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Research Paper

Foraging substrate use of American Three-toed Woodpeckers (*Picoides dorsalis*) in white spruce-dominated forests of the Black Hills of South Dakota

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ABSTRACT. Isolated, sedentary species with low population densities are at increased risk of population declines because of habitat disturbances relative to common, widely distributed species. The American Three-toed Woodpecker (*Picoides dorsalis*) population in the Black Hills of South Dakota is of conservation concern because of its geographic isolation, sedentary behavior, and association with relatively small, patchily distributed, white spruce (*Picea glauca*) habitats. The presence of sufficient suitable foraging habitat may positively affect fitness in birds, but because few foraging studies exist for American Three-toed Woodpeckers, and none have occurred in the Black Hills, understanding foraging habitat needs is critical for management and conservation planning for this isolated population. During the breeding seasons of 2006–2008 we recorded foraging observations of American Three-toed Woodpeckers in the Black Hills and examined foraging substrate preferences by comparing foraging substrate use to availability using initial and sequential observations of individual focal birds. We found that American Three-toed Woodpeckers foraged on large living and dead white spruce and large ponderosa pine (*Pinus ponderosa*) trees in higher proportion than their availability and on small living spruce and pine in lower proportion than their availability. Foraging event durations were longer on large spruce snags than on other tree species, size, and status (living or dead) categories. These results suggest that mature white spruce forests, and especially those with large living and dead white spruce trees, are important foraging habitats for the American Three-toed Woodpecker during the breeding season in the Black Hills. Recent proposed, but subsequently withdrawn, forest management plans that would have reduced white spruce forest extent in the Black Hills would likely have negative impacts on foraging resources for this bird species of regional conservation concern.

L'utilisation des substrats de recherche de nourriture par le Pic à dos rayé (*Picoides dorsalis*) dans les forêts dominées par l'épinette blanche des Black Hills dans le Dakota du Sud

RÉSUMÉ. Les espèces isolées et sédentaires, dont la densité de population est faible, sont davantage exposées au risque de déclin démographique en raison des perturbations de leur habitat que les espèces courantes et largement répandues. La population du Pic à dos rayé (*Picoides dorsalis*) dans les Black Hills du Dakota du Sud suscite des inquiétudes en matière de conservation en raison de son isolement géographique, de son comportement sédentaire et de son association avec des habitats d'épinettes blanches (*Picea glauca*) relativement petits et dispersés. La présence d'un habitat de recherche de nourriture suffisant et adapté peut avoir un effet positif sur la condition physique des oiseaux. Toutefois, en raison du faible nombre d'études sur les habitudes alimentaires du Pic à dos rayé, et de l'absence d'études dans les Black Hills, il s'avère essentiel de bien comprendre les besoins de cette population isolée en matière d'habitat de recherche de nourriture pour assurer sa gestion et planifier sa conservation. Au cours des saisons de reproduction de 2006 à 2008, nous avons relevé des observations concernant la recherche de nourriture chez les pics à dos rayé dans les Black Hills et nous avons étudié leurs préférences en matière de substrats de recherche de nourriture en comparant l'utilisation des substrats à leur disponibilité, à partir d'observations initiales et successives d'individus ciblés. Nous avons constaté que les pics à dos rayé se nourrissaient sur les grandes épinettes blanches, vivantes ou mortes, et sur de grands pins jaunes (*Pinus ponderosa*) dans une proportion supérieure à leur disponibilité, et sur de petites épinettes et pins vivants dans une proportion inférieure à leur disponibilité. La durée des séances de recherche de nourriture était plus longue sur les grandes épinettes sur pied que sur les autres espèces d'arbres, quel que soit leur taille ou leur état (vivants ou morts). Ces résultats suggèrent que les forêts matures d'épinettes blanches, et en particulier celles qui abritent de grandes épinettes blanches vivantes et mortes, constituent des habitats de recherche de nourriture importants pour les pics à dos rayé pendant la saison de reproduction dans les Black Hills. Les plans de gestion forestière récemment proposés, puis retirés, qui auraient réduit l'étendue des forêts d'épinettes blanches dans les Black Hills, auraient probablement eu des répercussions négatives sur les ressources alimentaires de cette espèce d'oiseau, dont la conservation revêt une importance régionale.

Key Words: *Black Hills; foraging; habitat selection; white spruce; woodpecker*

INTRODUCTION

The range of the American Three-toed Woodpecker (*Picoides dorsalis*) includes mature high elevation forests in the western U. S. and boreal forests in Canada (Virkkala 1987, Imbeau et al. 1999, Tremblay et al. 2020). Throughout its range, American Three-toed Woodpecker is dependent on older forests, especially those with large-diameter trees and an abundance of recently dead or dying trees (Mannan et al. 1980, Aulén 1991, Nappi et al. 2015, Kelly et al. 2019, Lamarre and Tremblay 2021). Dominant tree species in these forests may include black (*Picea mariana*), white (*Picea glauca*), and Engelmann (*Picea engelmannii*) spruce, Douglas (*Pseudotsugamenziesii*) and subalpine (*Abies lasiocarpa*) fir, and lodgepole pine (*Pinus contorta*; Tremblay et al. 2020). In these older forests, American Three-toed Woodpeckers may also inhabit areas of recent natural disturbance caused by fires, insect infestation, drought conditions or wind-throw (West and Speirs 1959, Yunick 1985, Kotliar et al. 2008, Dresser et al. 2013, Saab et al. 2014, Kelly et al. 2019). Such natural disturbances increase the abundance of bark (Scolytinae) beetle larvae, the primary prey of American Three-toed Woodpeckers (Murphy and Lehnhausen 1998, Wiggins 2004, Tremblay et al. 2020), which birds acquire by pecking and flaking bark (Bull et al. 1986, Tremblay et al. 2020) to access the shallow-feeding larvae (Pechacek 2006, Gitau et al. 2013). The association of American Three-toed Woodpecker with older forests, including spruce forests, extends to foraging behaviors (Tremblay et al. 2020). For example, this species preferred large, recently dead or dying black spruce for foraging in boreal forests of Quebec (Imbeau and Descorchers 2002, Gagné et al. 2007).

