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Big, sick, and rotting: Why tree size, damage, and decay are important to fisher reproductive habitat

Richard D. Weir^{a,*}, Mark Phinney^b, Eric C. Lofroth^c^a Artemis Wildlife Consultants, 4515 Hullcar Road, Armstrong, British Columbia, Canada V0E 1B4^b Louisiana-Pacific Canada Ltd., 116 – 116th Ave., Dawson Creek, British Columbia, Canada V1G 3C8^c British Columbia Ministry of Environment, P.O. Box 9338, Victoria, British Columbia, Canada V8W 9M1

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ABSTRACT

To gain a better understanding of the factors affecting selection of reproductive habitat by female fishers (*Martes pennanti*) in boreal mixed-wood forests, we identified structures, sites, and stands used by 12 radiotagged female fishers for reproduction between 2005 and 2009 near Dawson Creek, British Columbia, Canada. We deployed a used-unused design to evaluate the support by the data for a series of candidate models at each scale using information-theoretic inference. All dens occurred in internal cavities in large, diseased, and decaying trembling aspen (*Populus tremuloides*; $\bar{x}_{DBH} = 50$ cm, $SD = 11$, $n = 20$) or balsam poplar trees (*Populus balsamifera* spp. *balsamifera*; $\bar{x}_{DBH} = 58$ cm, $SD = 11$, $n = 11$). Female fishers appeared to select reproductive denning structures based upon the difference between the diameter of the tree (cm) from the mean DBH of trees within the site and whether the tree showed signs of damage and visible signs of decay. At the site scale, selection was positively related to mean DBH of aspen and balsam poplar trees and vertical diversity index, and negatively related to density of hard logs (pieces ha^{-1}). Females selected stands for reproduction based upon mean DBH of trees ≥ 15 cm and the position of the stand within their non-denning home range. In the boreal mixed-wood forests of north-eastern British Columbia, reproductive habitat for fishers was strongly linked to infection courts in large, diseased, and decaying aspen and balsam poplar trees. Our data suggests that tree size, damage, and decay play critical roles in the suitability of habitat for reproduction, and forest managers should consider retaining and promoting ecological processes that result in the recruitment of trees with these features if conservation of reproductive habitat for fishers is a concern.

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1. Introduction

Fishers (*Martes pennanti*) are medium-sized carnivores of the weasel family that occur throughout the boreal and temperate forests of North America. Fishers are rare but important members of the forest ecosystems that they occupy, and as mesocarnivores play an essential role in regulating populations of many mid-sized mammals in these forests (Roemer et al., 2009). Fishers are also habitat specialists that rely on many components of forested ecosystems to fulfil their life requirements, with reproduction being most closely tied to specific forest attributes (Lofroth et al., 2010).

Reproductive dens are critical habitat features in which female fishers give birth and rear offspring. These reproductive dens must provide shelter for female and young from challenging climatic conditions found in early spring, in addition to providing protection from potential predators. In British Columbia, female fishers

care for their young exclusively in cavities in trees (Lofroth et al., 2010) that they use continuously for periods of up to 3 months after giving birth. Fishers will occasionally use up to three different den trees during the rearing period between April and June (Paragi et al., 1996; Weir and Corbould, 2008).

Trees need to have two very specific features for females to use them as reproductive dens. Some form of damage must occur to the tree bole to provide a pathway for decay organisms to access the interior of the tree. This damage must be of particular dimensions to also provide predator-secure access for the female to the interior of the tree, typically through frost cracks, fire-scars, large anchored branches pulling out from the tree bole, and woodpecker holes (Lofroth et al., 2010). With a body mass between 2 and 3.5 kg and overall length approaching 1 m, female fishers are among the largest obligate-tree cavity users in North America and trees used as dens need to be large enough to provide a cavity that has an inside diameter of >30 cm (Weir and Corbould, 2008).

The specific features of reproductive dens appear to occur in a narrow range of tree sizes and types. Most dens in British Columbia are in live, declining, deciduous trees that have developed

* Corresponding author. Tel.: +1 250 546 0531; fax: +1 250 546 0532.

E-mail addresses: rweir@artemiswildlife.com (R.D. Weir), mark.phinney@lpcorp.com (M. Phinney), Eric.Lofroth@gov.bc.ca (E.C. Lofroth).

sufficient decay to form a large internal cavity (Lofroth et al., 2010). In the sub-boreal forests of central British Columbia, reproductive dens are most frequently found in large-diameter black cottonwood (*Populus balsamifera* spp. *trichocarpa*) trees (Weir and Harestad, 2003; Weir and Corbould, 2008). Fishers have also been documented using cavities in trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and Douglas-fir (*Pseudotsuga menziesii*) trees in the cold-dry Chilcotin region of the province (Davis, 2009).

Forest management has the potential to affect the supply of trees with features of reproductive dens for fishers throughout British Columbia. Loss of forested habitat from resource extraction and other human activities is believed to be the main long-term threat to fisher populations throughout their range (Proulx et al., 2004). Previous forest management activities have often resulted in the loss of trees with attributes suitable for use as reproductive dens. Short forest harvest rotations, repression or removal of “undesirable” tree species during forest operations, forest-health policies that strive to reduce tree disease, and removal of “danger” trees have all likely negatively affected the distribution and abundance of trees that have the features necessary for reproductive dens. Our objectives were to identify structures used by fishers for rearing offspring in boreal mixed-wood forests and evaluate the factors that affected selection of reproductive habitat at three spatial scales ranging from structures to stands. This information will assist land managers in better identifying reproductive habitat for fishers and informing their management decisions at several spatial scales, thereby lessening negative effects on the supply and distribution of reproductive habitats for fishers.

2. Materials and methods

2.1. Study area

Our study area covered 950 km² of the moist-warm subzone of the Boreal White and Black Spruce biogeoclimatic zone (Pojar

et al., 1987) to the south-west of Dawson Creek, British Columbia, Canada (55°45'N, 120°11'W; Fig. 1). Elevations in the study area range from 610 to 950 m above sea level and climate of the study area is cold and dry, which is typical of continental boreal forests. Mean annual temperature is 1.1 °C with 485 mm of precipitation each year, of which approximately 40% falls as snow (DeLong et al., 1990). Snow cover lasted from mid-November until mid-April and reached a peak average depth of 48 cm in March. Temperatures during the study ranged between −43 °C and 34 °C.

