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DWARF MISTLETOE AND BREEDING BIRD ABUNDANCE IN PONDEROSA PINE FORESTS

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ABSTRACT.—Southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*) parasitizes ponderosa pine (*Pinus ponderosa*). It can kill severely infected trees and induce the growth of dense masses of branches that can affect foraging and nesting habitat for wildlife. We tested the hypothesis that higher densities of breeding birds would be correlated with higher levels of southwestern dwarf mistletoe in ponderosa pine forests of Arizona. We estimated densities of 15 species of breeding birds and measured 26 habitat elements in 19 stands. Average dwarf mistletoe ratings (DMR) ranged from 0.0 (uninfested) to 3.7 (severely infested). Although we observed higher densities with higher infestation of dwarf mistletoe for 2 bird species and lower densities for 3 bird species, the effect of dwarf mistletoe on these was minor. Instead, higher snag density, an indirect measure of past mistletoe infestation, was a more important predictor of bird density. With greater snag size or density, the species richness and densities of 3 bird species increased. Because dwarf mistletoe infection can create snags, retaining groups of dwarf mistletoe-infected trees in ponderosa pine stands will provide a continued source of snags, which are important habitat for many wildlife species.

RESUMEN.—El muérdago *Arceuthobium vaginatum* subsp. *cryptopodum* parasita árboles de pino ponderosa (*Pinus ponderosa*) y puede matar a los individuos severamente infectados e inducir densas masas de ramas capaces de afectar el hábitat de forrajeo y anidación de muchos animales silvestres. Pusimos a prueba la hipótesis de que detectaríamos una mayor densidad de aves en reproducción en bosques de pino ponderosa con niveles más altos de muérdago en Arizona. Estimamos la densidad de 15 especies de aves en reproducción y medimos 26 elementos del hábitat en 19 puntos. El promedio de muérdago (DMR) osciló entre 0.0 (sin infestar) y 3.7 (severamente infestados). Aunque con una mayor infestación de muérdago observamos densidades mayores o menores para dos y tres especies de aves respectivamente, el efecto del muérdago fue mínimo para estas especies. En cambio, una mayor densidad de tocones, una medida indirecta de infestaciones de muérdago pasadas, fue un predictor más importante de la densidad de aves. Con un aumento en el tamaño o la densidad de los tocones, aumentó la riqueza de especies de aves y la densidad de tres especies. Debido a que la invasión de muérdago puede crear tocones, retener grupos de árboles infectados con muérdago en áreas de pino ponderosa proporcionará una fuente continua de tocones, los cuales funcionan como hábitats importantes para muchas especies silvestres.

In the southwestern United States, southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum;* hereafter mistletoe) parasitizes and is the most widespread and economically damaging disease agent of southwestern ponderosa pine (*Pinus ponderosa* var. *scopulorum;* Hawksworth et al. 1989). Mistletoe induces the formation of profusely branched, dense masses of distorted host branches known as witches' brooms (or brooms; Tinnin et al. 1982, Hawksworth and Wiens 1996) that contribute to reduced growth and increased mortality in ponderosa pine (Hawksworth 1961), which can substantially affect forest structure (Mathiasen 1996). Stand-replacement fires are more likely in severely infested pine forests (Alexander and Hawksworth 1975, Koonce and Roth 1985, Harrington and Hawksworth 1990, Parker et al. 2006, Stanton and Hadley 2010). Where timber production, fuels reduction, or forest restoration treatments are primary goals of forest management, managers attempt to control or remove mistletoe infestations (Hawksworth and Shaw 1988, Conklin and Fairweather 2010).