The presence of sufficient suitable foraging habitat is important to fitness in birds, including woodpeckers (Garabedian et al. 2014, Tremblay et al. 2014, Nappi et al. 2015). Because nesting and foraging habitats may differ for woodpeckers (Drever and Martin 2010) and other birds (Narango et al. 2017), comprehensive management planning for American Three-toed Woodpeckers requires addressing multiple ecological needs, including foraging habitats. Previous foraging studies of the American Three-toed Woodpecker have focused on foraging behavior and habitat associations in post-fire habitats (Murphy and Lehnhausen 1998, Hoyt and Hannon 2002, Kotliar et al. 2008), effects of forest cover and silvicultural treatments on foraging behavior (Gagné et al. 2007, Drever and Martin 2010), and local-scale foraging habitat characteristics in expansive contiguous western montane and boreal forests (Goggans et al. 1989, Loose and Anderson 1995, Imbeau and Desrochers 2002, Hammond and Theimer 2020). Relative to most western and boreal conifer forests in North America, conifer diversity is low in forests in the Black Hills, South Dakota, the focal region of this study, with most current forests dominated by ponderosa pine (*Pinus ponderosa*) and the only other prominent conifer being white spruce, which is the dominant conifer species for only about 5% of current forests in the Black Hills (Hoffman and Alexander 1987, USFS 2022a). Consequently, foraging behavior and substrate use by American Three-toed Woodpeckers in the Black Hills may be restricted by low conifer diversity in Black Hills forests relative to other regions.

Low density, sedentary, and isolated populations of habitat specialists, such as the American Three-toed Woodpecker in the Black Hills, face unique ecological and genetic challenges not

likely to be present in more widespread populations (Prugh et al. 2008, Khimoun et al. 2016, Morelli et al. 2020). American Three-toed Woodpeckers in the Black Hills are found primarily within the northern Limestone Plateau region (Drilling et al. 2018), which contains a limited subalpine belt of white spruce-dominated forests found on areas that are higher (typically above 1700 m), cooler, and wetter than southern portions of the Black Hills (Hoffman and Alexander 1987). Occupancy by American Three-toed Woodpeckers in the Black Hills of South Dakota and Wyoming was positively associated with coverage of white spruce in 500 m-radius plots, up to a maximum of 66% coverage (Mohren et al. 2016). American Three-toed Woodpeckers are not commonly found in recently burned areas outside of white spruce habitat in the Black Hills (Giroir et al. 2007), even though this species is known to irrupt into areas of recent disturbance, such as burned areas, that promote beetle infestations in other parts of its range (West and Speirs 1959, Yunick 1985, Hoyt and Hannon 2002, Hannon and Drapeau 2005, Edworthy et al. 2011, Dresser et al. 2013, Kelly et al. 2019). The majority of fires that occur in the Black Hills are located in the warmer, drier southern portions dominated by ponderosa pine, where white spruce forests are rare, and fires are uncommon in the higher elevation white spruce forests (USFS 2022a).

American Three-toed Woodpeckers are a species of conservation concern in the Black Hills because of their small population size, estimated as stable between 2009 and 2021 with mean population size of 1340 ± 796 (SE) individuals (Timmer et al. 2025), and reliance on the limited white spruce habitat (Anderson 2003, Giroir et al. 2007, Mohren et al. 2016). In South Dakota, three-toed woodpeckers are listed as imperiled because of rarity (few remaining individuals or hectares of specific habitat; South Dakota Natural Heritage Program 2018). White spruce forests have expanded in the Black Hills in recent decades from approximately 2% of total forest area in 1982–1986 (Hoffman and Alexander 1987) to approximately 5% in 2017–2019 (USFS 2022a), which may benefit local populations of American Three-toed Woodpeckers.

Recently, the Black Hills National Forest proposed a spruce vegetation management plan where spruce removal to assist aspen (*Populus tremuloides*) expansion, increase structural heterogeneity in white spruce forests, and reduce fire fuel loads would occur, with the goal of reducing the total forest area dominated by white spruce by approximately 57% (USFS 2022b). This management plan was withdrawn from current action in 2024 but could be re-initiated at a later date (USFS 2022b). Given that American Three-toed Woodpeckers are closely associated with white spruce forest habitats in the Black Hills (Ervin 2011, Mohren et al. 2016, Drilling et al. 2018), the proposed management activities seem likely to negatively impact populations of this species in the Black Hills, so data regarding use of white spruce habitats by three-toed woodpeckers for foraging, nesting, and other activities throughout the annual cycle are needed to help quantify impacts of any proposed spruce management plans on populations of this species in the Black Hills.

The purpose of this study was to determine which tree characteristics affect foraging preferences of the American Three-toed Woodpecker in the Black Hills, South Dakota. In this study we compared the use of foraging substrates to their availability

within the study area to determine foraging preferences (Zwicker and Walters 1999). We also examined whether the duration of foraging bouts was influenced by specific characteristics of the substrates used for foraging. Considering the high food value of large-diameter snags and close associations of three-toed woodpeckers in the Black Hills with white spruce (Mohren et al. 2016), we hypothesized that large-diameter living and dead spruce provide high quality foraging habitat compared to other substrates and should be used preferentially for foraging.

METHODS

Permits and approvals

All procedures in the study were carried out under approved protocols from the University of South Dakota Institutional Animal Care and Use Committee (Protocol Numbers 60-04-05-08B and 31-04-08-11B). Project activities were carried out under appropriate federal scientific collecting (USGS - MB758442) and banding (USGS Master Banding Permit 22199) permits and state collecting permits (SD-1-2005, SD-3-2006, SD-2-2007, SD-3-2008).