Forests in the study area were typical of boreal mixed-wood landscapes. Dominant tree species included trembling aspen, white spruce (*Picea glauca*), black spruce (*Picea mariana*), and lodgepole pine, with other deciduous components of balsam poplar (*P. balsamifera* spp. *balsamifera*) and paper birch (*Betula papyrifera*). Young forest stages were comprised primarily of trembling aspen or occasionally lodgepole pine, whereas later-successional stands were dominated by spruce or seral associations of trembling aspen. The natural disturbance regime of the project area was frequent, large-scale fires (up to 1000 km²) occurring about every 100 years (Wong et al., 2003). Mixed-wood forests differ from conifer-dominated boreal forests in that seral associations (British Columbia Ministry of Forests, 2002), typically dominated by aspens, are more widely spread and occupy up to 50% of the landscape mosaic.

Human alteration of the landscape was extensive despite the study area being largely comprised of young-forest or older structural stages (518 km²; 55%). Most land on the northern, western, and eastern edges of the study area were cleared for agriculture, accounting for 29% of the overall area. Forest harvesting of both conifer and deciduous stands has occurred throughout the study area, with approximately 7% of the study area harvested since 1980. Low-intensity ground fires have been periodically set to enhance understory forage production for cattle. Since 1990, exploration and development of oil and gas reserves has occurred. Specifically, 3-D seismic exploration of natural gas deposits in the area has resulted in a grid of 3- or 5-m wide cutlines, separated by 360 m, dissecting the entire study area.

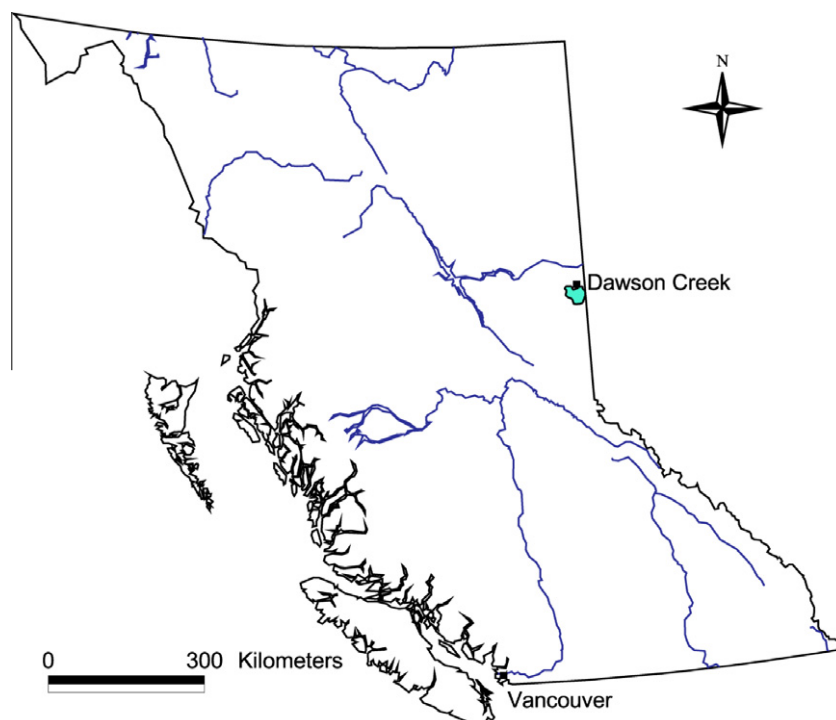


Fig. 1. Location of study area in the boreal mixed-wood forests of north-eastern British Columbia, Canada.

2.2. Capture and radiotelemetry monitoring

We captured, radiotagged, and radiolocated fishers throughout our study area between 2005 and 2009 (Weir et al., 2011). All capture, handling, and radiotagging protocols met or exceeded capture and handling guidelines outlined in the protocols for Wildlife Capture and Handling (Resource Inventory Committee, 1998) and were carried out under Wildlife Act permit FSJ05-9483. Reproductive dens were identified by homing-in on telemetry signals to identify structures used ≥ 3 times by adult female fishers during April and May (Weir, 1995; Paragi et al., 1996).

2.3. Experimental design

We examined the effects that various factors had on the probability of use at each of our three scales of examination: structures (i.e., trees), sites (or patches; Weir and Harestad, 2003), and stands (*sensu* Fig. 1; Slauson and Zielinski, 2009; Lofroth et al., 2010). At the structure scale, we considered use of a specific structure (i.e., reproductive den tree) relative to other structures within that specific site (i.e., patch). Likewise, selection of specific sites occurred when fishers selected from a choice of sites within their respective stands and selection of stands occurred when fishers selected from a choice of stands within their home ranges. We considered a structure, site, or stand used by each fisher for denning as the currency of use (Buskirk and Millspaugh, 2006).

At each scale of analysis, we used the next-broader scale of examination to identify the boundaries of “choice sets” (Buskirk and Millspaugh, 2006) for each selection event. That is, we identified features available to a fisher as those that occurred in the next scale “up”. Given the hierarchical nature of scale, resource selection at one scale is dependent upon selection decisions made at other scales (Weir and Harestad, 2003) and we designed our analyses to incorporate this dependence. We did not constrain choice sets, as done by Zielinski et al. (2004) and Aubry and Raley (2006), which allowed us to assess probability of use for all potential choice sets. Although constraining choice sets can reduce the effect of resource selection decisions at one scale on selection at another (i.e., cross-scale dependence), application of results from this type of analysis is more difficult because managers cannot predict the utility of all available sites. Since the objective of our work was to assist land managers in better identifying reproductive habitat for fishers, we traded a decrease in cross-scale dependence for an increase in management applicability, recognizing that this approach produced a different selection function than Zielinski et al. (2004) and Aubry and Raley (2006). At the structure scale, we compared the tree used by a fisher to simultaneously unused trees found within the same site. At the site scale, we compared a patch of forest used by a fisher (e.g., den tree and surrounding vegetation) to a simultaneously unused site within the same stand. We compared a stand (as delineated by Vegetation Resources Inventory [VRI] mapping; Ministry of Forests and Range, 2010) used by a fisher to simultaneously unused stands within its home range.

2.4. Habitat measurement

We measured a suite of characteristics for each tree that was used as a reproductive den. We documented tree species, diameter-at-breast-height (DBH), tree height, height to den entrance, entrance form (e.g., branch-hole, fire scar), diameter of the bole at the entrance and base of den cavity, depth of the den cavity from the entrance, and the length of the long and short axes of the entrance hole. We also estimated mean thickness of the cavity wall by using an increment borer to measure the width of the remaining holding wood at several points 5 cm above the cavity base. We estimated the inside diameter of the cavity at its base by

subtracting two times the mean wall thickness from the bole diameter at the cavity base.

