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Characteristics of aspen infected with heartrot: Implications for cavity-nesting birds

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ABSTRACT

Phellinus tremulae is an important fungal decay agent common to aspen and a critical component to the cavity-nesting bird complex found in western aspen stands. Little information exists on the conditions that facilitate infection and spread of *P. tremulae* in aspen forests. I used Forest Inventory and Analysis (FIA) data to explore the relationships of several tree and stand characteristics to the presence and frequency of *P. tremulae* in aspen measured across several western states of the United States. Results suggest a strong relationship between tree age, tree diameter, and compacted crown ratio with infection frequency in trees while stand purity, canopy cover and stand age had a positive relationship with the occurrence of *P. tremulae* in forest stands containing aspen. Logistic regression modeling identified stand age as the only variable that increased the odds of predicting infection at the stand-level while all tree-level variables were included in the tree model. Data also show that infection rates in the study area were lower than in other parts of aspen's range, and that average size of infected trees was smaller in the study area than those reported elsewhere. These results have important implications to management of aspen for wildlife, especially for birds that use decayed aspen for nesting.

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1. Introduction

Aspen (*Populus tremuloides*) is the most widely distributed tree species in North America and provides important habitat to a variety of organisms (Little, 1971; Debyle and Winokur, 1985). Aspen has been shown to be important habitat for breeding birds especially in the western contiguous United States, where it often provides food, cover, and nesting habitat disproportionate to its frequency on the landscape (Winternitz, 1980; Dobkin et al., 1995; Schieck et al., 1995; Hollenbeck and Ripple, 2008). Many of the bird species that breed in aspen forests are part of a system involving primary-cavity excavators, secondary-cavity-nesters, and aspen infected with the fungus *Phellinus tremulae* (Winternitz and Cahn, 1983; Daily et al., 1993; Martin and Eadie, 1999; Hart and Hart, 2001). *P. tremulae* causes white trunk rot (heartrot) in the trunk and stem of a tree without immediately killing it (Hiratsuka and Loman, 1984; Jones and Ostry, 1998). Although the specific mode of infection is not well understood, damage caused by natural pruning, animals, impacts from falling trees, and weather may facilitate infection (Basham, 1958; Hiratsuka, 1987). Infected aspen trees are sought out by several species of primary-cavity-nesting birds, some of the most important in the western United States being Red-naped sapsuckers (*Sphyrapicus nuchalis*) and Northern flickers (*Colaptes auratus*) (Crockett and Hadow, 1975; Winternitz and Cahn, 1983; Hart and Hart, 2001). These birds excavate new nest cavities throughout their life, often in the same tree, leaving old cavities for secondary-cavity-nesters to occupy (McClelland et al., 1979; Loeb, 1993; Newton, 1994; Sedgwick, 1997).

In Ontario, Canada Basham (1958) found the frequency of *P. tremulae* in aspen stands was related to tree age. Hiratsuka and Loman (1984) found a similar relationship in Alberta, Canada. However, few studies have investigated the relationship between stand and tree characteristics and the presence of *P. tremulae* in live trees in the western United States, where site characteristics can vary greatly from those in the northern and eastern extent of aspen's range. Since the presence of aspen trees infected by *P. tremulae* is a critical component of cavity-nesting bird communities, it is important for forest and wildlife managers to know what factors influence the frequency and extent of the fungus. Knowing what tree and stand characteristics are associated with *P. tremulae* can help predict where habitat might be lost or gained depending on naturally changing forest conditions. Stand treatments and other management practices could also be used to promote or maintain fungal activity. This information can then help land managers increase or

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maintain potential habitat for cavity-nesting birds in aspen stands in the western United States.