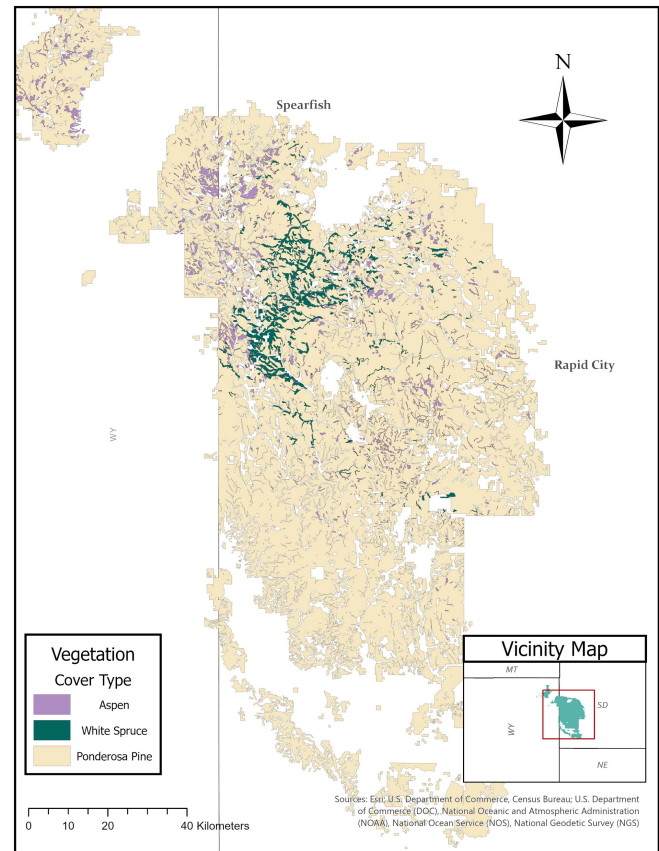
Study area

We conducted this study in the Black Hills National Forest within the Black Hills of South Dakota, an isolated mountain range situated in the Northern Great Plains (USFS 2005). The highest peak rises over 2215 m above sea level and the Black Hills span 200 km from north to south and 100 km from east to west (Froiland 1990). Ponderosa pine is the dominant overstory tree species in the Black Hills, and forests dominated by ponderosa pine make up almost 95% of the forested area, but white spruce and aspen are also important canopy tree species (Sheppard and Battaglia 2002, Brown and Cook 2006). White spruce forests cover approximately 5% of current Black Hills forest area, representing one of only a few areas south of Canada where pure populations of white spruce occur (Hoffman and Alexander 1987, Sheppard and Battaglia 2002). Most forest management in the Black Hills is directed toward ponderosa pine forests, with little management focus on white spruce forests (USFS 2022a). Because American Three-toed Woodpeckers are closely associated with white spruce habitats in the Black Hills (Tallman et al. 2002, Mohren et al. 2016, Drilling et al. 2018), we collected data on woodpecker foraging substrates in white spruce-dominated forests of the northern Limestone Plateau region of the Black Hills (Fig. 1).

Foraging substrates

We collected foraging data from mid-May to early August from 2006 to 2008. We focused searches for foraging American Three-toed Woodpeckers in areas where we had observed them previously during population playback surveys (Ervin 2011), during nest searches within previously identified woodpecker territories, or in areas where we observed trees with flaked bark typical of three-toed woodpecker foraging. We also collected foraging observations on American Three-toed Woodpeckers that we encountered opportunistically during our studies. When we visually located a foraging woodpecker, we recorded foraging substrate attributes including tree species, status (living or dead), and size category (based on diameter at breast height, DBH) for the tree on which we observed the bird. We classified trees as small (< 23 cm DBH) or large ($\geq$ 23 cm DBH) based on measurements

Fig. 1. The study area for recording foraging observations of American Three-toed Woodpecker (*Picoides dorsalis*) included white spruce (*Picea glauca*) forests (dark green), which primarily occur on the Limestone Plateau in the northwestern region of the Black Hills in South Dakota.



using tree calipers or rulers according to tree size thresholds established for conifer trees in the Black Hills National Forest (DeBlander 2002). We did not measure tree size for most observations in 2006, however, so we only include analyses for those observations where we recorded tree size in subsequent analyses of tree size category effects on foraging. We recorded the duration of individual foraging events, defined as the full time spent on a single foraging substrate, including time spent moving or searching while not actively pecking or flaking, but excluding time spent preening, to the nearest second with a stopwatch. We followed individual woodpeckers until we lost contact with them, and we recorded multiple foraging events for individual birds using the sequential observation method of Morrison (1984). This sequential observation method entailed separate measures of tree species, status (living or dead), size category (based on DBH) and duration of foraging event for each foraging substrate used by the focal bird.

We compared the use of foraging substrates to their availability within the study area by conducting vegetation sampling at random locations within white spruce habitats. Substrate availability was determined by randomly selecting 30 points from

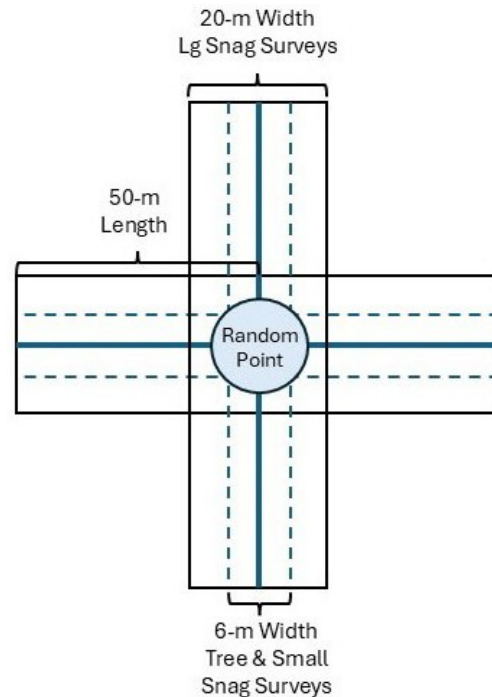
previously established random transects through white spruce habitat in the Black Hills (Panjabi 2003), where we had previously observed birds on the transect. We considered each random point as the survey center, and used strip transects beginning at the survey center to determine the number, status, and size category of each species of tree and snag according to a modification of the protocol of Bate et al. (1999; Fig. 2). In addition, we recorded the number and size category of downed logs, but because downed logs were often not identifiable to species, we did not record species of downed logs. We recorded the number of living trees, small snags, and downed logs within four 6 m x 50 m strip transects in each of the cardinal directions, with the random point as the starting point for the transects. Because large snags were rarer than living trees but may be especially important foraging substrates for American Three-toed Woodpeckers (Nappi et al. 2015), we recorded large snags (≥ 23 cm DBH) on four 20 x 50 m strip transects initiated at the survey center and extending in each of the four cardinal directions.

Statistical analyses

We assessed foraging substrate use by American Three-toed Woodpeckers both as single points and as a sequential series of observations for foraging durations (Morrison 1984). The single point observation method helps to mitigate the issue with non-independent samples, but sequential observation methods capture more rare foraging behaviors (Morrison 1984). Therefore, combining both methods provided a more robust overall representation of foraging preferences and substrate use. All individual birds that we included for foraging analyses were at different locations (or were different sexes if at the same location), so they were assumed to represent different individuals. We pooled foraging data across all three breeding seasons for subsequent analyses, but tree size category was only noted for two of the 2006 birds. Hence, for chi-square analyses related to tree size, we were only able to use 38 of the individuals, whereas for tree species and live vs. dead substrate, we used 51 individuals (we excluded the single individual in 2006 that was observed only foraging on a downed log). For all analyses, male and female data were combined because insufficient data were available for intersexual comparisons.

For single-point observations, we used chi-square goodness-of-fit tests to determine if American Three-toed Woodpeckers selected tree species, size, or status (living or dead) for foraging according to availability. We calculated expected cell values for chi-square tests by multiplying the mean proportional stem density of each tree species, status, and size category from vegetation analyses across 30 random points with the total number of foraging observations. For this analysis, we only included the first observed foraging substrate for each individual bird. To determine whether particular classes of foraging substrates differed significantly in terms of use (observed) vs. availability (expected), we conducted chi-square analyses on 2 x 2 tables, comparing the observed and expected frequencies for the class of interest (e.g., large live spruce) versus those for all other foraging substrates combined. For three comparisons in which small, expected values (< 5) precluded valid chi-square analyses, we used a likelihood-ratio (G) goodness-of-fit test statistic instead and generated exact *P*-values using the binomial null distribution.