Mistletoe has a more dominant role in present-day forest ecology than it did prior to Euro-American settlement (Parmeter 1978). Fire suppression, livestock grazing, and silvicultural practices have dramatically increased tree densities through parts of the Southwest (Cooper 1960, Covington and Moore 1994, Saab et al. 1995, Mast et al. 1999, Grissino-Mayer and Swetnam 2000). Mistletoe spreads more quickly in dense stands of evenly spaced

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trees (>175 trees · ha^{-1}) than in the open (<120 trees · ha^{-1}), clumped stands that are believed to have dominated before 1870 (Hawksworth 1961). Prior to fire suppression, mistletoe was reduced by the more frequent fires characteristic of historic fire regimes (Alexander and Hawksworth 1975, Harrington and Hawksworth 1990, Hoffman et al. 2007). Consequently, mistletoe infestations are found over larger areas and at a greater intensity than in the past (Maffei and Beatty 1988, Conklin and Fairweather 2010). In addition, ponderosa pine stands with mistletoe have higher surface-fuel loads than noninfested stands (Harrington and Hawksworth 1990, Hoffman et al. 2007, Stanton and Hadley 2010, Klutsch et al. 2014). As part of fuels reduction and forest restoration programs in western states, many ponderosa pine forests are actively managed to decrease risk of catastrophic fire (i.e., the Healthy Forests Restoration Act of 2003), affording the opportunity to also manage mistletoe to enhance wildlife habitat in many southwestern ponderosa pine forests (Conklin and Fairweather 2010).

Mistletoe is a valuable resource for some bird species (Hawksworth and Wiens 1996, Ganey et al. 2013). Several species of songbirds nest in brooms (Bennetts 1991, Bennetts et al. 1996). Songbirds foraged for insects attracted to mistletoe shoots in Colorado (Hudler et al. 1979), and insect abundance and richness was greater in witches' brooms than non-broomed branches of Douglas-fir (*Pseudotsuga menziesii*) in Arizona (Smith et al. 2013). Birds may also be attracted to heterogeneous canopy structures induced by mistletoe infestation (Reich et al. 2000). Cavity-nesting birds nest in snags created by mistletoe infection, and in Colorado 24 of 28 bird species studied were more abundant in ponderosa pine stands that were severely infested by mistletoe (Bennetts et al. 1996).

Information is needed on wildlife use of mistletoe-infested stands to help resource managers design prescriptions that incorporate mistletoe as a habitat component. We hypothesized that the presence of mistletoe and brooms in ponderosa pine stands would be correlated with higher species richness and higher densities of individual bird species because of the increased number of foraging and roosting substrates provided by mistletoe. Our objective was to determine whether the severity of mistletoe infestation influenced the diurnal breeding bird community in northern Arizona after adjusting for all other influential habitat attributes.

METHODS

Study Sites

We counted birds in ponderosa pine forests in northern Arizona in 1999 and 2000. The area was characterized by dry spring seasons, summer monsoons, and winter snow (Schubert 1974). Annual precipitation averaged 46.7 cm and 48.9 cm, and temperatures averaged 6.8 °C and 6.1 °C in 1999 and 2000, respectively (NOAA 2006). We used 4 criteria to select stands: each needed to be (1) dominated by ponderosa pine (≥95% by basal area), (2) an adequate size for bird counts (≥32 ha), (3) spaced ≥1 km away from other stands, and (4) representative of a range of mistletoe infection in ponderosa pine forests on public lands in northern Arizona. To select stands with these criteria, we surveyed 63 stands using ≥20 point-samples in each (Avery and Burkhart 2002). At each point-sample we used a 4.7 m^2 · ha^{-1} basal area factor prism and examined all "in" trees for mistletoe infection and recorded the tree species. Each "in" tree was assigned a dwarf mistletoe rating (DMR) using the 6-class system (Hawksworth 1977). This system divides the live crown of a tree into thirds and rates each third as 0 = no infection, 1 = less than half of the branches infected, or 2 = more than half of the branches infected. The ratings for each third are then summed to yield a DMR for the tree. DMRs can range from 0 (uninfected) to as high as 6 (severely infected). Totaling the DMRs for all trees sampled in a stand, including uninfected trees, and dividing by the total number of trees examined provided a mean DMR for each stand. The mean DMR provided an estimate of the severity of mistletoe infection at the stand level (Hawksworth 1977, Parker and Mathiasen 2004).