I explored the relationship between aspen and *P. tremulae* in eight western states by comparing aspen tree and stand characteristics where the fungus is present to those where it is not found. I used Interior West Forest Inventory and Analysis (IW-FIA) data to test whether certain tree and stand characteristics can predict the presence or frequency of *P. tremulae*. I tested whether age, diameter, or compacted crown ratio of aspen trees $\geq$2.54 cm diameter at breast height (1.40 m) (DBH) infected with heartrot differed from non-infected trees. To assess the potential value of external ocular cues to infection, I compared ages of trees showing external signs of infection (conks) to infected trees that showed no external signs. I also tested for differences in stand purity, stand age, crown cover and site quality between infected and uninfected forest stands containing aspen trees. I tested the hypothesis that where stand characteristics reflect higher quality sites for aspen growth, the incidence of infection would be higher. I hypothesized that older stands would be more prone to infection because of greater temporal opportunity for the fungus to infect suitable host trees. Stands of higher aspen purity were predicted to have higher rates of infection because close proximity to other trees increased opportunity for infection. I also tested the hypothesis that tree age and diameter would be higher in the infected population based on previous findings (Basham, 1958). I discuss findings as they pertain to the cavity-nesting bird community in the western United States.

2. Methods

2.1. Forest inventory and analysis program

The Forest Inventory and Analysis (FIA) program of the Forest Service, U.S. Department of Agriculture, is responsible for assessing the status and trends of all forested lands in the U.S. (Gillespie, 1999). The national FIA program conducts inventory on all forested lands of the U.S. using a nationally standardized plot design at an intensity of approximately one field plot (roughly 0.4 ha in size) per 2388 ha (USDA, 2007). Plots in each annual panel are distributed evenly across each state so as to be free of geographic bias. The Interior West region of FIA is responsible for data collection and analysis in Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming. Under the annual inventory protocol, approximately 10% of plots from the full sample set in a state are measured each year. FIA data have been used to quantify potential habitat and evaluate habitat quality for a variety of western wildlife species (Zielinski et al., 2006; Welsh et al., 2006; Witt, 2009). Here I used IW-FIA data gathered across the Interior West region under the current annual inventory program. In the cases where methodologies were similar to annual inventories, past periodic inventory data was used as well.

2.2. Tree- and stand-level attributes

I used tree and plot data collected between 1979 and 2008. Tree and plot data were gleaned from all eight states in the Interior West FIA region. Aspen trees that had all variables measured were used for the tree-level analysis. Stand data came from those plots where aspen trees contributed 50% or greater of the total basal area. Infection of individual aspen trees was determined by locating external fruiting bodies of the fungus on the bole and detecting internal rot from boring the tree. I tested whether age, diameter, and compacted crown ratio of trees $\geq$2.54 cm diameter at breast height (1.40 m) (DBH) infected with heartrot differed from non-infected trees. The data set contained 13,706 trees for the tree-level analyses. Tree age was measured by counting growth rings from a core sample extracted from the tree at 1.40 m above ground level. Where the tree was too young to take a core, the number of branch whorls (locations on a tree where branches originate) was counted to estimate age. Tree diameter was obtained by measuring the diameter of the tree bole with a tape measure at 1.40 m above ground level. Compacted crown ratio was expressed as the percent of the tree bole supporting live foliage when compared to the total height of the tree (Miles et al., 2001). A tree with excess branch pruning would have a small compacted crown ratio and comparatively more potential infection sites. Compacted crown ratio was ocularly estimated by field crews. There were 2709 trees used for comparing tree ages and diameters with external ($n = 1445$) and internal ($n = 1264$) signs of infection.

There were 1.397 plots used for the stand-level analyses. Of these, 869 had infection detected on the plot while 528 had no infection detected on them. Stand age was determined by averaging the live tree ages in the predominant size-class of the plot (Miles et al., 2001). Crown cover on a plot was estimated by the point-intercept method described in USDA (2007). Site quality was measured by using the IW-FIA cubic foot mean annual increment measurement (MAICF) of a plot. MAICF is an incremental growth rate that generally reflects soil moisture and other site quality metrics. This data was gathered by measuring tree ring growth over time. Ten years of tree ring growth are measured and the average growth per year calculated. This information is then entered into an algorithm that incorporates other stand data to produce a value (USDA, 2007). MAICF is reported here as $\mathrm{m^3\ ha^{-1}\ year^{-1}}$. Purity is defined as the percentage of basal area ($\mathrm{m^2}$) of all live trees $\geq$2.54 cm DBH on the plot that came from aspen trees.