Fig. 2. Vegetation sampling design around 30 random points in white spruce (*Picea glauca*) forests in the Black Hills. We conducted four 50-m strip transects in the cardinal directions from the random point, with all trees, small snags, and downed logs counted in 6-m wide transects, and large snags counted in 20-m wide transects.



We employed a multivariate approach for analyzing foraging duration data for different substrates. For this method, we rounded fractional minutes of foraging time for American Three-toed Woodpeckers to the nearest integer. We modeled foraging time represented by the count of minutes within a generalized linear mixed model with Poisson family distribution, log link function, and nested random effects for Bird ID within Year (Bolker et al. 2009). We fit models with the Laplace maximum-likelihood approximation using package glmmTMB (McGillcuddy et al. 2025) in the R statistical computing environment (Version 4.4.2). We omitted data from 2006 (as most observations did not include tree diameter measurements), as well as records for aspen tree type, and log and other tree types, providing sufficient data for two-way interactions between Size and Status covariates and resulting in repeated measures of foraging duration for 36 individual birds across two years ($n = 188$). We approximated hypotheses for tree structure and composition by specifying factor covariates for Size with two levels for small-diameter (< 23 cm) and large-diameter (≥ 23 cm) trees, Species with two levels for ponderosa pine and white spruce (by far the two species most used for foraging), and Status with two levels for dead (snag) and live trees. We constructed models for all subsets of covariates and two-way interactions (Doherty et al. 2012), but data were insufficient for interactions between Species and Status. We evaluated support for hypotheses and covariate relationships using information-

theoretic model selection (Burnham and Anderson 2002). We made multi-model inference by calculating cumulative AIC_c weights for main effects of predictor variables [$w_+(j)$] and model averaging estimates for a candidate set models with $\Delta_i < 2$ (Burnham and Anderson 2002). We estimated mean foraging duration by model averaging estimates for all combinations of the tree Size, Species, and Status covariates. We evaluated statistical support for beta coefficients of fixed covariate effects according to 90% Confidence Intervals (CI) with respect to zero ($\alpha = 0.1$). We used $\alpha = 0.1$ to calculate 90% Confidence Intervals for two reasons. First, because information-theoretic model selection is known to select coefficients in the top model with 85% Confidence Intervals (CIs) excluding zero (Arnold 2010), we did not wish to enforce the typical α used in hypothesis-testing. We chose an $\alpha = 0.1$ as a compromise between the typical $\alpha = 0.05$ and the model selection compliant $\alpha = 0.157$.

We calculated Manly selection ratios (Manly et al. 2002) to compare foraging substrate use vs. availability by estimating proportion of cumulative time spent on each substrate category (species, size, status) for all individual woodpecker observations of foraging. We used only foraging observations and individuals for 2007–2008, when tree-size category was noted ($n = 36$ birds). We also only included foraging observations on standing trees (logs were excluded). Based on the foraging duration model described above, we then calculated the ratio between the proportion of cumulative time spent on each foraging substrate for all individual birds to the proportional frequency of substrates (relative stem density) from random tree data to calculate the Manly selection ratios for each substrate. We elected to use the model averaged estimates in place of direct empirical estimates of proportional use because the estimates of foraging duration were derived from an appropriate non-normal distribution, accounted for repeated measures, and had higher precision (lower standard errors). We used the delta method (Powell 2007) and standard errors for proportional use and availability to approximate standard errors for the Manly selection ratios for each substrate category (tree species, size, status), computed 95% confidence intervals on natural log-transformed values of the selection ratios (using z-scores), and then back-transformed the confidence limits into the original units. Substrate use that is proportional to availability results in a Manly selection ratio of 1.0, so if 95% confidence intervals include 1.0, then use does not differ from availability (Manly et al. 2002). Confidence intervals with values < 1 indicate avoidance whereas those > 1 indicate preference for particular substrates. We only report selection ratios for spruce and pine as only one of the 36 birds from 2007–2008 was observed foraging on a deciduous tree (a small aspen snag). Aspen and other deciduous tree species constituted 12.5% of available trees.

We used Microsoft Excel for chi-square goodness-of-fit tests and Manly selection ratio analyses of substrate use vs. availability and R Studio with R 4.4.2 for developing models of foraging duration by tree Species, Size, and Status, and for computing likelihood-ratio (G) goodness-of-fit tests with exact P -values. We defined statistical significance as $P \leq 0.05$, except for chi-square tests of initial foraging observations, for which we used a sequential Bonferroni method (Rice 1989) to adjust alpha-levels for multiple individual tests to maintain a family-wise alpha-level of 0.05.

Table 1. American Three-toed Woodpecker (*Picoides dorsalis*) foraging usage (total duration and % of total duration) and availability (estimated % of stems in the study area) of foraging substrate by tree species, status (living or dead), and tree size (large, small) for observations in 2007–2008. Usage data are restricted to spruce and pine. Total foraging duration and % use estimates are based on the best model from the analysis of sequential foraging observations. Foraging observations represent use by an individual bird of an individual foraging substrate for a single interval of time in the field. Note: A single observation of a bird that foraged on a small aspen snag in 2008 for 20 seconds (0.33 minutes, or 0.06% of the total) is not included.

Tree species	Tree status	Tree size	# foraging obs.*	Total foraging duration (minutes)	% Use (SE)	% Available (SE)
Spruce	Living	Large	65	186.1	33.7 (3.9)	14.2 (1.8)
Spruce	Living	Small	25	59.4	10.7 (1.5)	42.9 (2.7)
Spruce	Dead	Large	46	178.5	32.3 (3.8)	0.9 (0.2)
Spruce	Dead	Small	16	51.5	9.3 (1.3)	12.6 (1.9)
Pine	Living	Large	32	70.1	12.7 (1.9)	6.6 (1.7)
Pine	Living	Small	4	7.3	1.3 (0.2)	7.4 (1.9)
Pine	Dead	Large	0	0.0	0	0.7 (0.2)
Pine	Dead	Small	0	0.0	0	2.2 (0.9)
Total			188	552.9	100%	87.5%

