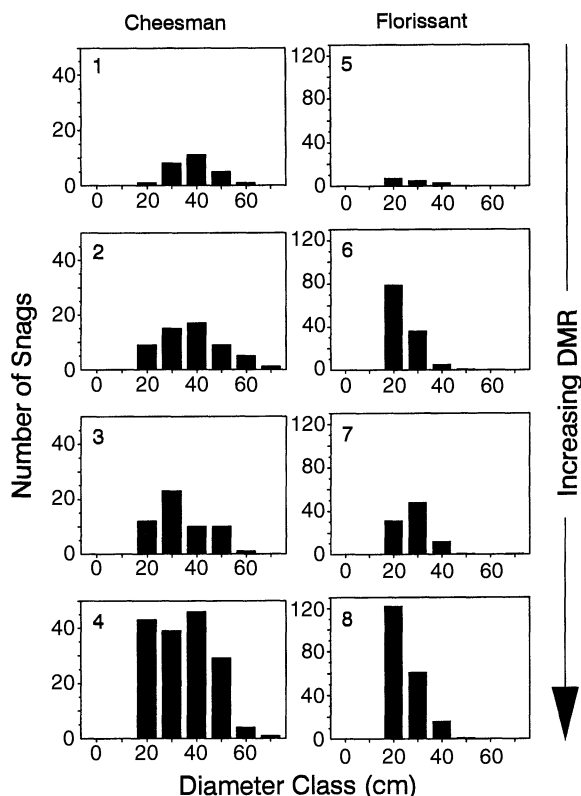


FIG. 2. The distribution of snag diameters on each of the eight stands, in 10-cm size classes. Note the association with dwarf mistletoe rating (DMR).

infected trees because those in the later stages of decay are less likely to retain evidence.

The size distribution of snags (based on dbh) differed among stands at both Cheesman (MRPP, test statistic =  $-2.39$ ,  $P = 0.024$ ) and Florissant (MRPP, test statistic =  $-9.51$ ,  $P < 0.001$ ) (Fig. 2). At both locations there were disproportionately more smaller snags in infested vs. uninfested stands (Fig. 2).

#### Bird abundance

We accumulated a total of 3036 bird registrations of 47 species (Table 1). In our exploratory assessment, DMR was the factor that most influenced the total number of bird registrations (Table 2). This was true regardless of whether we included DMR as we have shown here, or used alternative model selection procedures (e.g., forward or backward stepwise procedures). We also found effects of year and location (in the interaction term with DMR). We did not find a significant survey effect for the total number of registrations either in our univariate or our saturated models. Our  $\log(x + 1)$  transformation for this analysis did not achieve compliance with the assumption of normality ( $P < 0.05$ ) based on a Shapiro-Wilk test (Shapiro and Wilk 1965). However, these data were well fitted to a negative binomial distribution (Bennetts 1991), and Mitchell (1977) has shown that ANOVA

procedures are relatively robust to violations of normality when the data are distributed as a negative binomial.

The average slope from the 30 regression models for the total number of bird registrations regressed on DMR separately for each survey, each year, at each location, was 0.15. None of these 30 models had a negative slope, indicating a consistent positive association between numbers of birds and dwarf mistletoe for all species combined (sign test,  $P < 0.001$ ). The slopes of these models differed from zero ( $t = 3.78$ ,  $P = 0.03$ , 3 df). This was a moderately powerful test ( $1 - \beta = 0.88$ ,  $H_A$ : slope = 0.15,  $\alpha = 0.05$ ).

DMR also explained considerably more of the variation in numbers of CNBs than location, year, or individual survey (Table 3). However, we did find evidence for effects of year, and for location and survey (in the interaction terms). If the number of snags per stand is substituted for DMR in the final model, it shows a similarly significant effect ( $F = 68.98$ ,  $P < 0.001$ ); however if both terms are included DMR is significant ( $F = 4.49$ ,  $P = 0.032$ ), but not the number of snags ( $F = 2.37$ ,  $P = 0.127$ ). The effects of DMR and number of snags on abundance of CNBs are confounded because DMR also is highly correlated with the number of snags ( $r = 0.92$ ,  $P = 0.001$ ).

The mean slope of the 30 individual regression models of CNB counts vs. DMR for each survey, each year, at each location, was 2.23. This differed significantly from zero ( $t = 5.47$ ,  $P = 0.012$ , 3 df) and was a relatively powerful test ( $1 - \beta = 0.94$ ,  $H_A$ : slope = 2.23,  $\alpha = 0.05$ ). Twenty-nine of the 30 slopes were positive (sign test,  $P < 0.001$ ), suggesting that the number of CNBs increased with increasing mistletoe level and that this relationship was generally consistent among locations, years, and repeated surveys.