Of the 63 stands we surveyed, we selected 19 that fit our criteria. Mean DMR, elevation, and slope ranged from 0.0 to 3.7, 2218 m to 2545 m, and 2° to 14°, respectively. These stands were dominated by ponderosa pine (99.2% by basal area); remaining species were Gambel oak (*Quercus gambelii*), New Mexican locust (*Robinia neomexicana*), southwestern white pine (*Pinus strobiformis*), Douglas-fir, junipers

(*Juniperus* spp.) or pinyon pine (*Pinus edulis*). Basal area of stands ranged from 19.7 to 43.5 $m^2 \cdot ha^{-1}$, tree density from 219 trees $\cdot$ ha^{-1} to 964 trees $\cdot$ ha^{-1}, and quadratic mean diameter from 22 cm to 37 cm. There was little (<0.01%) understory shrub cover; dominant species were Fendler ceanothus (*Ceanothus fendleri*) and creeping barberry (*Berberis repens*). Cover of understory forbs and grasses ranged from 7.1% to 30.3% and included common mullein (*Verbascum thapsus*), white pussytoes (*Antennaria parvifolia*), mountain muhly (*Muhlenbergia montana*), columbine (*Aquilegia* spp.), silvery lupine (*Lupinus argenteus*), Arizona fescue (*Festuca arizonica*), pine dropseed (*Blepharoneuron tricholepis*), and blue grama (*Bouteloua gracilis*). Densities of snags >12.7 cm diameter at breast height (dbh, 1.4 m above ground level) and >1 m tall ranged from 1.8 to 70.4 per ha; 99.7% of snags were ponderosa pine. In stands with a mean DMR ≥1.0, 79% of ponderosa pine snags in decay class 1 and 2 (Raphael and White 1984) had evidence of past mistletoe infection (e.g., basal cups, distorted branches, dead brooms). For all stands, 56% of ponderosa pine snags in decay class 1 and 2 had evidence of past mistletoe infection.

The stands had a similar management history, and they had not been thinned or burned by prescribed fire or wildfire in the 5 years prior to our study. Fire suppression and livestock grazing occurred in the area since the 1800s, and wild ungulates (elk [*Cervus canadensis*] and mule deer [*Odocoileus hemionus*]) had access to all stands.

Bird Surveys

We established 8 point-count stations in each stand. One station originated at a random start location, and the remaining 7 stations were placed using a random compass bearing to establish direction and were ≥100 m from the stand boundary and ≥200 m apart. We surveyed birds using a modified version of a variable-radius point-count technique (Ralph et al. 1993), recording all birds detected by sight or by sound ≤100 m from the station. We estimated distance to the bird to the nearest meter using a handheld laser rangefinder (Haglöf Laser Pro 300XL, Haglöf Inc., Madison, MS). We surveyed stations 6 times per year between 22 May and 2 July in 1999 and 2000, with at least 6 d separating repeated surveys at a station. Sites were visited in random order within each survey period. We began counts 30 min after sunrise and completed them by 0830. Two observers per year counted birds with one observer common to both years. To minimize bias, this observer also trained the other observer and observers rotated among all sites. After arriving at the station, we counted birds for 5 min after waiting a 1-min settling period (Szaro and Balda 1982, Ralph et al. 1993). We stopped counts when wind was ≥13 km $\cdot$ h^{-1} and when it was raining (Robbins et al. 1986).

We identified 15 bird species known or believed to be associated with mistletoe infestation that had large enough sample sizes for analyses. These species were categorized into 3 groups: birds that nested in foliage and thus could be affected by broom volume (n = 7, Table 1), birds (primary and secondary cavity nesters and one flake nester) that nested in snags that might have resulted from mistletoe infection (n = 7, Table 1), and one ground-nesting bird that is affected by decreased stand density (i.e., greater understory development with lower overstory canopy; Griffis et al. 2001; Table 1). We estimated densities for those species with adequate sample sizes (≥60 detections within a stand; Dark-eyed Junco, Mountain Chickadee, Yellow-rumped Warbler; for scientific names see Table 1) using Program DISTANCE (Buckland et al. 1993). For the 12 species without adequate detections, we tested whether the probability of detection between stands was similar by comparing detection distances for birds in the 5 most severely infested stands with those in the 5 least severely infested stands. Mean detection distances varied <1 m between severely infested and uninfested stands ($F_{1,3232}$ = 1.84, P = 0.18). For this reason, and because average truncation distance in DISTANCE was 76.6 m, detections beyond 75 m were removed from the data set and total counts were used as an index of avian abundance.