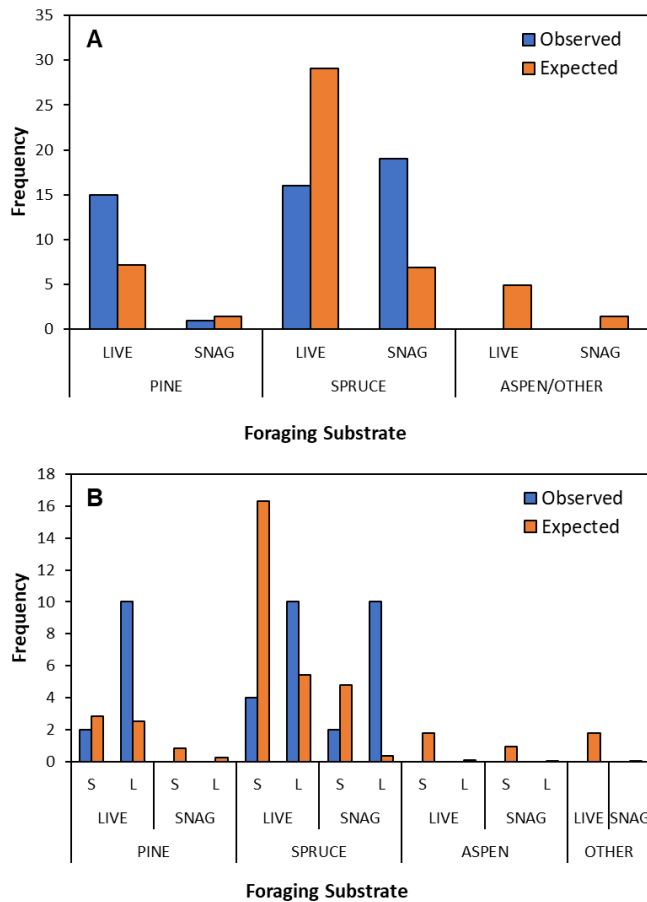
RESULTS

Foraging substrates

Vegetation analyses across the 30 random vegetation points revealed that spruce was dominant, representing 70.6% of total tree density (Table 1). Most (81%) spruce were live, and most (79% overall, 75% of live spruce and 93% of spruce snags) were small (< 23 cm DBH). Large (≥ 23 cm DBH) dead spruce made up less than 1% of all trees, while large live spruce composed 14%. Ponderosa pines composed 17% of all trees, with most (83%) of them living. Size categories were more evenly split with pine than in spruce, as 59% of pine trees were small and 41% large. Aspen (not shown in Table 1) made up 7.6% of all trees and other deciduous tree species composed another 4.9%. Most aspen trees were in the small size category.

We recorded a total of 302 foraging observations from 51 birds as follows: 15 individual birds (105 observations) in 2006, 24 individual birds (114 observations) in 2007, and 12 individual birds (83 observations) in 2008. For single-point, initial foraging locations across all breeding seasons ($n = 51$ individual birds), 68.6% (35 of 51) of total foraging substrates consisted of spruce trees, 54% (19) of which were on dead spruce and 46% (16) on living spruce (Fig. 3A). Additionally, 31.4% of foraging substrates were ponderosa pine, with nearly all (15 of 16) on living trees. Although a few birds used aspen snags (and one on a live aspen) during sequential foraging bouts, none used aspen (or any other species besides pine or spruce) for the initial foraging substrate. Overall, birds used living trees as initial foraging substrates more frequently (60.8%, 30 of 51) than dead trees (39.2%, 20 of 51), but live trees were used significantly less frequently than expected and dead trees were used significantly more frequently than expected relative to their densities in the study area (Table 2).

Fig. 3. Breeding-season American Three-toed Woodpecker (*Picoides dorsalis*) foraging substrate observed frequencies of use compared to expected frequencies (based on relative stem densities) from random vegetation samples in white spruce (*Picea glauca*) forests in the Black Hills, South Dakota. Panel A (n = 51) includes 2006 data for which tree size category was not recorded; Panel B (n = 38) includes only 2006–2008 data for which tree size category (S = small, < 23 cm DBH; L = large, > 23 cm DBH) was recorded.



Frequency of overall spruce use did not differ significantly from expected, but live spruce was used less frequently, and spruce snags were used more frequently than expected, given their relative stem densities in the study area. Ponderosa pine was used as an initial foraging substrate almost twice as often as expected based on its relative stem density in the study area. This was based on preferential use of live pine, as pine snags occurred at low relative densities in the study area and only one bird out of the 16 using pine as an initial foraging substrate was observed on a pine snag. Given that no species other than spruce or pine was used as an initial foraging substrate, other species as a group (primarily aspen) were significantly underused for foraging Fig. 3A, Table 2).

Using only the observations for which tree size category was recorded (n = 38, mostly in 2007–2008), large spruce or pine trees were used as the initial foraging substrate by 78.9% (30) of birds, whereas small trees were the initial foraging substrate for only 21.1% (8) of individuals (Fig. 3B, Table 2). This contrasts with the much higher proportion of small trees (77%, here include 5% of “other” species for which size was unspecified) than large trees (23%) in the study area. Hence, large trees were used significantly more and small trees significantly less than expected based on their relative frequencies (Table 2). Large spruce trees (both live and snags) were used significantly more frequently (3.5 times) than expected, and small spruce trees were used less frequently (0.28 times) than expected. Large pine trees were also used more frequently than expected, whereas proportional use of small pine trees did not differ significantly from their relative abundance in the study area (Table 2). Large live spruce trees were used significantly more frequently than expected and small live spruce were used significantly less than expected (Fig. 3B, Table 2). Frequency of use of large dead spruce was about 29 times what was expected, based on high use by birds (10 of 38 individuals) and very low relative stem densities in the study area (< 1% of all trees). No foraging observations occurred on large or small pine snags, although there was one observation in 2006 on a pine snag where size was not recorded.

For Manly selection ratios estimated from all foraging observations for 36 individual birds (from 2007–2008) included in the foraging duration model, three-toed woodpeckers showed significant preferences for live large pines and both live and dead large spruce, with selection values particularly high for large spruce snags (Table 3). Small live pine and spruce were used as foraging substrate less than their availability, suggesting general underutilization of these substrates, while small spruce snags were used according to their availability (Table 3). Selection ratios could not be estimated for small or large pine snags, as they were not used for foraging by any of the birds in 2007–2008 and occurred at low densities in the study area (together less than 2.9% of total tree density; Table 1). We also calculated Manly selection ratios directly from the empirical use data (with 37 individuals, including one from 2006), rather than those derived from the foraging duration model. These estimates differ slightly from those derived from the foraging duration models and generally have wider confidence intervals but produce the same interpretations of substrate preference and avoidance (Appendix 1).