Of the 47 species observed, 28 had a sufficient number of registrations to enable estimation of the slope for at least one survey. The average slope of 24 of these 28 species was positive (Table 1; sign test,  $P < 0.001$ ), suggesting that the abundance of most species was positively (or at least not negatively) associated with levels of mistletoe. The mean slope for 4 of 25 (0.16) of the species with a sufficient number of slopes to permit a test statistic, differed from zero with  $\alpha = 0.05$ . However, the power of these tests was relatively low ( $\bar{X}_{1-\beta} = 0.34$ ). If  $\alpha$  is therefore relaxed to 0.10, then the mean slopes for 9 of 25 (0.36) species differed from zero. No species whose slopes were negative, had slopes that differed from zero at either  $\alpha$  level.

#### Bird diversity

DMR was positively correlated with both the number of species observed in each stand ( $r = 0.87$ ,  $P = 0.005$ ) and the number of species estimated from program CAPTURE ( $r = 0.86$ ,  $P = 0.006$ ). This positive association was consistent within, as well as among, locations (Fig. 3). Program CAPTURE consistently in-

TABLE 1. The relationship between bird species abundance and mistletoe level, as shown by mean slopes of individual regression models relating bird abundance and dwarf mistletoe rating (DMR) for each species.

Common name	Scientific name	Total no. registrations	$\bar{X}_{\text{slope}}$	P
Mourning Dove	<i>Zenaida macroura</i>	24	0.47	—‡
Hairy Woodpecker	<i>Picoides villosus</i>	37	0.49	0.039
Downy Woodpecker	<i>Picoides pubescens</i>	1	—§	—‡
Three-toed Woodpecker	<i>Picoides tridactylus</i>	3	—§	—‡
Yellow Bellied Sapsucker	<i>Sphyrapicus varius</i>	1	—§	—‡
Williamson's Sapsucker	<i>Sphyrapicus thyroideus</i>	55	0.19	0.065
Northern Flicker	<i>Colaptes auratus</i>	32	0.36	0.176
Common Nighthawk	<i>Chordeiles minor</i>	23	71.43	—‡
White-throated Swift	<i>Aeronautes saxatalis</i>	1	—§	—‡
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	59	0.37	0.887
Olive-sided Flycatcher	<i>Contopus borealis</i>	3	—§	—‡
Western Wood-pewee	<i>Contopus sordidulus</i>	66	0.49	0.035
Western Flycatcher	<i>Empidonax difficilis</i>	14	—§	—‡
Hammond's Flycatcher	<i>Empidonax hammondi</i>	148	0.36	0.399
Steller's Jay	<i>Cyanocitta stelleri</i>	87	0.38	0.017
Gray Jay	<i>Perisoreus canadensis</i>	10	—§	—‡
Clark's Nutcracker	<i>Nucifraga columbiana</i>	29	18.08	0.496
Brown-headed Cowbird	<i>Molothrus ater</i>	210	0.22	0.148
Common Grackle	<i>Quiscalus quiscula</i>	1	—§	—‡
Evening Grosbeak	<i>Coccothraustes vespertinus</i>	17	-0.56	—‡
Cassin's Finch	<i>Carpodacus cassinii</i>	45	4.19	0.537
Red Crossbill	<i>Loxia curvirostra</i>	55	0.42	0.584
Pine Siskin	<i>Carduelis pinus</i>	14	—§	—‡
Chipping Sparrow	<i>Spizella passerina</i>	195	0.74	0.064
Dark-eyed Junco	<i>Junco hyemalis</i>	170	5.14	0.386
Song Sparrow	<i>Melospiza melodia</i>	1	—§	—‡
Green-tailed Towhee	<i>Pipilo chlorurus</i>	31	—§	—‡
Western Tanager	<i>Piranga ludoviciana</i>	240	30.19	0.184
Tree Swallow	<i>Tachycineta bicolor</i>	1	—§	—‡
Violet-green Swallow	<i>Tachycineta thalassina</i>	177	0.72	0.003
Warbling Vireo	<i>Vireo gilvus</i>	4	—§	—‡
Solitary Vireo	<i>Vireo solitarius</i>	78	-0.20	0.221
Virginia's Warbler	<i>Vermivora virginiae</i>	1	—§	—‡
Yellow-rumped Warbler	<i>Dendroica coronata</i>	216	-0.08	0.472
House Wren	<i>Troglodytes aedon</i>	54	0.71	0.071
Brown Creeper	<i>Certhia americana</i>	1	—§	—‡
White-breasted Nuthatch	<i>Sitta carolinensis</i>	72	0.58	0.374
Red-breasted Nuthatch	<i>Sitta canadensis</i>	6	—§	—‡
Pygmy Nuthatch	<i>Sitta pygmaea</i>	228	0.15	0.348
Mountain Chickadee	<i>Parus gameli</i>	213	0.73	0.144
Golden-crowned Kinglet	<i>Regulus satrapa</i>	1	—§	—‡
Ruby-crowned Kinglet	<i>Regulus calendula</i>	1	—§	—‡
Townsend's Solitaire	<i>Myadestes townsendi</i>	116	13.46	0.430
Hermit Thrush	<i>Catharus guttatus</i>	66	-0.07	0.787
American Robin	<i>Turdus migratorius</i>	139	0.47	0.084
Western Bluebird	<i>Sialia mexicana</i>	86	1.07	0.090
Mountain Bluebird	<i>Sialia currucoides</i>	4	—§	—‡