Habitat Sampling

Slope and aspect (precision to 1°) were measured at each of the 152 point-count stations. We sampled vegetation at five 11.3-m radius plots (0.04 ha) at each point-count station with one sampling plot centered on the point-count station and the 4 other plots placed 40 m from the point-count station. The first of these

TABLE 1. Models for diurnal breeding birds observed in 19 mistletoe-infested ponderosa pine stands, northern Arizona, 1999 and 2000. Bird species were organized by nesting and foraging guild; *n* = number of bird detections. Variables were habitat features that best predicted increase or decrease in bird detections. The sign (+ or −) for dead wood and mistletoe variables represents the relationship between bird detections or richness and the variable. *P* = probability that the addition of mistletoe variables to the reduced model was significantly different from zero (i.e., probability that there was an effect of mistletoe on habitat selection). Variables used to measure mistletoe or dead wood (snags, logs) are indicated in bold font.

Species common name	Scientific name	*n*	Variables in best model[a]	χ^2	*P*
Richness		—	**+SNGDBH**	3.3	0.19
Primary cavity nesters					
Hairy Woodpecker	*Picoides villosus*	130	BA	1.2	0.55
Secondary cavity nesters					
Cordilleran Flycatcher	*Empidonax occidentalis*	124	**VBI, +MSTOE, +CWD**	6.1	0.05
Mountain Chickadee	*Poecile gambeli*	1293	**−VBI, −MSTOE**	10.3	0.01
Pygmy Nuthatch	*Sitta pygmaea*	1654	**+SPH>10, +SNGDBH, +VBI, +MSTOE**	6.0	0.05
White-breasted Nuthatch	*Sitta carolinensis*	756	HERB, TPH>38	5.2	0.07
Western Bluebird	*Sialia mexicana*	455	BA, avgLCR, HERB	2.1	0.35
Flake nesters					
Brown Creeper	*Certhia americana*	359	ELEV, **+SPH>45**, TPH3145	0.3	0.86
Foliage nesters					
American Robin	*Turdus migratorius*	225	ELEV, DIRT, TPH>60	4.5	0.11
Mourning Dove	*Zenaida macroura*	271	DIRT, QMD	4.7	0.10
Olive Warbler	*Peucedramus taeniatus*	187	no model	2.5	0.29
Plumbeous Vireo	*Vireo plumbeus*	214	**−SPH>45**	4.5	0.11
Western Tanager	*Piranga ludoviciana*	296	BA, TPH, TPH4660	0.2	0.90
Western Wood-Pewee	*Contopus sordidulus*	175	totLCR, TPH<13, **−SPH>45**	3.8	0.15
Yellow-rumped Warbler	*Dendroica coronata*	1709	ROCK, **−SPH>10, −VBI, −MSTOE**	6.7	0.04
Ground nesters					
Dark-eyed Junco	*Junco hyemalis*	1105	BA, TPH<13, **VBI, −MSTOE**	9.0	0.01

[a]Variables were transformed using log(variable+1) or square root(variable). Variables were average live crown percent (avgLCR), total basal area (BA), coarse woody debris volume (CWD), percent dirt cover (DIRT), elevation (ELEV), percent herbaceous ground cover (HERB), quadratic mean diameter (QMD), percent rock cover (ROCK), average snag dbh (SNGDBH), snags per ha >10 m tall (SPH>10), snags per ha >45 cm dbh (SPH>45), total live crown percent (totLCR), trees per ha (TPH), trees per ha <13 cm dbh (TPH<13), trees per ha 31 to 45 cm dbh (TPH3145), trees per ha >38 cm dbh (TPH>38), trees per ha 46 to 60 cm dbh (TPH4660), trees per ha >60 cm dbh (TPH>60). Mistletoe variables believed to be important in predicting bird density were VBI (broom volume of trees infected with dwarf mistletoe) and MSTOE (a derived variable from 5 strongly positively correlated mistletoe variables: BRM, DMI, DMRavg, TIP, and VBA—definitions in text).