Foraging duration

Cumulative AIC_c weights [$w_+(j)$] supported all three hypotheses for the effects of tree structure and composition on foraging substrate use for American Three-toed Woodpeckers (Fig. 4). Tree Status [$w_+(j) = 0.98$] was the most important predictor of foraging duration, followed by moderate predictive ability of tree Species [$w_+(j) = 0.63$] and Size [$w_+(j) = 0.57$]. The best approximating model included fixed effects of tree Species, Size, and Status (Table 4). Evidence ratios indicated the top model representing all three hypotheses was 1.5 times more plausible than the second-best model without the Size covariate, 1.9 times more probable than the third-best model without Species, and 2.1 times more plausible

Table 2. Summary of chi-square goodness-of-fit analyses about American Three-toed Woodpecker (*Picoides dorsalis*) initial foraging substrate use. Observed (OBS) values refer to the number of birds that were observed using a particular initial foraging substrate. Expected (EXP) refers to the expected frequency of usage based on the proportion of that substrate type (based on relative stem density) in the study area based on random vegetation surveys. The first seven models are based on all 51 individual birds, whereas the last eight models are based only on 38 birds for which tree size was noted in the initial foraging observation. All chi-square analyses have a single degree of freedom. P-values in bold represent significant differences in foraging use from expected values based on tree abundance. Asterisks indicate tests where expected values were < 5, so we calculated the likelihood-ratio (G) goodness-of-fit statistic and computed exact P-values based on the binomial distribution, instead of using the chi-square goodness-of-fit test.

Comparison Group 1	OBS	EXP	Comparison Group 2	OBS	EXP	Chi-square	P-value
Live Trees	31	41.26	Dead Trees	20	9.74	13.35	<0.001
Spruce	35	36.01	All Other Trees	16	14.99	0.10	0.757
Live Spruce	16	29.13	All Other Trees	35	21.87	13.80	<0.001
Dead Spruce	19	6.88	All Other Trees	32	44.12	24.70	<0.001
Pine	16	8.63	All Other Trees	35	42.37	7.57	0.006
Live Pine	15	7.18	All Other Trees	36	43.82	9.93	0.002
Other Tree Species	0	6.36	Pine and Spruce	51	44.64	7.27	0.007
Large Trees	30	8.65	Small Trees	8	29.35	68.23	<0.001
Large Spruce	20	5.75	All Other Trees	18	32.25	41.63	<0.001
Small Spruce	6	21.08	All Other Trees	32	16.92	24.23	<0.001
Large Pine*	10	2.77	All Other Trees	28	35.23	12.81	<0.001
Small Pine*	2	3.66	All Other Trees	36	34.34	0.98	0.432
Large Live Spruce	10	5.41	All Other Trees	28	32.59	4.55	0.033
Small Live Spruce	4	16.30	All Other Trees	34	21.70	16.24	<0.001
Large Dead Spruce*	10	0.34	All Other Trees	28	37.66	51.03	<0.001

Table 3. Means, standard errors, and 95% lower (LCL) and upper (UCL) confidence limits for Manly selection ratios based on the ratio of proportional substrate use vs. availability for foraging substrates for American Three-toed Woodpeckers (*Picoides dorsalis*) in the Black Hills. Substrate use values were based on model-averaged estimates from the foraging duration model for birds from 2007–2008. No estimates are given for dead ponderosa pine (*Pinus ponderosa*), as no birds were observed foraging on dead pines in 2007–2008. Confidence intervals that do not overlap 1.0 indicate significant preference (> 1.0; +) or avoidance (< 1.0; -). Tree categories include species (ponderosa pine or white spruce [*Picea glauca*]), status (living or dead [snag]), and size (small = < 23 cm DBH, large = ≥ 23 cm DBH).

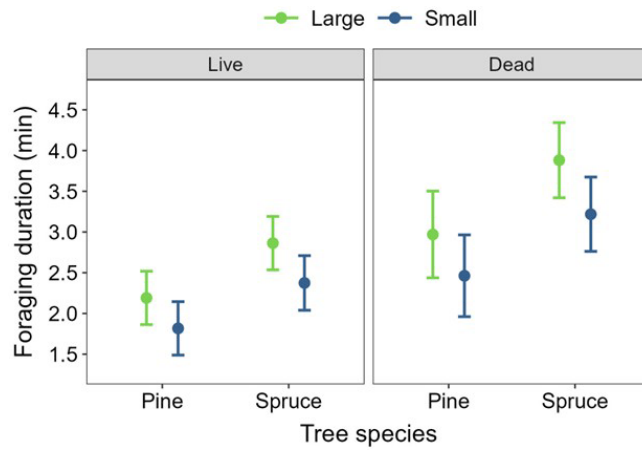
Tree category	Manly selection ratio estimates				Pref/Avoid
	Mean	SE	LCL	UCL	
Small Live Pine	0.200	0.065	0.105	0.379	-
Small Live Spruce	0.258	0.042	0.187	0.356	-
Small Dead Spruce	0.786	0.166	0.520	1.189	=
Large Live Pine	2.024	0.604	1.127	3.634	+
Large Live Spruce	2.288	0.395	1.630	3.210	+
Large Dead Spruce	35.258	9.034	21.338	58.259	+

than the fourth-best model with Status alone (Table 4). Beta coefficients from the competing models confirmed predictions for the tree structure and composition hypotheses (Table 5). Accordingly, beta coefficients in the best model indicated foraging time was greater for large-diameter trees than for small-diameter trees, greater for white spruce than for ponderosa pine, and greater for dead than for live trees (Table 5). The confidence intervals for beta coefficients in the best model did not cover zero, indicating measurable effect sizes for the covariates (Table 5).

DISCUSSION

Our results suggest that American Three-toed Woodpeckers in the Black Hills, South Dakota, prefer large (> 23 cm DBH) dead white spruce trees and, to a lesser degree, large live spruce and ponderosa pine trees as foraging substrates, and select against living small spruce and pine. Most studies of American Three-toed Woodpecker foraging ecology do not compare foraging substrate use to availability as we did in this study (but see Imbeau and Desrochers 2002, Gagné et al. 2007, Nappi et al. 2015). The foraging preference for large dead spruce trees documented in the present study is consistent with previous findings for American Three-toed Woodpeckers at other locations. For example, Imbeau and Desrochers (2002) and Gagné et al. (2007) found that three-toed woodpeckers in boreal forests of Quebec preferred large recently dead or dying black spruce for foraging. In contrast, Nappi et al. (2015) noted that American Three-toed Woodpeckers in black spruce forests in Quebec foraged 60% of the time on live healthy trees, 10% on live decaying trees, and only 30% on dead trees, although dead trees were used in greater proportion than their availability, and mostly on trees < 20 cm DBH. American Three-toed Woodpeckers in the Deschutes National Forest, Oregon, selected mature and over-mature trees and avoided small trees (Goggans et al. 1989). However, the Oregon birds tended to forage on lodgepole pine (63%) rather than Engelmann spruce (25%), whereas in the present study, about 70% of foraging bouts occurred on white spruce and only about 30% on ponderosa pine, although large spruce and large ponderosa pine were both used in greater proportion than their availability at our study sites. Thus, a preference for large dead and dying spruce trees is apparent in many regions throughout the range of the American Three-toed Woodpecker, highlighting the dependence of this species on older forest habitats where these conditions are present

Fig. 4. Mean $\pm$ SE foraging bout durations for all combinations of the tree Size (large or small), Species (pine or spruce) and Status (living or dead) covariates from model-averaged estimates of forage duration during the breeding season for American Three-toed Woodpeckers (*Picoides dorsalis*) in white spruce forest habitats of the Black Hills, South Dakota, 2007–2008.