To characterize habitats selected by fishers for reproduction, we measured structural and vegetative attributes of both used and unused structures, sites, and stands. We did this by pairing each used structure, site, or stand in which a fisher established a reproductive den with a simultaneously unused structure, site, or stand elsewhere within the same scale using a paired approach. This is not to suggest that the fisher never used the simultaneously unused structure, site, or stand; only that it was not used at the exact moment that the fisher was at its den. This temporal stratification was key to our analytical design and involved the use of generalized estimating equations (Zeger et al., 1988); it allowed us to compare used and unused structures, sites, or stands within the temporal stratum, recognizing that a structure, site, or stand that was unused at one point in time may have been used by fishers at another time.

We collected structure- and site-scale data using standardized measurement techniques at two types of 400-m² plots: *fisher-site plots* and *comparison plots*. At fisher-site plots (i.e., reproductive sites), we measured physical, structural, and vegetative characteristics of the site and structure used and all other unused structures within the plot. At the comparison plots, we measured the same characteristics, plus site and stand descriptors (British Columbia Ministry of Environment Lands and Parks and British Columbia Ministry of Forests, 1998a). We used comparison plots to characterize a site that was simultaneously not used by the fisher within the same stand. For our analyses, we treated a stand as a contiguous area (i.e., mapped polygon) that had the consistent vegetative characteristics, as delineated by 1:20,000-scale VRI mapping (Ministry of Forests and Range, 2010). We centered fisher-site plots on the structure used by the fisher; comparison plots were centered on random geo-coordinates within their respective stand polygons. We used 400-m² circular plots because this is the standard size used for vegetation inventory in British Columbia (British Columbia Ministry of Environment Lands and Parks and British Columbia Ministry of Forests, 1998b).

We assessed physical, vegetative, and structural characteristics at both plot types using standard methods (British Columbia Ministry of Environment Lands and Parks and British Columbia Ministry of Forests, 1998b). We assessed vegetation composition at each plot using ocular cover estimates for tree (stems >10 m tall), high-shrub (2–10 m), low-shrub (0.15–2 m), herb, and moss layers (British Columbia Ministry of Environment Lands and Parks and British Columbia Ministry of Forests, 1998c). We also estimated the percent cover of coniferous shrubs and the total percent of overhead cover (tree and shrub layers) during summer (leaf-on) and winter (leaf-off). We estimated an index of vertical diversity of the vegetation layers by calculating the Shannon–Weiner function (Krebs, 1989, p. 361) using the percent cover provided by each layer of woody plants (i.e., tree, high shrub, low shrub).

We measured stocking densities of trees ≥ 15 cm DBH at the site scale using variable-radius prism plots (7–11 trees per plot; Resources Information Standards Committee, 2004). We recorded species, DBH, appearance code, crown code, extent of infection courts, notable pathogens, and damage severity and type for each tree (British Columbia Ministry of Environment Lands and Parks and British Columbia Ministry of Forests, 1998d). We measured coarse woody debris (CWD) ≥ 7.5 cm diameter encountered along two 24-m transects emanating at perpendicular angles on a random azimuth from the plot center. For each piece of CWD, we recorded its distance along the transect, species, diameter at the intercept point, decay class, tilt angle, and height above ground (British Columbia Ministry of Environment Lands and Parks and British Columbia Ministry of Forests, 1998e).

We used fisher-site and comparison plot data to quantify characteristics of used and unused sites. We calculated stem density

(stems ha^{-1}) for declining or dead trees, trees ≥ 40 cm DBH, and deciduous trees ≥ 40 cm DBH with visible signs of decay. We also estimated the crown index for each plot as the average cover provided by each tree within the plot. We estimated the density of hard pieces of CWD (i.e., decay class 1–3; British Columbia Ministry of Environment Lands and Parks and British Columbia Ministry of Forests, 1998e) per plot (*sensu* Marshall et al., 2000).

We identified stand-scale polygons using 1:20,000 scale VRI spatial data. We used land cover classification, overstory tree species and coverage, soil moisture, and soil nutrient regime (British Columbia Ministry of Forests and Range, 2008) to classify each polygon into 1 of 13 ecosystem associations. Each polygon was further assigned 1 of 8 structural stages, ranging from non-vegetated to old forest. We used the combination of ecosystem association and structural stage to classify stands, which we considered to be relatively homogeneous assemblages of vegetation structure and composition ≥ 2 ha (i.e., areas with similar CWD, closure of vegetation strata, and other structural attributes).

We also used structural data from ≥ 3 randomly located comparison plots to calculate mean values for structural conditions found in each ecosystem association and structural stage. We did not include data from plots that fell in atypical sites (e.g., roads, landings, creeks) in the calculation of stand-averaged structural values.

Finally, we assessed the location of each stand within the non-denning home range of each female fisher. To accomplish this, we estimated the utilization distribution (UD) during non-denning periods (i.e., June–March) generated from the fixed kernel method with the smoothing parameter selected by least-squares cross-validation on a minimum of 30 temporally independent radiolocations (Worton, 1989; Seaman and Powell, 1996) during these periods (see Weir et al. in submission for additional telemetry sampling and home range calculation methods). We then overlaid the stand polygons with the UD to determine the area-weighted average UD score for each polygon for each fisher. Scores ranged between 0.02 for the most-used area to 0.95; thus, proximity to center of home range decreased as the UD score increased. For example, a stand that had a UD score of 0.25 was closer to the center of the home range than a stand with a UD score of 0.75.

2.5. Analysis

We analysed the factors that affected selection by radiotagged fishers in discrete analyses at the structure, site, and stand spatial scales. We considered selection as a binary process and modelled it as a logistic function. Because we used temporal stratification to identify used and unused structures, sites, and stands, the derived function was a resource selection probability function (RSPF; Manly et al., 2002).

We developed different sets of candidate models to evaluate relationships between habitat factors and selection of structures, sites, and stands for reproduction (Appendix A). We used information from previous studies of fisher ecology and suspected ecological relationships to develop a priori models that we tested using information-theoretic inference (Burnham and Anderson, 1998), in which several competing hypotheses (i.e., models) were simultaneously confronted with data (Johnson and Omland, 2004). Information-theoretic inference allowed us to compare the support by the data among several hypothetical models and determine the probability of each model in the candidate set being closest to the underlying process that affected selection (i.e., selection decisions by the animal). We limited the minimum events per variable for our model building to 10 (Peduzzi et al., 1996). We assessed multicollinearity among variables at each scale by ordinary least-squares regression and considered combinations of variables with $r^2 \geq 0.4$ sufficiently correlated to exclude the combination from the same model (Ballinger, 2004).