4 sampling plots was located at random and the other 3 points located at 90°, 180°, and 270° offsets from the randomly located plot.

Live trees and snags ≥12.7 cm dbh were measured in each of the five 11.3-m-radius plots established at each sample point. Tree species, dbh (measured to the nearest cm), dwarf mistletoe rating (DMR, Hawksworth 1977), and tree height (estimated to the nearest m) were recorded for each live tree. Percent live crown (percentage of the total height of the tree that had living branches) was visually estimated to the nearest 10% by the same person during both years of the study. The percentage of the live crown occupied by witches' brooms (broom volume) was visually estimated to the nearest 10% for each live tree in each of the 5 plots by the same person. The approximate volume occupied by brooms in the live crown of a tree was visually compressed and the approximate volume of the live crown occupied by brooms was then estimated.

Because measures of mistletoe were developed to quantify mistletoe infection rather than wildlife habitat, we derived 6 measures of mistletoe infection to characterize habitat: (**1**) Broom index (BRM), an index of broom volume, was calculated by multiplying the percent of live crown occupied by mistletoe brooms (the approximate volume of the live crown volume occupied by witches' brooms estimated to the nearest 10%) by the percent live crown (the ratio of the length of the live crown to the total height of the tree estimated to the nearest 10%) by the tree height, and then summing this value for all live trees in all plots established for each study site. Broom index was necessary to quantify broom development because severely infected trees do not always develop brooms, and broom development may depend partially on forest conditions such as basal area (Hawksworth 1961, Parker and Mathiasen 2004). Broom index can quantify the degree of broom development available for nesting and foraging more accurately than can other methods of quantifying broom development (e.g., broom volume rating or total broom volume), because it accounts for differential tree heights among forest stands (Parker and Mathiasen 2004). In general, the higher the broom index value for a study site, the greater the number of large trees with brooms in their crowns. (**2**) Average dwarf mistletoe rating for each stand (DMRavg) was calculated by averaging the DMRs for all live trees (infected and uninfected) by species. (**3**) Average mistletoe rating of trees infected with dwarf mistletoe (DMI, an average that excluded uninfected trees), (**4**) percent of trees with mistletoe infection (TIP), and (**5**) broom volume estimated to the nearest 10% for all live trees (VBA) were also calculated, as well as (**6**) broom volume of live trees infected with dwarf mistletoe (VBI), which was similar to VBA except for excluding trees without mistletoe infection.

For each snag, we measured height, dbh, and decay class. We used 5 decay classes: (1) recently dead tree with needles, twigs, and limbs present; (2) needles absent, twigs and limbs present; (3) needles and twigs absent, limbs present and mostly intact; (4) limbs present but mostly broken; and (5) without limbs (after Raphael and White 1984). Evidence of mistletoe infection was noted only for class 1 and 2 snags (class 3, 4, and 5 snags no longer showed clear evidence of mistletoe infection due to bark degradation and related difficulty in identifying basal cups).

We measured woody plants ≥0.5 m tall and <12.7 cm dbh on 5-m-radius plots within each 11.3-m-radius plot. We recorded species, height (to nearest 0.1 m), and width in the widest direction (to nearest 0.1 m) for each woody plant.

We used two 40-m transects at each point-count station to measure canopy cover, ground cover, and downed woody debris. One transect was established on a random azimuth from the station, and another 180° from the random azimuth. Presence or absence of canopy cover at 1-m intercepts was determined using a vertical sighting periscope (Rosenstock 1996). Ground cover was estimated on the same transects and at the same locations as canopy cover intercepts. We noted presence or absence of the following classes of ground cover: grasses, forbs, litter, shrubs, rock, and logs. In addition, we recorded diameter and length of logs with a diameter ≥12.7 cm at midpoint. We generated 34 vegetation and physiographic characteristics (e.g., basal area, trees per hectare by diameter class, elevation) for each study site to use in models of bird–habitat relationships.