I performed a stepwise logistic regression on both tree and stand-level variables to identify which suite of characteristics best-predicted heartrot infection. Using the variables described above, a four-predictor logistic model was fitted to the stand-level data while a three-predictor model was tested for the tree-level data. Tree age, tree diameter, crown ratio, crown cover, MAICF, stand age and stand purity data were also tested individually using one-way ANOVAs (Zar, 1996). Detailed methods of all tree and stand data collection are described in USDA (2007). All statistical procedures were performed using SAS software (Ver. 9.02, SAS Institute, Cary, NC).

3. Results

3.1. Tree-level characteristics

Tree ages ranged from 6 to 292 years (mean ± SD = 74.7 ± 34.6). Infected aspen trees were older than uninfected aspen trees (Table 1). Tree diameters ranged from 2.54 to 72.9 cm (mean ± SD = 19.6 ± 10.4). Diameters of infected aspen trees were larger than those of uninfected aspen trees (Table 1). Compacted crown ratios ranged from zero to 90% (mean ± SD = 28.7 ± 13.8). Ratio distribution showed differences between groups (Table 1). The average age of infected trees showing no external signs of heartrot (fungal conks) was younger than the mean age of trees having conks detected on their stems ($F(1, 268) = 46.76$, $P < 0.0001$) (Fig. 1). The average diameter of infected trees showing no external signs of heartrot (fungal conks) was smaller than trees having conks detected on their stems ($F(1, 675) = 52.29$, $P < 0.0001$) (Fig. 2). I found 9% of aspen trees had fungal conks observed on their stems, with 2% of all aspen trees showing no external signs of infection but having heartrot detected though bore samples, for an 11% infection rate overall.

The best fitting stepwise multiple logistic regression model indicated the odds of an aspen tree having heartrot was positively

Table 1
Tree and stand characteristics of infected and uninfected aspen trees in the Interior West, 1979–2008. *F* and *P* values are derived from ANOVAs. All effects were considered significant at $P \leq 0.05$.

Characteristics	Infected				Uninfected				F (df = 1)	P
	n	Mean	Median	SD	*n*	Mean	Median	SD		
Stand										
Crown cover (%)	417	52.75	51.00	19.65	417	49.68	50.00	21.17	4.72	0.0301
MAICF (m^3 ha^{-1} $year^{-1}$)	1.180	2.75	2.59	1.34	773	2.53	2.31	1.33	16.53	<0.001
Purity (% of basal area)	392	48.99	44.76	34.00	392	31.64	17.85	33.36	52.11	<0.001
Stand age (years)	417	85.52	85.00	40.24	417	79.67	80.00	41.32	4.28	0.0388
Tree										
Age (years)	660	78.61	77.00	37.75	660	74.37	71.50	32.41	4.80	0.0286
DBH (cm)	3.023	21.21	20.07	9.29	3,023	17.89	17.02	8.31	213.66	<0.001
Compacted crown ratio (%)	2231	26.60	25.00	12.81	2,231	26.89	25.00	13.74	0.53	0.4660

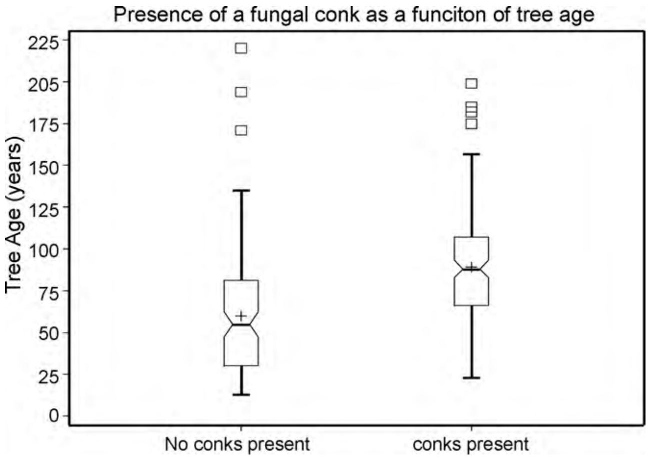

Fig. 1. Box plot comparison of age distribution between trees having fungal conks present and those with no external signs of fungal infection. Whisker endpoints represent maximum and minimum observations above and below 1.5 * the InterQuartile range (75–25th percentile); edges of box represents the 25th (bottom) and 75th (top) percentiles; notches represent the 95% confidence intervals of the medians, plus signs represent the sample mean; hollow squares represent outliers, horizontal lines between notch midpoints represent the sample median.

related to tree age, diameter, and compacted crown ratio, with tree diameter contributing more to the probability of infection than the other variables (Table 2). However, the predictive power of the best model was only slightly better than chance.