We dealt with the longitudinal nature of repeated observations on a fixed number of radiotagged fishers by employing generalized estimating equations to generate a population-averaged model (Hu et al., 1998). Because generalized estimating equations are not likelihood-based, we used a modification to the Akaike information criterion to produce a quasi-likelihood information criterion (QIC_u) to identify the most parsimonious model (Pan, 2001). Furthermore, generalized estimating equations allowed us to temporally stratify each radiolocation, which was key to our analytical design. We assumed that correlation among data points occurred within individuals and time, which necessitated the use of exchangeable correlation (Ballinger, 2004) as our working correlation structure. The number of estimated parameters in each model (K) equalled the number of variables in the model plus 2 for estimated parameters (i.e., model intercept and working correlation matrix). We calculated the QIC_u score for each model and ranked the relative support for each by comparing the scores among competing models. We then identified the “best” model from this candidate set by selecting the model with the lowest QIC_u score. We assessed whether selection occurred by comparing the QIC_u scores of models in the candidate set to a null model that predicted no selection. We considered selection to have occurred if the null model was outside the 95% confidence set of best models.

We used Akaike weights (w_i) to quantify strength of evidence for candidate models (Burnham and Anderson, 1998). The 95% confidence set of best models was identified using the fewest top models where $\sum w_i$ was ≥ 0.95 . We used multi-model inference to estimate model-averaged parameters and unconditional 95% confidence intervals for each of the variables in the production of a best predictive model (Burnham and Anderson, 1998). This inferential process allowed us to determine if selection occurred and, if so, to estimate the changes in probability of use of a structure, site, or stand based upon increases or decreases of identified habitat features. Because our modelling approach employed a used-unused design, we evaluated performance of each model by estimating the area under its receiver-operating characteristic (ROC) curve (Hosmer and Lemeshow, 2000).

3. Results

We identified 12 fishers using 31 different trees as reproductive dens on 39 occasions to successfully rear 23 litters between 2005 and 2009. All dens occurred in cavities in trembling aspen ($n = 20$) or balsam poplar trees ($n = 11$) that were accessed through branch-holes ($n = 20$), unhealed fire-scars ($n = 6$), or split branch/leader separations ($n = 3$). Cavities used as dens were, on average, 68 cm deep ($\text{SD} = 31$ cm, $n = 24$), had an inside diameter of 41 cm ($\text{SD} = 11$, $n = 17$), and were accessed through an opening that had a long axis of 17.9 cm ($\text{SD} = 12.5$ cm, $n = 28$) and short axis of 6.3 cm ($\text{SD} = 1.4$ cm, $n = 28$; Table 1). None of the entrances or cavities showed signs of being excavated by primary excavating birds, such as woodpeckers. The mean DBH of trees used as reproductive dens was 50 cm ($\text{SD} = 11$) for aspens and 58 cm ($\text{SD} = 11$) for balsam poplars (Table 1). We recorded den trees in a number of different ecosystems and structural stages, but predominately in young- or mature-forest stages of deciduous-dominated mesic or moist ecosystems.

Although fishers used 31 different trees as reproductive dens, this represented 32 selection events because 1 den tree was selected by 2 unrelated fishers (as determined through DNA fingerprinting, see Weir et al. in submission) in different years. Thus, we used a sample size of 32 for our selection analyses, recognizing that the tree data was not entirely independent.

Radiotagged female fishers were highly selective at the structure spatial scale for trees that they used as reproductive dens within

Table 1

Characteristics of trees and cavities used by radiotagged female fishers as reproductive dens near Dawson Creek, British Columbia, Canada between 2005 and 2009.

Variable	Aspen			Balsam poplar			All dens		
	\bar{x}	SD	<i>n</i>	\bar{x}	SD	<i>n</i>	\bar{x}	SD	<i>n</i>
DBH (cm)	50	11	20	58	11	11	53	11	31
Tree height (m)	24	5	20	21	5	11	23	5	31
Height to entrance (m)	5.0	2.6	20	6.0	3.8	10	5.3	3.0	30
Bole diameter at entrance (cm)	49	11	20	50	11	10	50	11	30
Bole diameter at cavity base (cm)	53	11	18	54	13	6	53	11	24
Entrance long axis (cm)	17.2	12.8	20	19.7	12.6	8	17.9	12.5	28
Entrance short axis (cm)	6.3	1.5	20	6.5	1.4	8	6.3	1.4	28
Cavity depth (cm)	72	32	19	51	24	5	68	31	24
Mean wall thickness (cm)	6	4	13	6	2	5	6	3	18
Estimated diameter inside cavity ^a (cm)	42	12	12	41	12	5	41	11	17

^a Estimated as: bole diameter at cavity base – 2 × mean wall thickness.

sites. The model most-supported by the data, and the only model in the 95% confidence set, predicted probability of use based on the difference between DBH of the identified tree and the mean DBH of trees within the site, and whether the stem had damage and showed visible signs of moderate or severe stem decay. This best model scored 14.67 QIC_u units better than the next-best model, ≥ 52 QIC_u units better than the null model (i.e., no selection), and had excellent discriminatory power (ROC curve area = 0.87). Model parameterization indicated that the probability of female fishers using a specific tree as a reproductive den was positively associated with the difference in diameter of the tree from the mean DBH of trees within the site (odds ratio: 1.11, 95% CI: 1.04–1.17) and whether the tree showed signs of damage and visible signs of decay (odds ratio: 8.47, 95% CI: 3.81–18.81). Application of the best model suggested that female fishers, when selecting a reproductive den, were 20 times more likely to select a tree that had a DBH that was 20 cm larger than the site-average and showed signs of damage with moderate or severe visible decay (probability of use = 0.68; 95% CI: 0.44–0.85) than a tree of average size without damage or visible decay (probability of use = 0.03; 95% CI: 0.02–0.06; Fig. 2).

Female fishers were also highly selective for the sites in which they situated their reproductive dens. The model best-supported by the data predicted probability of use of a site based on the mean DBH of aspen or balsam poplar trees ≥ 15 cm DBH, vertical diversity index, and density of hard logs. This model had excellent discriminatory power (ROC curve area = 0.84) and scored 42.6 QIC_u units better than the null model, although the 95% confidence set of best models contained three other similar models (Table 2). Multi-model parameterization indicated that the probability of using a specific site for reproduction was positively associated with the mean DBH of aspen or balsam poplar trees and vertical diversity index, but negatively associated with the density of hard logs (Table 3). Application of the parameterized best model suggested that female fishers were 146 times more likely to select a patch of trees where the mean DBH of aspen or balsam poplar trees was 50 cm, vertical diversity index was 0.9, and no hard CWD occurred (probability of use = 0.99; 95% CI: 0.60–0.99) than one where the mean DBH of aspen or balsam poplar trees was 30 cm, vertical diversity index was 0.5, and density of hard CWD was 1000 pieces ha⁻¹ (probability of use = 0.01; 95% CI: 0–0.41; Fig. 3).