(Tremblay et al. 2020, Lamarre and Tremblay 2021), but some regional variation in tree species and status (i.e., live vs. dead) preferred for foraging is evident.

Our data suggest that tree size is also an important foraging selection attribute of the American Three-toed Woodpecker in the Black Hills. Mohren (2002) concluded that the average DBH of foraging trees for three-toed woodpeckers in the Black Hills was 22.9 cm, but this average was smaller than the average DBH of trees (including both white spruce and ponderosa pine) at random sites within their study area. The high use of spruce trees for foraging relative to larger ponderosa pine trees likely explains the selection of trees with smaller diameters than the overall average DBH for both pine and spruce at random sites in Mohren (2002). American Three-toed Woodpeckers in Quebec also foraged preferentially on recently dead spruce trees, but with a smaller median diameter of 9.5 cm (Nappi et al. 2015), although other studies in Quebec suggest a foraging preference for larger spruce trees (Imbeau and Desrochers 2002, Gagné et al. 2007). Bull et al. (1986) noted that American Three-toed Woodpeckers foraged on dead lodgepole pine trees with an average DBH of 24 cm in northeastern Oregon. Beetle infestations typically occur in snags and larger diameter trees (USFS 1996, Mohren 2002), so increased prey availability in larger trees is a probable explanation for the selection of trees ≥ 23 cm for foraging in the present study. Although a different species on a different continent, the Eurasian Three-toed Woodpecker (*Picoides tridactylus*) is closely related to the American Three-toed Woodpecker and has similar overall habitat associations (del Hoyo et al. 2020), so data on habitat and foraging ecology for this species might also complement data for the American Three-toed Woodpecker. Eurasian Three-toed Woodpeckers in Sweden preferred foraging on large freshly dead trees in both unburned and prescribed-burned conifer forest patches, and preferred foraging on Norway spruce (*Picea abies*) relative to Scots pine (*Pinus sylvestris*; Versluijs et al. 2020).

Table 4. Model selection for the effects of tree Size (large ≥ 23 cm DBH; small < 23 cm DBH), Species (white spruce [*Picea glauca*] and ponderosa pine [*Pinus ponderosa*]) and Status (living or dead) on foraging time of American Three-toed Woodpeckers (*Picoides dorsalis*) in the Black Hills of South Dakota, 2007–2008. The model selection metrics are log-likelihood [$\log(L)$], number of parameters (K), second order Akaike's information criterion adjusted for sample size (AIC_c), difference between AIC_c of the best model and model i (Δ_i), and AIC_c weights for model i (w_i). Models with $\Delta_i < 4$ are shown.

Model	$\log(L)$	K	AIC_c	Δ_i	w_i
Size + Species + Status	-461.69	6	935.85	0.00	0.259
Species + Status	-463.14	5	936.61	0.76	0.177
Size + Status	-463.40	5	937.14	1.29	0.136
Status	-464.54	4	937.30	1.45	0.125
Size + Species + Status + Size*Status	-461.47	7	937.57	1.72	0.110
Size + Species + Status + Size*Species	-461.68	7	937.97	2.13	0.089
Size + Status + Size*Status	-463.32	6	939.10	3.25	0.051
Size + Species + Status + Size*Species + Size*Status	-461.41	8	939.63	3.78	0.039

American Three-toed Woodpeckers in the present study foraged on snags for 39.2% of initial foraging observations and 42% of the total foraging time. This is lower than previous reports of 78–93% (Imbeau and Desrochers 2002) and 88% (Goggans et al. 1989) of foraging events on snags at other locations. Therefore despite the effect size of snags vs. live trees being the largest effect size in the foraging duration analyses in this study, snags did not compose a similarly high proportion of foraging events for the Black Hills population. One potential reason for this difference might be that snags occurred at relatively low densities, compared to live trees, at our study sites (Table 1). An additional possibility for the relatively low degree of foraging on snags by American Three-toed Woodpeckers in the Black Hills may be their responses to fire patterns within the Black Hills National Forest. In contrast to other western North American populations of three-toed woodpeckers, but similar to eastern North American populations (Murphy and Lehnhausen 1998, Hannon and Drapeau 2005, Kotliar et al. 2008), the Black Hills population does not seem to shift its distribution in response to recent fires (Mohren 2002), most of which occur in ponderosa pine-dominated forests in the Black Hills (USFS 2005). This may be because the thicker bark of ponderosa pine relative to white spruce (Jackson et al. 2019, Malone and Liang 2009) is not conducive to the pecking/flaking foraging strategy of three-toed woodpeckers, even in burned areas. Thus, the absence of colonization of burned habitats in the Black Hills and the general preference for foraging on large living and dead white spruce and, to a lesser extent, on large living ponderosa pine might explain why snags compose a smaller fraction of foraging events in the Black Hills than in other western portions of the range. Similarly, in Quebec's boreal black spruce forests only 30% of American Three-toed Woodpecker foraging bouts were on dead trees, whereas 60% of foraging bouts were on living healthy conifers, with close to 20% of foraging time devoted to sap-licking (Nappi et al. 2015). Throughout its range, the American Three-toed Woodpecker forages on large living trees (Tremblay et al. 2020). Even when it occurs in burns, three-toed woodpeckers forage mainly on lightly to moderately burned stands that offer a mixture of live trees and uncharred portions

Table 5. Parameter estimates, Standard Errors (SE), and Lower (LCL) and Upper (UCL) 90% Confidence Limits, respectively, from the best five models ($\Delta_i < 2$) for the effects of tree Size, Species, and Status on foraging time of American Three-toed Woodpeckers (*Picoides dorsalis*), Black Hills, South Dakota, 2007–2008. The parameters Year and Bird ID : Year are error terms (Standard Deviations) for nested random effects.