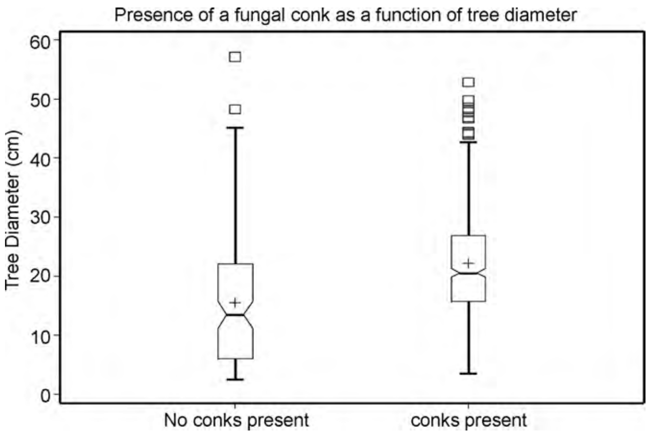

Fig. 2. Box plot comparison of diameter distribution between trees having fungal conks present and those with no external signs of fungal infection. Whisker endpoints represent maximum and minimum observations above and below 1.5 * the InterQuartile range (75–25th percentile); notches represent the 95% confidence intervals of the medians, plus signs represent the sample mean; hollow squares represent outliers, horizontal lines between notch midpoints represent the sample median.

3.2. *Stand-level characteristics*

Stands having at least 50% of their tree basal area composed of aspen ranged from 50 to 100% pure (mean ± SD = 83.0 ± 17.3). Purity scores of infected plots did not differ from uninfected plots (Table 1). Crown cover ranged from 1% (recent disturbance) to 99% cover (mean ± SD = 51.87 ± 22.15). Crown cover of infected plots did not differ from uninfected plots (Table 1). Stand age ranged from zero to 155 years old (mean ± SD = 68.7 ± 31.6). Mean age of infected plots was greater than uninfected plots (Table 1). MAICF scores ranged from 0.07 to 12.17 m^3 ha^{-1} $year^{-1}$ (mean ± SD = 2.70 ± 1.34). MAICF in infected aspen stands was greater than in uninfected stands (Table 1).

The stepwise multiple logistic regression model for stand-level variables indicated that the best predictive model include only stand age. This model has a positive relationship with the probability of heartrot infection (Table 2). No other stand-level variable contributed significantly to the model. The stand-level model using stand age alone predicted a 1 year increase in stand age increased the odds of a stand being infected by 1.01 times.

4. Discussion

Results of the present study are in general agreement with the earlier findings of Basham's (1958) Ontario research that suggested age and diameter had positive relationships with both incidence and total volume of infected trees. However, the frequency of infection in western aspen trees (11%) is lower than that found in the northeast (Basham, 1958) and Midwest estimates (Jones and Ostry, 1998). Jones and Ostry found that 14% of 295 destructively sampled trees in a Minnesota study had *P. tremulae* conks. They also reported that 55% of infected trees showed no external signs of infection by any decay agent. The authors did not report the proportion of these trees that were infected by *P. tremulae* and not some other agent. Basham (1958) conducted destructive sampling on 1754 trees and found *P. tremulae* decay in 63% of the sample. In the present study, FIA crews identified infected trees by external conks found on stems and by boring trees at breast height. While all tallied Trees 2.54 cm or greater DBH were inspected for conks, comparably fewer trees were bored on a plot. Only one tree for each size-class encountered on a plot is bored. These trees are chosen based on how well they represent the overall condition of the trees in their respective size-class. Therefore, FIA procedures may underestimate the frequency of infection because no destructive sampling is conducted, not all trees are bored, and not all infected aspen have heartrot at the location the sample is extracted from (1.40 m above the base of the tree). The two studies noted above sampled trees 12.7 cm or greater DBH while I used data from all sampled trees 2.54 cm or greater DBH. Since it appears age and diameter have a positive relationship with infection rate, the inclusion of smaller and younger trees in a sam-

Table 2
Logistic regression analysis of tree- and stand-level variables as predictors for the presence of heartrot infection.