Notes: DMR is a measure of mistletoe abundance; for description of method see *Study area and methods*. P values are from two-tailed t tests of the null hypothesis that slope = 0.

† Based on degrees of freedom for location (1 df), year (1 df), and the interaction between location and year (1 df).

‡ Insufficient number of slopes for test.

§ Insufficient number of bird registrations to enable parameter estimation.

licated a generalized jackknife estimator (Burnham and Overton 1979) as being appropriate for these data.

There were no significant differences in evenness among stands at either location (Kolmogorov-Smirnov k-sample test,  $P > 0.1$ ) (Fig. 4).

#### DISCUSSION

Although our data are correlative, and thus do not necessarily imply causality, they suggest that both bird abundance and species richness are positively associated with the presence of dwarf mistletoe. There are

several potential explanations for this pattern. At least at some scales of patchiness, habitat heterogeneity may enhance bird diversity (Levin 1974, Roth 1976). The variation we observed in DMR does not represent uncertainty about our estimate because virtually all trees within each stand were rated (i.e., sampling error is effectively zero), but rather, reflects the patchy distribution of mistletoe throughout a stand. Thus, a stand with a moderate DMR is not generally a homogeneous stand of trees with moderate DMR values, but rather an interspersed of trees with varying DMR levels. This

TABLE 2. Analysis of variance table from multiple regression model using the  $\log(x + 1)$  number of bird registrations as the dependent variable. ss values are all Type III partial sums of squares (i.e., they are adjusted for all other terms in the model and are not dependent on the order of entry (SAS 1988)).

Source	df	ss	ms	F	P
Dwarf Mistletoe					
Rating (DMR)	1	35.189	35.189	64.78	<0.001
Year	1	2.317	2.317	4.27	0.039
Location	1	0.655	0.655	1.21	0.272
DMR $\times$ Year	1	0.093	0.093	0.17	0.678
DMR $\times$ Location	1	5.661	5.661	10.42	0.001
Error	1074	583.182	0.543		

patchy distribution of mistletoe results from a combination of localized spread via a pressure-propelled seed with colonization of new infection centers via animal (primarily bird) carriers (Hawksworth 1961a, Hudler 1976). The resulting influence on habitat structure is to create a mosaic of habitat patches of varying characteristics depending on the nature of the infestation.

Dwarf mistletoe may have enhanced the nesting opportunities of several bird species. Several previous studies (e.g., Mannan et al. 1980, Raphael and White 1984) have shown strong associations between the number of snags and the abundance of CNBs. The average slopes for the number of all cavity-nesting bird (CNB) species and DMR were positive, and Bennetts (1991) reported that the highest number of CNB nests on our study area were found in stands with the highest DMR. The number of snags also was highly correlated with DMR. Although the correlation between DMR and snags does not ensure that dwarf mistletoe caused the numbers of snags, the high percentage of snags that had been infected with mistletoe ( $\approx 78\%$ ) make it highly probable that mistletoe at least contributed to the number of snags. These correlations also do not ensure that DMR caused the higher numbers of CNBs; however, these relationships are consistent with previously reported associations between snags and CNBs (e.g., Mannan et al. 1980, Raphael and White 1984).