Model	Parameter	Estimate	SE	LCL	UCL
Size + Species + Status					
	Intercept	0.597	0.181	0.300	0.895
	Size - large	0.187	0.112	0.003	0.371
	Species - spruce	0.268	0.147	0.025	0.511
	Status - dead	0.304	0.098	0.143	0.465
	Year	<0.001	-	-	-
	Bird ID : Year	0.483	-	-	-
Species + Status					
	Intercept	0.767	0.148	0.523	1.010
	Species - spruce	0.241	0.146	0.000	0.482
	Status - dead	0.297	0.097	0.137	0.458
	Year	<0.001	-	-	-
	Bird ID : Year	0.469	-	-	-
Size + Status					
	Intercept	0.805	0.137	0.579	1.031
	Size - large	0.165	0.111	-0.018	0.349
	Status - dead	0.362	0.093	0.209	0.516
	Year	<0.001	-	-	-
	Bird ID : Year	0.472	-	-	-
Status					
	Intercept	0.938	0.101	0.772	1.105
	Status - dead	0.350	0.092	0.198	0.503
	Year	<0.001	-	-	-
	Bird ID : Year	0.459	-	-	-
Size + Species + Status + Size * Status					
	Intercept	0.531	0.207	0.191	0.872
	Size - large	0.261	0.158	0.000	0.522
	Species - spruce	0.280	0.148	0.036	0.524
	Status - dead	0.416	0.195	0.095	0.736
	Size - large * Status - dead	-0.150	0.226	-0.523	0.223
	Year	<0.001	-	-	-
	Bird ID : Year	0.474	-	-	-

of burned trees (Murphy and Lehnhausen 1998, Nappi et al. 2010). Such foraging behavior may be linked with higher numbers of bark beetles and bark beetle predators in lightly to moderately burned stands than in severely burned stands (Nappi et al. 2010). These differences in foraging behavior throughout the range of American Three-toed Woodpecker might indicate that Black Hills populations are adjusting to the low conifer diversity in the Black Hills, where preferred foraging habitat essentially exists as small islands of spruce in a sea of ponderosa pine.

Our study focused on foraging substrate use during the breeding season and because foraging preferences may vary seasonally, we cannot necessarily extrapolate foraging preferences during the breeding season to other periods of the year. However, the primary foraging method of American Three-toed Woodpeckers involves flaking bark to find prey rather than excavating, so this species tends to prefer thin-barked species, such as white spruce, rather than thicker-barked species such as ponderosa pine, for foraging (Tremblay et al. 2020). Noteworthy in this regard is that white spruce and ponderosa pine comprise the only two widespread conifer tree species in the Black Hills (USFS 2005). The high foraging use of spruce, including a preference for large

spruce, and the significantly greater mean foraging duration on large spruce snags compared to other tree species and size/status categories in this study is consistent with differences in tree bark thickness and primary foraging methods of American Three-toed Woodpeckers. Thus, it seems likely that the foraging preferences that we documented during the breeding season in the Black Hills population extend to other seasons.

Conservation implications

The preference of American Three-toed Woodpeckers for foraging on large living and, especially, dead spruce and, to a lesser degree, large living ponderosa pine in greater proportion than their availability in this study underscores the importance of mature and older forest habitats containing large trees to this species. The isolated population of American Three-toed Woodpeckers in the Black Hills combined with its strong association with limited mature white spruce habitat (5% of total forest cover; DeBlander 2002, USFS 2022a) make it a key species of conservation concern in South Dakota. Because of the relatively low incidence of fires occurring within these white spruce forests (USFS 2005) and the promotion of climax spruce forests by fire exclusion practices in the Black Hills (USFS 2022a), post-burn salvage logging is not as much of a direct threat to white spruce habitat as other management activities that involve the harvesting of live trees (e.g., cutting trees to reduce insect outbreaks or fire intensity). Approximately 90% of the white spruce habitat in the Black Hills is considered late successional mature forest (USFS 2005). These mature white spruce forests, including standing snags, are important American Three-toed Woodpecker foraging habitats within the Black Hills National Forest and therefore should be an important conservation consideration of future forest management plans. This is highlighted by the recent proposed spruce forest management plan by the Black Hills National Forest, which has been at least temporarily withdrawn, that would have reduced white spruce-dominated habitats by more than half to expand aspen and pine forest habitats in the northern Black Hills (USFS 2022b). Our data suggest that such management actions would reduce important foraging habitat for the isolated population of American Three-toed Woodpeckers in the Black Hills. Moreover, fire management or silvicultural treatments may be needed to increase availability of large dead spruce and improve foraging habitat for American Three-toed Woodpeckers in the Black Hills. Continuing fire exclusion could result in catastrophic wildfires, even in white spruce habitats, which could negatively influence American Three-toed Woodpeckers given their foraging reliance on large trees, although given associations of this species with post-fire habitats in the western portion of their range, such fires might conceivably provide short-term positive impacts on Black Hills populations.

Although American Three-toed Woodpeckers are primarily associated with white spruce forests in the Black Hills and large living spruce trees and snags serve as the most often used foraging substrates, the Black Hills population is also associated with mixed forest types of ponderosa pine, white spruce, and aspen and nesting substrates include pine snags and, especially, living and dead aspen (Mohren 2002, Ervin 2011). Consideration of nesting substrate requirements in addition to foraging resources are needed to fully evaluate habitat suitability for the American

Three-toed Woodpecker population in the Black Hills, so management activities should consider not only foraging habitat needs but full annual cycle habitat requirements for appropriate conservation and management plans (Mohren 2002, Ervin 2011).

Author Contributions:

AE: Designed the study and collected the data, wrote and revised the manuscript.

DP: Designed and conducted analyses, wrote and revised the manuscript.

MD: Designed and conducted analyses, wrote and revised the manuscript.

DS: Designed the study and collected the data, provided input to statistical analyses, wrote and revised the manuscript.

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Data Availability:

Data from this project are publicly available in the Dryad depository at <https://doi.org/10.5061/dryad.34tmgp50j>.

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Appendix 1. Means and 95% lower (LCL) and upper (UCL) confidence limits for Manly selection ratios based on the ratio of proportional substrate use vs. availability for foraging substrates for American Three-toed Woodpeckers (n=37) in the Black Hills. Substrate use values were empirical estimates of cumulative time spent on each substrate averaged across observations of 36 individual birds from 2007-2008 and one bird from 2006 for which tree-size data were recorded. No estimates are given for dead ponderosa pine, as no birds were observed foraging on dead pine. Confidence intervals that do not overlap 1.0 indicate significant preference (> 1.0; +) or avoidance (< 1.0; -). Tree categories include species (ponderosa pine or white spruce), status (living or dead [snag]), and size (small = < 23 cm DBH, large = ≥ 23 cm DBH).

Tree Category	Manly Selection Ratio Estimates			
	Mean	LCL	UCL	Pref/Avoid
Small Live Pine	0.134	0.027	0.666	-
Small Live Spruce	0.261	0.124	0.549	-
Small Dead Spruce	0.702	0.299	1.651	=
Large Live Pine	3.309	1.585	6.910	+
Large Live Spruce	2.349	1.556	3.546	+
Large Dead Spruce	26.323	14.525	47.704	+