Predictor variable	df	Estimate	SE	Wald's x^2	P	Odds ratio
Tree-level						
Intercept	1	−1.9938	0.0768	673.3557	<0.0001	–
Diameter (cm)	1	0.0083	0.0030	7.5126	0.0061	1.0080
Age (years)	1	0.0031	0.0009	11.3916	0.0007	1.0030
Crown ratio (%)	1	0.0066	0.0016	17.4650	<0.0001	1.0070
Percent concordant	59.7	Somers' D 0.207				
Percent discordant	39.1	Gamma 0.209				
Percent tied	1.2	Tau-a 0.097				
		c (AUC) 0.603				
Stand-level						
Intercept	1	−0.2473	0.1374	3.2404	0.0718	–
Stand age (years)	1	0.0112	0.0019	36.3949	<0.0001	1.0110
Percent concordant	54.6	Somers' D	0.109			
Percent discordant	43.6	Gamma	0.111			
Percent tied	1.8	Tau-a	0.035			
		c (AUC)	0.555			

ple could produce smaller infection estimates than those sampling only larger aspen trees. For these reasons, the frequency estimates reported here should be considered conservative in comparison.

Average diameter of infected trees in study area was smaller than what has been reported to be preferred by cavity-nesting birds in aspen in British Columbia (Merkens and Booth, 1998; Steeger and Dulisse, 2002; Aitken and Martin, 2004) and Wyoming (Hart and Hart, 2001). But similar to the results of other aspen studies conducted in Colorado (Crockett and Hadow, 1975; Winternitz and Cahn, 1983), and Southeast Oregon (Dobkin et al., 1995) (Table 3). None of the studies listed in Table 3 quantified production of nesting pairs so it is unclear whether nesting in larger trees results in higher productivity. Larger trees might provide better security from predators (Kilham, 1971; Harestad and Keisker, 1989; Jackson and Jackson, 2004), higher residency time before the tree decays and falls down (Steeger and Dulisse, 2002), and better thermal insulation than smaller trees (Joy, 2000).

The results of Daily (1993) suggest tree diameter did not matter as much as tree height and the presence of infected heartwood for Red-naped sapsuckers in Colorado. Keisker (1987) and Savignac and Machtans (2006) both showed that presence of a fungal conk (an indicator of heartrot) was the best indicator of nest tree quality in British Columbia. Trees with fungal conks in my study were older and larger than infected trees without conks (Figs. 1 and 2, respectively). However, many of the trees showing no external signs of infection were large enough to meet the reported preferences of many cavity-nesting birds (Fig. 2). Although studies in New Hampshire (Kilham, 1971) and Colorado (Winternitz and Cahn, 1983) show that some cavity-nesting birds use the presence of a fungal conk as an indicator of suitability, less is known about how often aspen with no external signs of infection are utilized. Heartrot might be present for many years, perhaps decades, before fungal conks form and provide an ocular cue to infection (Jackson and Jackson, 2004). Cavity-nesting species that employ no other means to find suitable trees for excavation might be underutilizing this portion of the aspen population. In contrast, those species which create "exploratory" excavations or that peck on trees that have no external signs of heartrot (Conner et al., 1976) may have a competitive advantage over those that do not employ such behavior. There are obvious thresholds to how small a tree can be effectively used as a nest cavity, regardless of a bird's willingness to attempt excavation. A nest cavity must be large enough to accommodate one or both parents, and their offspring (Jackson and Jackson, 2004). Even so, these results indicate that smaller diameter trees infected with heartrot may not be utilized to the fullest extent possible. Further research into which species use visual cues exclusively and which use a suite of techniques would be valuable.