Data Analysis

To test our hypothesis that the habitat and mistletoe variables (explanatory variables) were

TABLE 2. Habitat variables evaluated as covariates predicting response of diurnal breeding birds and bird species richness to dwarf mistletoe infestation in ponderosa pine forests in northern Arizona, 1999–2000.

Category	Variable	Definition
Year	YEAR	Year the data were collected (1999 or 2000)
Canopy	BA	Total basal area ($m^2 \cdot ha^{-1}$)
	CANOPY	Percent canopy cover
	avgLCR	Average live crown percent
	totLCR	Total live crown percent
Ground	ELEV	Elevation (m)
	DIRT	Percent dirt cover
	HERB	Percent herb cover
	LITTER	Percent litter cover
	ROCK	Percent rock cover
Dead wood	CWD	Course woody debris volume ($m^3 \cdot ha^{-1}$)
	SNGDBH	Average snag dbh (cm)
	SPH>10	Snags per ha >10 m tall
	SPH>1	Snags per ha >1 m tall
	SPH>45	Snags per ha >45 cm dbh
Small tree	TPH	Trees per ha
	TPH<13	Trees per ha <13 cm dbh
	TPH1330	Trees per ha 13 to 30 cm dbh
Small tree	TPH3145	Trees per ha 31 to 45 cm dbh
	TPH>30	Trees per ha >30 cm dbh
	TPH>38	Trees per ha >38 cm dbh
Large tree	TPH>45	Trees per ha >45 cm dbh
	TPH4660	Trees per ha 46 to 60 cm dbh
	TPH>50	Trees per ha >50 cm dbh
	TPH>60	Trees per ha >60 cm dbh
Stand descriptor variables for trees	DbhCOV	Coefficient of variation for dbh
	HgtCOV	Coefficient of variation for tree height
	QMD	Quadratic mean diameter (cm)
Mistletoe	MSTOE	Variable for mistletoe derived from a combination of BRM, DMI, DMRavg, TIP, and VBA[a]
	VBI	Broom volume of trees infected with dwarf mistletoe

[a]Definitions in text.

related to bird counts or species richness, we analyzed stand-level averages of habitat characteristics, bird density estimates, and species richness (Zar 1999). We transformed variables using square root or log (log[variable+1]) transformations to meet assumptions of normality. We used Pearson's correlation coefficient to illustrate direction and strength of the association between mistletoe and dead wood variables in models and estimates of bird densities and species richness (Neter et al. 1996). Because 5 measures of mistletoe infection (BRM, DMI, DMRavg, TIP, and VBA) were positively correlated ($r \geq 0.83$, $P < 0.0001$), we used a principal component analysis (PROC PRINCOMP; Khattree and Naik 2000) to reduce these measures to one synthetic variable (MSTOE) that explained 94% of the variation in the original data. For species that are primary or secondary cavity nesters, we also considered indirect measures of mistletoe infection (e.g., snags per ha >1 m tall, snags per ha >10 m tall, snags per ha >45 cm dbh) as these variables were positively correlated with the mistletoe variable MSTOE ($r \geq 0.67$, $P < 0.001$).

To develop a model that included habitat variables that best predicted species richness or the density estimate for each bird species, we divided the habitat variables with the potential to influence density or richness into 6 groups (Table 2): canopy (e.g., total live crown, percent canopy cover), ground, dead wood, small-tree variables, large-tree variables, and stand-descriptor variables for trees. We then reduced the number of variables in each group to the subset that we considered to have explanatory power ($P \leq 0.15$). Next, we created a model for each response variable that included all habitat variables identified in the first step, and retained those variables where $P \leq 0.05$. Therefore, this "reduced" model included all explanatory variables that explained variation in each response, except mistletoe variables. Finally, we added the 2 mistletoe variables (MSTOE and VBI) to each reduced model to create a "full" model and computed the difference in the amount of variation in the response explained by full and reduced models with a drop-in-deviance test (Ramsey and Schafer 2002). This provided a test of the effect of mistletoe on bird density after accounting for other important habitat variables. Because we sampled each stand for 2 years, we used year as a covariate in all models and all steps regardless of its explanatory power.