Furthermore, fishers were highly selective for stands in which they established reproductive dens. The model best-supported by the data, and the only model in the 95% confidence set, predicted probability of use for reproductive denning based upon the stand's position within the non-denning home range and mean DBH of trees. This best model scored 11.3 QIC_u units better than the next-best model, ≥ 73 QIC_u units better than the null model (no selection), and had acceptable discriminatory power (ROC curve area = 0.70). Multi-model parameterization indicated that the probability of using a specific stand for reproduction was positively

associated with mean DBH of trees ≥ 15 cm (odds ratio: 1.15; 95% CI: 1.09–1.22) and that female fishers were more likely to use a stand situated near the center of their non-denning home range than on the periphery (odds ratio for 10% change in UD: 0.61; 95% CI: 0.54–0.70). Parameterization of the best model suggested that female fishers were 52 times more likely to select a stand with mean DBH of 50 cm situated at the 20% isopleth of the non-denning home range (probability of use = 0.311; 95% CI: 0.012–0.940) than one situated at the 80% isopleth of the non-denning home range where the mean DBH was also 50 cm (probability of use = 0.006; 95% CI: 0–0.123; Fig. 4).

4. Discussion

We observed radiotagged female fishers exhibiting very pronounced selection for specific features of trees, sites, and stands in which to give birth and rear their young in the boreal mixed-wood forests of north-eastern British Columbia. Female fishers showed the highest specificity for reproductive habitat at fine scales and less specificity at coarser scales. The strong selection at fine scales may be linked to very distinct conditions not found in other habitat assemblages, specifically, the occurrence of large, injured, and decaying trees, whereas the selectivity at coarser scales is likely linked to the distribution and abundance of these features within the home range.

Across their range, fishers are well known for using large trees that have cavities with small entrance holes as reproductive dens (e.g., Paragi et al., 1996; Lofroth et al., 2010). Fishers in the boreal mixed-wood forests also used trees with these two critical characteristics. This was reflected in strong, specific, fine-scale decisions that radiotagged female fishers made for reproductive habitat based upon tree species, size, and prevalence of decay. Given the ecology of decay in trees, large cavities and small entrance holes likely develop only under very specific circumstances related to the species of tree and the rate, intensity, and duration of infection of the tree by decay-causing fungi and other organisms.

Certain tree species are likely more susceptible to internal decay and cavity formation than others and this was reflected in the selection patterns that we observed. Aspen and balsam poplar trees, unlike conifers, do not have relatively decay-resistant heartwood and as such have much lower resistance to wood-decay fungi (Sinclair and Lyon, 2005). Several species of decay-causing fungi infect trembling aspen and balsam poplar trees (Callan, 1998), with up to 69% of aspens being infected with at least 1 species of fungus (Basham, 1958). Aspen trunk rot (*Phellinus tremulae*) and hardwood trunk rot (*P. ingriarius*) are the primary fungi that cause extensive decay in aspen and balsam poplar trees in the boreal forests of western Canada (Hiratsuka and Loman, 1984). Trembling aspen and balsam poplar trees are well adapted to tolerate fungal

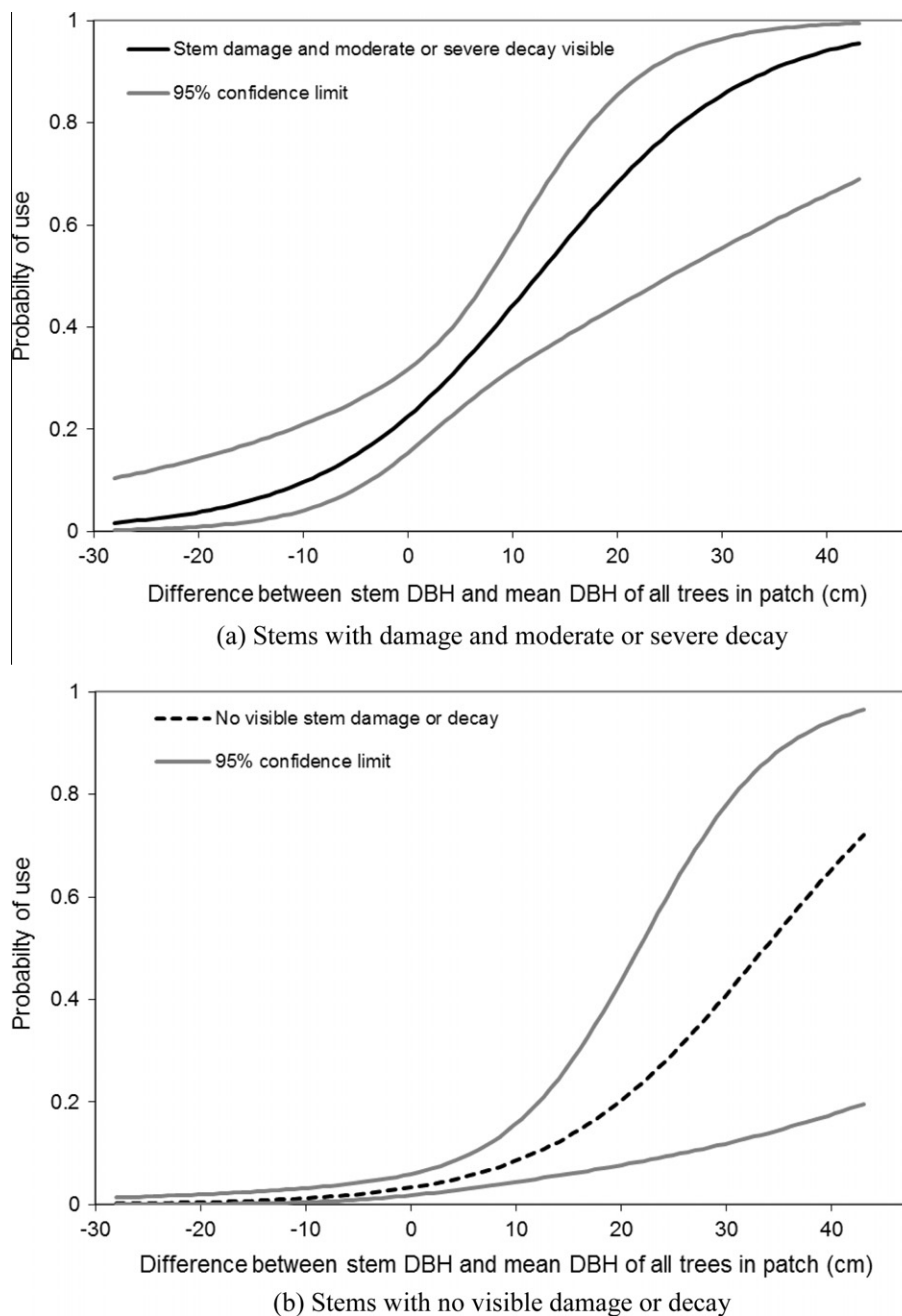


Fig. 2. Predicted relationships between relative tree size, amount of stem damage, and extent of decay on the probability of use of a tree as a reproductive den by female fishers near Dawson Creek, British Columbia, Canada between 2005 and 2009. Trees that were much larger than the average tree DBH and had stem damage and moderate or severe decay (a) were more likely to be used than those with average DBH and no stem damage or decay (b).