If the presence of heartrot in aspen is paramount in importance when cavity site selection is made, then minimum diameters might not be the best guide for management decisions. Bunnell et al. (2002) suggest that since nest tree diameters selected by cavity-nesting birds in the Pacific Northwest had long-tailed distributions, medians should be used to detect central tendencies of tree selection. They note that using minimum diameters fails to take central tendency into account. In the present study mean and median diameter values for western aspen are similar (Table 1) and selection of one over the other would not likely change the effectiveness of a management decision for the entire region. There may be intra-regional differences in these values that should be identified before using these results for management on smaller scales. Unfortunately, most studies do not report median tree diameters so comparisons to other investigations are difficult.

In many parts of the west, aspen has experienced declines, die-off, and encroachment from conifer species (Kay, 1997; Bartos and Campbell, 1998). Many land managers and researchers are calling for the treatment of large areas of aspen "invaded" by conifers by removing conifers from the stand. Removing conifers from mixed-species stands to promote aspen persistence could create better conditions for *P. tremulae* infection in these stands. This would allow aspen trees to persist longer, thus providing more opportunities for heartrot to decay trees, which would provide more cavity sites and higher temporal availability of snags. However, these treatments could have detrimental impacts to birds such as Williamson's sapsuckers because they require nearby conifers for foraging during the breeding season (Crockett, 1975; Sousa, 1983; Smith, 1982; Conway and Martin, 1993). The aspen die-off phenomenon in the west coupled with suppressed recruitment might also create temporal gaps of suitable sized and aged trees for many cavity-nesters (Hollenbeck and Ripple, 2008), leaving only smaller and younger trees as options in some areas. Birds might be able to shift their preferences to smaller infected trees without a loss in productivity. However, we could still expect constrictions of nest tree availability knowing that larger and older trees appear to have higher infection rates.

The multiple logistic regression modeling exercises indicated that all tree-level variables were positively related to the probability of infection (Table 2). However, the AUC (area under the curve) score of 0.555 indicates that this might not prove very useful from a management perspective. The stand-level model indicated stand age as the only significant predictor of heartrot infection. This

Table 3
Diameter measurements of nest tress for various western cavity-nesting birds reported in the literature. The results of this study are listed on the top for comparison. All values are in centimeters.

	Mean DBH	Min. DBH	Max DBH	Pct of all IW aspen ≥ Min. DBH	Pct of infected IW aspen ≥ Min. DBH	Source	Location
Infected aspen in interior west	21.2	2.5	72.9	–	–	This study	IW USA[a]
	27.4	–	–	–	–	Dobkin et al. (1995)	Southeast Oregon
	31.2	–	–	–	–	Martin et al. (2004)	British Columbia, Canada
Red-naped sapsucker (*Sphyrapicus nuchalis*)	36.5	14.0	74.0	71.1	80.0	Steeger and Dulisse (2002) [b]	British Columbia, Canada
	–	23.0	–	24.3	37.1	Hart and Hart (2001)	Wyoming
	–	27.0	–	13.6	23.6	Keisker (2000)	British Columbia, Canada
	29.1	–	–	–	–	Dobkin et al. (1995)	Southeast Oregon
	31.9	19.8	48.7	37.4	51.1	Keisker (1987)	British Columbia, Canada
Northern flicker (*Colaptes auratus*)	34.7	–	–	–	–	Martin et al. (2004)	British Columbia, Canada
	37.3	–	–	–	–	Aitken and Martin (2004)	British Columbia, Canada
	39.9	25.4	63.5	17.6	28.7	Flack (1976)	IW Canada and IW USA[c]
	–	30.0	–	8.5	16.4	Keisker (2000)	British Columbia, Canada
Hairy woodpecker (*Picoides villosus*)	27.6	17.4	44.5	49.5	62.7	Keisker (1987)	British Columbia, CAN
	29.2	20.3	40.6	35.2	48.8	Flack (1976)	IW Canada and IW USA[c]
	–	27.0	–	13.6	23.6	Keisker (2000)	British Columbia, Canada
	25.0	–	–	–	–	McClelland et al. (1979)	Montana
	25.1	15.2	30.4	63.9	74.6	Flack (1976)	IW Canada and IW USA[c]
Downy woodpecker (*Picoides pubescens*)	26.3	19.1	31.4	39.8	53.5	Keisker (1987)	British Columbia, Canada
	–	15.2	–	–	–	Thomas et al. (1979)	Oregon
	–	30.0	–	–	–	Keisker (2000)	British Columbia, Canada
Lewis' woodpecker (*Melanerpes lewis*)	41.3	20.1	103.5	35.2	48.8	Newlon (2005)	Southern Idaho
Williamson's sapsucker (*Sphyrapicus thyroideus*)	23.5	18.0	32.4	46.5	60.0	Crockett and Hadow (1975)	Colorado
Red-breasted nuthatch (*Sitta canadensis*)	23.2	–	–	–	–	Martin et al. (2004)	British Columbia, Canada
	–	23.0	–	24.3	37.1	Hart and Hart (2001)	Wyoming
	–	30.0	–	8.5	16.4	Thomas et al. (1979)	Oregon
Mountain chickadee (*Poecile gambeli*)	24.9	–	–	–	–	Martin et al. (2004)	British Columbia, Canada
	–	30.0	–	8.5	16.4	Keisker (2000)	British Columbia, Canada
House wren (*Troglodytes aedon*)	27.6	–	–	–	–	Dobkin et al. (1995)	Southeast Oregon
	31.0	15.2	50.8	63.9	74.6	Flack (1976)	IW Canada and IW USA[c]
Mountain bluebird (*Sialia currucoides*)	27.4	–	–	–	–	Dobkin et al. (1995)	Southeast Oregon
	31.3	–	–	–	–	Martin et al. (2004)	British Columbia, Canada
	34.3	20.3	76.2	35.2	48.8	Flack (1976)	IW Canada and IW USA[c]
Tree swallow (*Tachycineta bicolor*)	29.2	20.3	63.5	35.2	48.8	Flack (1976)	IW Canada and IW USA[c]
	30.2	–	–	–	–	Dobkin et al. (1995)	Southeast Oregon
	32.1	–	–	–	–	Aitken and Martin (2004)	British Columbia, Canada