We used a repeated-measures, mixed-model approach for all analyses (PROC MIXED; Littell et al. 2006) to account for data collected from the same stand in both years, and used a first-order autoregressive covariance structure. We identified stands as a random effect and all other variables as fixed effects.

RESULTS

We observed 45 species during the 2-year study. We did not detect a relationship between bird species richness with mistletoe variables after adjusting for all other habitat variables (Table 1). Five of 15 bird species were positively ($n = 2$) or negatively ($n = 3$) associated with mistletoe. Two cavity-nesting species (Cordilleran Flycatcher and Pygmy Nuthatch) were more abundant with increased presence of mistletoe (Table 1). However, the relationships between these cavity nesters and mistletoe were weak relative to the influence of habitat elements, based on parameter estimates and their confidence intervals (Table 3). Although we detected fewer Yellow-rumped Warblers, Dark-eyed Juncos, and Mountain Chickadees with higher levels of mistletoe (Table 1), the negative influence of mistletoe in these models was also weak (Table 3).

Bird species richness was greater with increased numbers of larger-sized (dbh) snags ($P = 0.02$), and models for 3 of 7 cavity- and flake-nesting birds included some measure of snag density (Table 1, Table 3). Abundance of Pygmy Nuthatches was greater with higher numbers of larger-sized (dbh) snags ($P = 0.01$) and with higher density of snags >10 m tall ($P = 0.05$) (Table 3). Abundance of Cordilleran Flycatchers was greater with increased amounts of coarse woody debris ($P = 0.04$) (Table 3). Abundance of Brown Creepers was greater with increased numbers of snags >45 cm dbh ($P = 0.02$). We also noted relationships between 3 foliage-nesting birds and dead wood. Abundances of Plumbeous Vireo and Western Wood-Pewee decreased with higher numbers of snags >45 cm dbh (Plumbeous Vireo: $P = 0.02$; Western Wood-Pewee: $P = 0.01$), and abundance of Yellow-rumped Warblers decreased with an increase in snags >10 m tall ($P = 0.79$; Tables 1, 3).

DISCUSSION

Historically, ponderosa pine forests in the Southwest probably had lower levels of mistletoe than at present (Maffei and Beatty 1988, Conklin and Fairweather 2010), which may explain why we found little dependence of birds on mistletoe in our study. Although Bennetts et al. (1996) reported significant ($P < 0.05$) positive associations between mistletoe, bird species richness, and 4 bird species (Hairy Woodpecker, Western Wood-Pewee, Steller's Jay [*Cyanocitta stelleri*], and Violet-green Swallow [*Tachycineta thalassina*]), we found none of these relationships. Parks et al. (1999) and Garnett et al. (2006) documented use of brooms by several mammal species, including squirrels (*Sciurus* spp.). The presence of squirrels may deter broom use by birds since squirrels can be nest predators (e.g., Saab and Vierling 2001, Ibarzabal and Desrochers 2004).

However, mistletoe may still represent an important resource for birds. We found nests of Mourning Dove and Yellow-rumped Warbler in brooms (Parker 2001). Many birds in northern Arizona are permanent residents or short-distance migrants, so brooms may provide roosting or foraging substrates during the colder winter months.

The 2 bird species in our study with positive, albeit weak, mistletoe associations were cavity nesters (Cordilleran Flycatcher and Pygmy Nuthatch) that were also positively associated with measures of coarse woody debris, snag density, or snag size. Bennetts et al. (1996) found a positive correlation between mistletoe levels and snag numbers, and they speculated that mistletoe led to snag creation in the stands they studied. Given the strong correlation we found between severity of mistletoe infection and snag density, mistletoe could be an important factor in recruiting snags as wildlife habitat for some species. However, other cavity-nesting birds in our study showed no or a negative association

TABLE 3. Fixed effects (β) and lower (LCI) and upper (UCI) confidence interval limits for models predicting habitat relationships (CWD, SNGDBH, SPH>10, ROCK, BA, TPH<13; variables defined in text) where effects of dwarf mistletoe (VBI, MSTOE) were significant (see Table 1) on breeding birds in ponderosa pine forest, northern Arizona, 1999–2000.