infection and can continue to survive and grow despite the presence of extensive advanced decay within their boles (Peterson and Peterson, 1992), which likely makes them especially suited as dens for fishers. In our study area, internal decay was most prevalent in trembling aspens and balsam poplar trees and female fishers were highly selective for these two tree species when they made selection decisions at the site spatial scale. Most of the trees that fishers used as reproductive dens displayed evidence of *Phellinus* decay such as conks or obvious white-rot decay. Unlike elsewhere in the western range of fishers (e.g., Aubry and Raley, 2006; Davis, 2009), we did not detect fishers using conifer trees as dens, likely because these species did not appear to develop internal decay frequently; only 5 of 309 conifer trees that we surveyed

showed signs of internal decay and none of these trees were sufficiently large or had entrances suitable for fishers.

Internal decay requires that decay-causing organisms gain access to dead tissue inside the tree bole. This is achieved through infection courts, which are wound sites where fungi can invade the tree's protective barriers (Basham, 1958). These infection courts play a dual role in making trees suitable as reproductive dens for fishers. First, infection courts are a necessary avenue for decay-causing fungi to penetrate the tree's defences, infect the vulnerable dead inner tree tissues, and develop sufficient advanced decay for a cavity to form. Second, infection courts also form the critical access point that fishers need to gain entrance to the internal cavity.

Table 2
Ninety-five percent confidence set of models explaining selection of sites by radiotagged fishers for reproductive dens near Dawson Creek, British Columbia, Canada between 2005 and 2009.

Model ID	Probability of use of site for reproductive den related to:	K^a	QIC_u^b	Δ_i^c	w_i^d	Area under ROC curve
PW22	Mean DBH of aspen and balsam poplar trees, vertical diversity, and density of hard logs	5	50.102	0	0.817	0.84
PW14	Mean DBH of aspen and balsam poplar trees, vertical diversity	4	55.138	5.035	0.066	0.88
PW11	Mean DBH of aspen and balsam poplar trees, depending upon maximum DBH of aspen and balsam poplar trees in site	3	56.274	6.172	0.037	0.90
PW21	Mean DBH of aspen and balsam poplar trees, vertical diversity, and crown index	5	57.000	6.898	0.026	0.88

^a Number of estimated parameters in associated model.

^b Quasi-likelihood Information Criterion for small samples (Pan, 2001).

^c Difference in QIC_u scores between model and best-selected model.

^d Relative likelihood of model; Akaike weight (Burnham and Anderson, 1998).

Table 3
Multi-model parameterization of factors affecting selection of sites within stands used by radiotagged fishers for reproductive dens near Dawson Creek, British Columbia, Canada between 2005 and 2009.

Variable	Model-averaged estimate	Unconditional SE	Odds ratio (95% CI)	Relationship
Intercept	−10.624	3.523		
Mean DBH of aspen and balsam poplar trees (cm)	0.197	0.045	1.218 (1.113–1.333)	Positive
Vertical diversity index	5.738	2.322	1.775 ^a (1.126–2.798)	Positive
Density of hard logs (pieces ha ^{−1})	−0.003	0.002	0.729 ^b (0.537–0.991)	Negative

^a Odds ratio for 0.1 change in vertical diversity index.

^b Odds ratio for 100 pieces ha^{−1} change in density of hard logs.

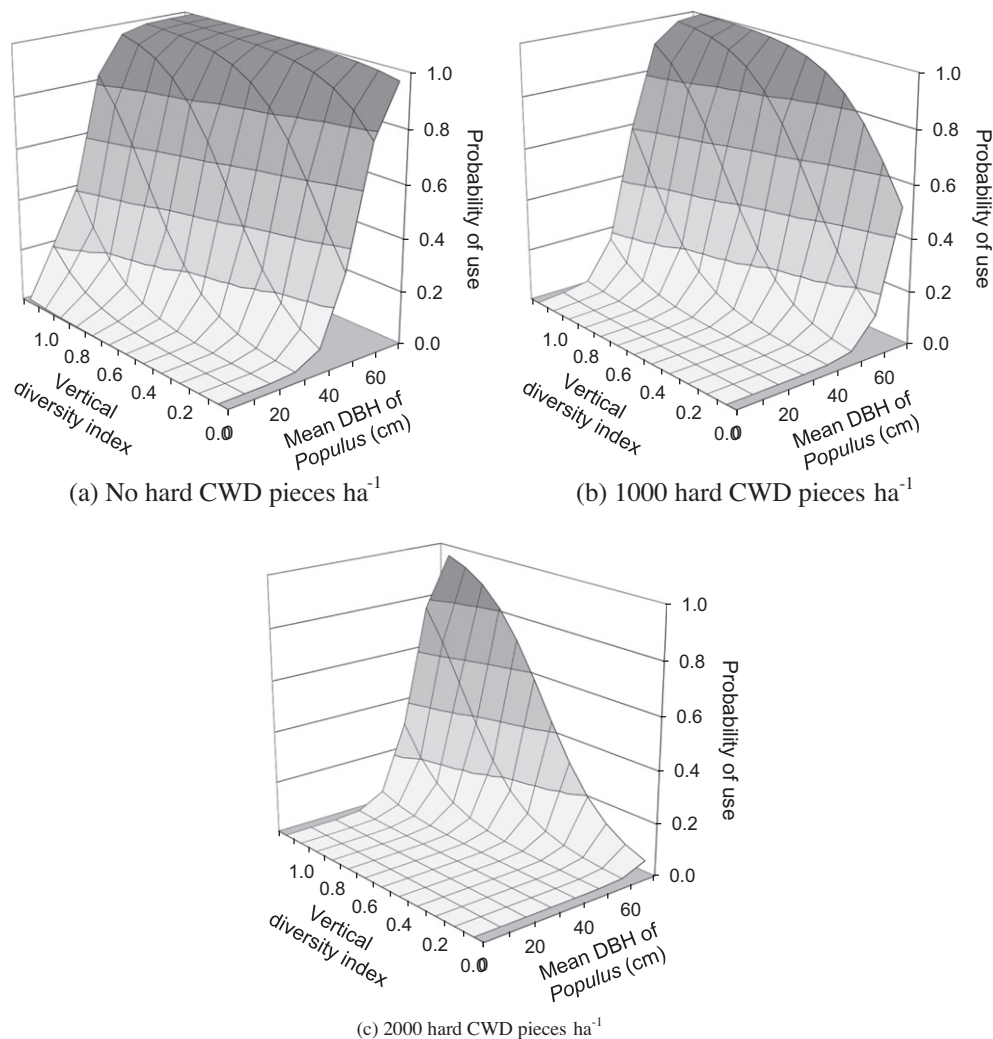


Fig. 3. Predicted probability of use of a site as a reproductive den by radiotagged fishers as a function of mean DBH of aspen and balsam poplar trees and vertical diversity for three different densities of hard CWD near Dawson Creek, British Columbia, Canada between 2005 and 2009. Fishers were most likely to select sites with greater average DBH, more vertical diversity, and less hard CWD than other sites within the same stand.