It has also been widely reported that CNBs tend to select larger snags for cavity excavation (e.g., McClelland and Frissell 1975, Scott 1978, Mannan et al. 1980, Raphael and White 1984). Bennetts (1991) found this relationship on our study area as well. Even though

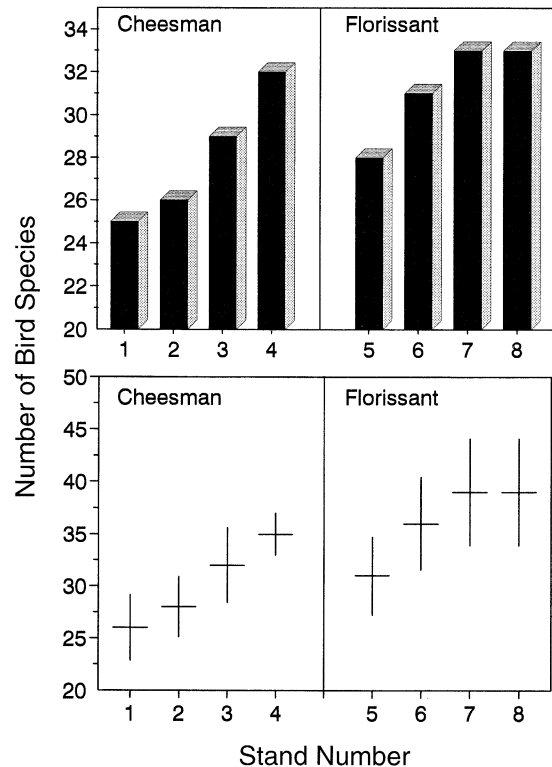


FIG. 3. The actual number of species observed on each stand (bars) and a generalized jackknife estimate of that number (perpendicular lines: means  $\pm$  1 SE) (Burnham and Overton 1979).

our data show a disproportionate increase in smaller snags with dwarf mistletoe, there was also a substantial increase in the total number of snags including larger ones. Sedgwick and Knopf (1990) suggested that a mosaic of different age structures is desirable to accommodate all species of CNBs.

Species other than CNBs also may have had enhanced nesting opportunities from dwarf mistletoe. Bennetts (1991) reported a positive correlation between DMR and the number of nests found on our study area. Dwarf mistletoe causes the formation of dense witches' brooms (Hawksworth and Wiens 1995), which may increase the concealment of nests. Bennetts (1991) reported that 50% of the cup nests found in infected trees on our study area were in witches' brooms. Numerous

TABLE 3. Analysis of variance table from multiple regression model using the  $\log(x + 1)$  number of cavity-nesting bird (CNB) registrations as the dependent variable. Sums of squares (ss) values are all Type III partial sums of squares (i.e., they are adjusted for all other terms in the model and are not dependent on the order of entry) (SAS 1988).

Source	df	ss	ms	F	P
Dwarf Mistletoe Rating (DMR)	1	16.040	16.040	67.70	<0.001
Year	1	1.231	1.231	5.19	0.025
Location	1	0.091	0.091	0.38	0.538
Survey	7	1.509	0.216	0.91	0.502
DMR $\times$ Location	1	1.281	1.281	5.41	0.022
Location $\times$ Survey	7	3.099	0.443	1.87	0.082
Error	101	23.937	0.237		



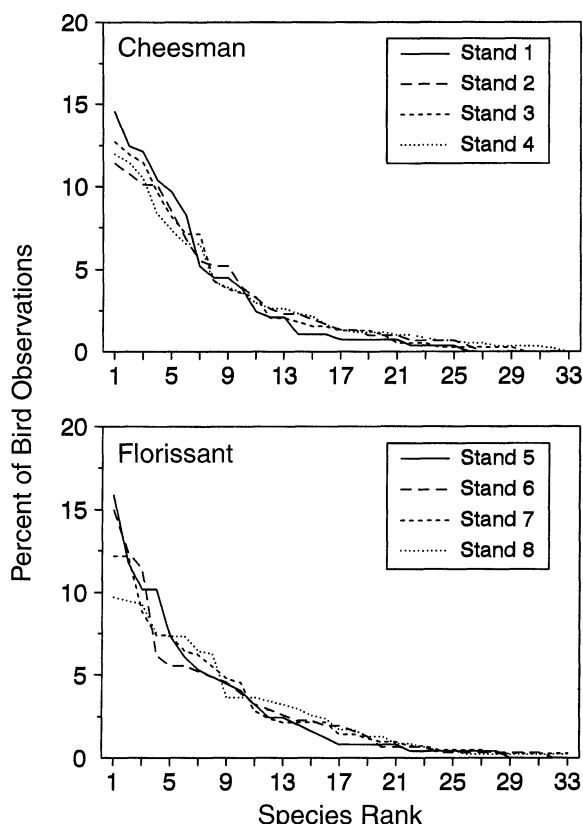


FIG. 4. The percentage of the total number of bird observations from each stand at Cheesman and Florissant accounted for by each avian species. Species are shown in rank order from the highest to the lowest number of individual observations. Complete equitability among species would result in a horizontal line.

species in other areas also have been reported to heavily use witches' brooms as a nest substrate (reviewed by Hawksworth and Wiens 1995).