Species	β	LCI	UCI
Positive response to dwarf mistletoe			
Cordilleran Flycatcher			
Intercept	−2.2999	−6.2172	1.6173
Year 1999	−0.1	−0.4304	0.2304
Year 2000	0	—	—
CWD	0.8371	0.06483	1.6093
VBI	−0.05416	−0.1856	0.07725
MSTOE	0.03168	−0.1732	0.2365
Pygmy Nuthatch			
Intercept	−104.93	−215.29	5.4346
Year 1999	−38.1053	−45.4236	−30.787
Year 2000	0	—	—
SNGDBH	107.03	34.6329	179.43
SPH>10	19.633	0.2602	39.0058
VBI	0.7204	-2.0931	3.5339
MSTOE	−1.5167	−7.1548	4.1214
Negative response to dwarf mistletoe			
Mountain Chickadee			
Intercept	0.9829	0.7097	1.256
Year 1999	−0.02105	−0.2399	0.1978
Year 2000	0	—	—
VBI	0.006324	−0.04323	0.05588
MSTOE	−0.02825	−0.0981	0.0416
Yellow-rumped Warbler			
Intercept	1.3067	0.767	1.8464
Year 1999	−0.4105	−0.5719	−0.2491
Year 2000	0	—	—
ROCK	−0.03275	−0.06799	0.002486
SPH>10	−0.04705	−0.4244	0.3303
VBI	0.03295	−0.02688	0.09277
MSTOE	−0.09469	−0.2144	0.02501
Dark-eyed Junco			
Intercept	2.7022	1.3309	4.0735
Year 1999	0.2895	−0.00454	0.5835
Year 2000	0	—	—
BA	−0.03219	−0.05692	−0.00745
TPH<13	−0.4664	−0.8871	−0.04565
VBI	0.02272	−0.03034	0.07578
MSTOE	−0.04503	−0.1216	0.03159

with ponderosa pine snags and down wood. White-breasted Nuthatches, Mountain Chickadees, and Western Bluebirds did not appear to be dependent on presence of ponderosa pine snags, possibly because they can nest in excavated and natural cavities of dead or live trees (Balda 1975, Cunningham et al. 1980).

The dependence of several cavity nesters on snags indicates the importance of maintaining this habitat element across the landscape to provide nesting sites, and mistletoe appears to be an important contributor to snag formation. Recommendations for snag densities in ponderosa pine have varied from 4.2 to 7.4 per hectare (United States Forest Service 1996, Ganey 2016). Because ponderosa pine snags remain standing only a short time (i.e., up to 90% of ponderosa pine snags fall ≤10 years after creation; Ganey et al. 2015) and because mistletoe kills trees in a very slow manner (Hawksworth and Geils 1990), mistletoe infestation can be a long-term source of snags. Therefore, we recommend retaining groups of mistletoe-infected ponderosa pines to help create snags on a continuing basis because they create important habitat for many wildlife species.

As forests become more severely infested with a parasite such as mistletoe, the structure and composition of the plant community may shift; for example, dominant trees may die and less susceptible tree and shrub species may then derive a competitive advantage and become more common (Press and Phoenix 2005). As plant species diversity increases, avian diversity may also increase (MacArthur and MacArthur 1961, Rotenberry 1985). In our study, although overstory canopy cover decreased with increasing mistletoe infestation (MSTOE, $r = -0.52$, $P = 0.0008$), herbaceous cover did not increase ($r = -0.21$, $P = 0.2$). Our sites represented simple plant communities; they were primarily ponderosa pine with little understory. Although snags were more common in severely infested stands, snag formation did not significantly affect the understory plant community.

We tried 6 measures of mistletoe to explain habitat associations. Although the relationships we found between bird density and dwarf mistletoe were weak, the variables we used (MSTOE and VBI) were useful in explaining habitat relationships for some birds. Because 5 were highly correlated (combined as MSTOE), any of these measures of dwarf mistletoe infection can be used. Resource managers can use the measures that are the easiest to take in the field or the most accepted in practice (e.g., DMR) as a tool to assess mistletoe's effect on breeding birds in the Southwest.

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