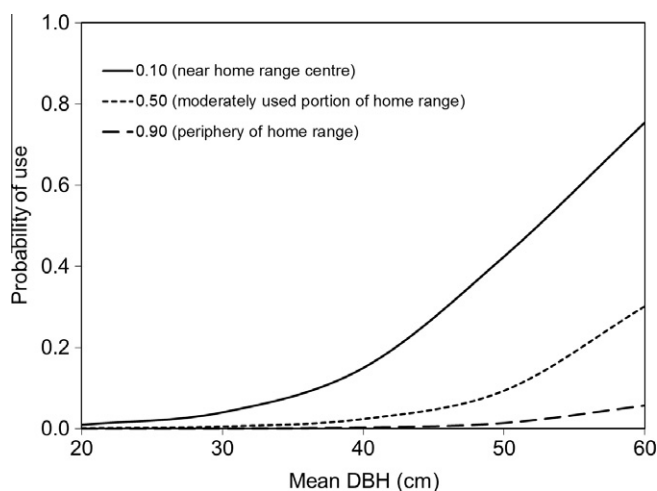


Fig. 4. Predicted relationship among mean DBH and location within the non-denning home range on probability of a radiotagged female fisher selecting a stand for reproduction in the Kiskatinaw Plateau region south of Dawson Creek, British Columbia, Canada between 2005 and 2009. Fishers were most likely to select stands with large mean DBH that were located near the center of their non-denning home range.

The intensity and duration of fungal infection needed for sufficient advanced decay to form a suitable cavity inside aspen or balsam poplar trees is unclear. All of the trees that we observed fishers using as reproductive dens had large, persistent injuries such as branch-holes, fire scars, or limb/leader splits. These types of chronic, non-healing infection courts consistently expose the tree interior to fungal spores over long periods of time (Basham, 1958), which may explain why older trees typically have more advanced decay than younger trees (Witt, 2010). Decay may be further accelerated by specific types of infection courts, such as branch stubs and fire-scarred wood, that persistently shunt moisture and spores to the unprotected deadwood thereby creating a favorable microenvironment for continued infection (Basham, 1958). However, unlike other cavity-users such as woodpeckers, fishers are not primary cavity excavators; they may require decay to be significantly progressed beyond that achieved by fungi and may need additional physical breakdown of the dead interior wood by arthropods (e.g., Hammond et al., 2003) for a suitable cavity to form. The features of balsam poplar trees used by fishers as dens in our study were similar to those found in black cottonwood trees elsewhere in British Columbia, where the majority of dens occurred in cavities accessed through branch-hole infection courts (Weir and Harestad, 2003; Weir and Corbould, 2008). Unlike southern portions of their range where activities of primary cavity excavators are important sources of inoculation and cavities used by fishers (Raley et al., in press), fishers in the boreal forest used entrances and cavities that showed very little or no evidence of excavation by other vertebrates.

Not only do infection courts have the vital role of providing decay organisms access to the heart of the tree, but they form the entrance point to the cavity that fishers also require. Female fishers used infection courts with very specific dimensions to gain secure access to the internal tree cavity. Indeed, the minor axis of all entrances to den cavities ranged between 4.5 and 9.5 cm, which is only slightly larger than the distance between the ventral side of the mandible and the vertex of the frontal bone of female fishers (i.e., $\bar{x} = 4.3$ cm, $SD = 1.9$ cm, $n = 74$ skinned adult female fisher carcasses; R.D. Weir, unpublished data). This supports the hypothesis that female fishers select trees with infection courts of specific dimensions that provide access to the cavity, but which excludes larger animals such as potential predators (Leonard, 1986).

Furthermore, infection courts that are suitably sized may need to occur in the lower regions of aspen and balsam poplar trees in the boreal forest because this portion of the bole is most likely to reach the size needed to form a cavity ≥ 40 cm inside diameter, as our data suggests, within the normal disturbance cycle of 100 years. This hypothesis is supported by our observation that most entrances to dens were in the lower third of the tree bole and within 10 m of ground level.

Infection courts likely developed and produced reproductive habitat for fishers through a number of mechanisms. Internal cavities in several den trees were accessed through large injuries resulting from low-intensity surface fires. These non-lethal injuries initially formed extensive areas of damage that often reached several meters up the tree bole and allowed for persistent infection by decay fungi. As the scar healed, cambium tissue partially grew over the scar, forming suitably sized entrances to the interior cavity. Most other reproductive dens occurred in trees with persistent infection courts that were the result of large anchored limbs pulling out from the bole, resulting in a branch hole leading to the deadwood. The exact mechanism by which branch holes formed is unknown, but presumably a large architectural limb (i.e., ≥ 10 cm diameter that is rooted to the center of the tree) pulled out from the tree bole, likely through some sort of mechanical damage, such as nearby falling trees, snow load, or wind. Prior to mechanical damage of these limbs, advanced decay may also have been present so that the architectural limb pulled out of the bole, rather than simply breaking at the base.

Tree diameter also played a significant role in the selection of reproductive habitat by female fishers at all scales of examination. Both aspen and balsam poplar trees have vigorous growth rates and can reach diameters >40 cm in less than 100 years on highly productive sites (Peterson and Peterson, 1992; Harper, 2008). Larger and older trees are also more likely to develop advanced decay (Witt, 2010). Tree diameter was positively related to reproductive habitat for female fishers because large aspen and balsam poplar trees are those most likely to develop decay and grow to a size large enough to form a cavity to hold a female and her young (i.e., bole diameter ≥ 50 cm at cavity height). These large trees appeared to be rare in our study area; we encountered only 27 aspen or balsam poplar trees that were ≥ 50 cm dbh in 153 randomly located plots.

Factors other than those related to large cavities with appropriate entrances within a single tree affected selection of sites by fishers for reproduction. We observed that females selected sites with increased vertical cover around the dens, which may provide important security cover for the female and young. Fishers also selected sites with lower densities of hard CWD than expected; this may be related to providing good horizontal visibility and predator-detection for young when loafing at the base of the den trees while the female is away from the den. Reduced density of CWD may also allow the female to better detect potential predators upon leaving the den area. Alternatively, large hard CWD may not accumulate in areas frequented by fires, such as which occurred in the study area over the past 100 years.