Dwarf mistletoe also may enhance insect populations that feed on or pollinate mistletoe or that take advantage of the weakened condition of trees infected by mistletoe (Stevens and Hawksworth 1970, Scharpf 1975). Some species of insects are even host specific to dwarf mistletoes (Stevens and Hawksworth 1970, Scharpf 1975). Thus, the abundance of some insectivorous bird species may at least partially reflect enhanced foraging opportunities.

Although in almost all of our analyses, DMR showed a substantially greater influence than other variables we tested, several other sources of variation were detected. The limited scope of this study (i.e., two locations and eight stands) precludes a detailed exploration of secondary effects; however, we can suggest some plausible hypotheses for future testing. Our exploratory analysis showed an effect of location. This is likely due to local variation within and adjacent to our study stands at each location. For example, the Cheesman site was generally contiguous coniferous-

forest habitat. Adjacent habitats generally were other coniferous forest types (e.g. Douglas-fir or mixed conifer). In contrast, at Florissant adjacent habitats (beyond our buffer zones) often were open meadow. This could also explain the DMR  $\times$  Location interaction we observed in our exploratory regression model. Because the Florissant landscape already had numerous patches of open habitats, the effect of open patches created by mistletoe may not have been as pronounced. (The effects of DMR on bird numbers were greater at Cheesman.)

In addition to location, we also observed year effects in our exploratory analysis. We do not, however, consider year effects surprising given the potential for many species to show high annual variation in numbers (e.g., Holmes and Sherry 1988). We did not measure local resources (e.g., food) that may have helped explain these differences. Similarly, survey effects also were not surprising because the seasonal chronologies (e.g., arrival times of migrants, timing of breeding initiation, and degree of multiple nesting) among species differ.

The death of an individual tree from dwarf mistletoe may take several decades (Hawksworth and Geils 1990) and widespread infestation of a forest stand may take centuries (based on rates of spread described by Hawksworth [1961a]). Thus, the experimental manipulation that would be required to infer with a high degree of certainty a causal relationship between mistletoe and bird abundance is highly impractical. Consequently, we were limited to a retrospective study that used correlative and comparative data to show the secondary effects of dwarf mistletoe. It is possible to reduce the number of mistletoe shoots in small areas using chemical agents (Johnson and Hawksworth 1988); however, this would be effective only for assessing the direct effects of the plant's presence. Our intention here was to examine broader patterns, which included several potential indirect effects.

The number of registrations will be a biased measure of bird abundance if detectability is not equal among treatment groups. Differences in visual detectability among stands of different mistletoe levels is likely. Detectability in open patches created by mistletoe probably is increased, but detectability in foliage probably is decreased because of the dense witches' brooms. Witches' brooms in some conifers created by sources other than dwarf mistletoes often form as a single or few brooms (Hawksworth 1961b). In contrast, the brooms of dwarf mistletoes may occur on virtually all branches in a heavily infested patch (Hawksworth 1961b). Thus, visual detectability of birds may be greatly reduced in heavily infested patches. The extent to which these biases counter each other is unknown; however, most of our detections (75%) included aural detection. Although some biases probably also exist for such detection, it is doubtful that they could account for the large differences in the number of individuals

observed among stands. Thus, we are confident that our results are not an artifact of detectability bias.

Our data suggest that dwarf mistletoe may have some positive influences on bird communities. In light of an emerging emphasis on forest conservation and biodiversity among many land management agencies (e.g., Thomas 1987, Thomas and Salwasser 1989), an alternative perspective to dwarf mistletoe primarily being viewed as a forest pest may be warranted. Where a priori management goals emphasize timber production or protection of trees in recreation areas or home sites, dwarf mistletoe reduction programs may be warranted. In areas where management goals are not strictly focused on timber production, control of dwarf mistletoe may not be justified, practical, or even desirable. Wickner (1984) states "Dwarf mistletoe is a slow, insidious pest that fights a war of attrition. It wears down our interest, the visibility of our efforts, and thus the financial support of our control programs." Given that dwarf mistletoe has existed as part of ponderosa pine communities for a very great many years, we suggest that when consistent with management objectives, an alternative to fighting a "war" with dwarf mistletoe is to view it as having a "place" in healthy diverse forest ecosystems rather than as an invading "enemy".

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