[a] Interior West: Includes Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming.

[b] Results of Steeger and Dulisse (2002) included various primary excavators, the majority of which were *S. nuchalis*. Minimum and Maximum values are estimated from author's figures.

[c] Includes IW states, Alberta, Saskatchewan, and one site in California.

model's AUC score of 0.603 suggests it would be slightly more useful to a manager who is interested in modeling infection probability on a large spatial scale than the model using tree-level variables (Table 2).

Although site productivity based on MAICF score was higher in infected stands, this variable did not contribute significantly to the regression model. Although the statistical analysis shows differences between infected and uninfected stands, this difference might not be enough to have practical applications for management of cavity-nesting birds. The positive relationship between MAICF and infection rate might be partially explained by larger (and older) trees present on higher quality sites but soil moisture and chemistry could play a role as well. The fact that MAICF is a metric that reflects unmeasured physical and chemical attributes of the plot makes it difficult to discern what factors are influencing the frequency of heartrot in this case. Future research that explores how microclimate affects *P. tremulae* would help address these unanswered questions.

5. Conclusions

Infection of aspen by *P. tremulae* occurred more often in older and larger trees and in older stands with higher productivity. From a forest management perspective the results of these analyses provide mixed and sometimes conflicting information. Stand age, tree age, tree diameter and MAICF score could be used to some extent to predict heartrot infection and quantify the extent of the potential resource currently on the landscape. However, the results of the regression models suggest that these variables are only slightly better than chance. There are likely physical, biophysical, and perhaps genetic factors not investigated in the present study that influence the frequency and susceptibility of aspen to heartrot infection. Controlling for some of these potential confounding variables in future investigations might result in a clearer picture of the interactions between aspen and *P. tremulae*.

Aspen is a dynamic forest type and current trends in climate and management might change the status of “suitable” stands relatively quickly. Aspen forests persist in a wide variety of climates, soils and elevations and as such, behave differently from one area to another. Smaller, more focused analyses would be useful for making localized treatment and management prescriptions. In addition, researching bird productivity in stands with a range of age, diameter, and site quality classes are research endeavors needed to provide more useful tools for the managers of the aspen resource wherever it may occur.

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