Female fishers may have reproduced in stands that were near the center of their non-breeding home range for a number of reasons. Situating reproductive sites near the center of a well-known area may allow females to reliably access sites of known prey resources during denning periods. Alternatively, dispersing females may decide where to establish their home range based upon the distribution of suitable den sites. Only 2 of 32 reproductive dens used by radiotagged females overlapped the 80% UD of another female (Weir et al., in submission), which supports the hypothesis that denning opportunities are a resource that females defend and females may establish home ranges based upon the

distribution of this resource or adjust their home ranges to be centered on stands with denning opportunities.

5. Conclusions

In the boreal mixed-wood forests of north-eastern British Columbia, reproductive habitat for fishers was strongly linked to large, diseased, and decaying aspen and balsam poplar trees. Trees with the two attributes necessary for use as a den by fishers appeared to be relatively rare and these trees probably developed under very specific circumstances of tree growth, persistent infection with decay-causing fungi, and appropriate-sized disturbance, damage agents, and site conditions. Maintaining the natural processes of tree growth, damage, disease, and decay that produce these trees are important to the continued conservation and recruitment of reproductive habitat for fishers at all spatial scales. Conserving the mechanisms by which fire-scar and branch-hole infection courts develop, such as low-intensity surface fires and appropriate crown development, is critical to ensure the continued recruitment and conservation of reproductive habitat for fishers. Using this information, land managers will be able to better plan and implement effective forest management strategies to help ensure sufficient reproductive habitat for fishers is available within forest rotations over the long-term.

If it is an objective, we recommend that land managers in the mixed-wood boreal forest adopt a multi-scale approach to conserving reproductive habitat for fishers. When deciding upon areas within the landscape to schedule for timber harvest, managers should consider conserving high-quality stands that have large trembling aspen or balsam poplars as the primary species (e.g., stand with quadratic mean diameter ≥ 20 cm, age ≥ 100 years, and height ≥ 20 m). Anecdotal information from our study suggests that female fishers may be able to reproduce successfully if ≥ 600 ha of these high-quality stands occur within a typical 30-km² female home range (R. Weir, unpublished data). Additionally, reproductive habitat can be retained at finer scales within

timber-harvest units by identifying sites that have high densities of large declining deciduous trees surrounded by dense vegetation that provides good cover, and setting aside these areas from harvest. At the finest scale, large, diseased, and rotting trees can be conserved within harvested cutblocks through single-tree retention, rather than these trees being felled and yarded to cull-piles.

Although our work has furthered our understanding of the relationships between tree size and species, infection courts, decay-causing fungi, cavity formation, and the supply of reproductive habitat for fishers, considerable knowledge gaps still remain. Future work should focus on elucidating the relationship between infection courts and cavity development, specifically the duration and intensity of infection at which different types of wounds infect the interior deadwood of the tree with decay-causing fungus. Emphasis should also be placed on identifying attributes of tree morphology and development that may facilitate infection courts that cause the den cavity and access points needed by fishers for reproductive dens.

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Appendix A

See Table A1.

Model ID	Number of variables	Probability of use related to
Structure		
E-1	1	DBH
E-2	1	DBH ≥ 40 cm
E-3	2 ^a	DBH ≥ 40 cm depending upon tree species
E-4	1	Difference between structure DBH and mean DBH of <i>Populus</i> in site
E-5	1	Difference between structure DBH and mean DBH
E-6	1	Extent of infection courts on bole of tree
E-7	2 ^a	Extent of infection courts depending upon severity and presence of stem or root disease on <i>Populus</i> trees
E-8	1 ^a	Extent of infection courts depending upon severity and presence of stem or root disease
E-9	1 ^a	Extent of infection courts depending upon height to live crown aka bole length
E-10	1	Extent of conks on bole of tree
E-11	1 ^a	DBH ≥ 40 cm depending upon extent of infection courts and severity (binary) and presence of stem or root disease
E-12	1 ^a	DBH depending upon tree status
E-13	1 ^a	DBH ≥ 40 cm depending upon extent of infection courts
E-14	1 ^a	DBH depending upon extent of infection courts
E-15	1 ^a	Difference between DBH and mean DBH depending upon DBH ≥ 40 cm and presence of damage
E-16	2	Difference between DBH and mean DBH and presence of infection courts

Table A1 (Continued)

Model ID	Number of variables	Probability of use related to
E-17	2 ^a	Difference between DBH and mean DBH and presence of moderate or severe stem decay
E-18	2	Difference between DBH and mean DBH and presence of conks
E-19	1 ^a	Extent of infection courts depending upon stand age
E-20	2 ^a	Difference between DBH and mean DBH depending on average crown index and presence of stem decay depending upon average crown index
E-Null	0	No selection (null model)
Site		
P-1	1	Mean DBH
P-2	1	Average DBH of aspen or balsam poplar in site
P-3	1	Deciduous cover
P-4	1	Density of trees with infection courts
P-5	1	Density of <i>Populus</i> \geq 40 cm DBH
P-6	1	Density of trees \geq 40 cm DBH that have infection courts
P-7	1	Largest DBH of tree in site
P-8	1	Density of declining deciduous trees \geq 40 cm DBH
P-9	1	Density of trees with advanced decay
P-10	1	Potential den density
P-11	1	Mean DBH of <i>Populus</i> depending upon maximum DBH of <i>Populus</i> in site
P-12	2	Maximum DBH and shrub cover
P-13	2	Density of trees \geq 40 cm DBH that have infection courts and crown index
P-14	2	Mean DBH of <i>Populus</i> and vertical diversity measure
P-15	2	Maximum DBH and density of elevated logs
P-16	2	Mean DBH of <i>Populus</i> in site depending on difference from stand average and vertical diversity
P-17	2	Size of largest tree in site and density of infection courts
P-18	2	Mean DBH of <i>Populus</i> and leaf-on cover
P-19	2	Density of <i>Populus</i> \geq 40 cm DBH and leaf-on cover
P-20	3	Density of trees \geq 40 cm DBH with infection courts and leaf-on cover
P-21	3	Mean DBH of <i>Populus</i> , vertical diversity, and crown index
P-22	3	Mean DBH of <i>Populus</i> , vertical diversity, and density of hard logs
P-23	3	Density of trees with advanced decay, vertical diversity, and crown index
P-Null	0	No selection (null model)
Stand		
SR1	1	Deciduous cover
SR2	2	Density of den-sized deciduous trees and leaf-off cover
SR3	1	Density of trees with advanced decay
SR4	1	Structural stage
SR5	1	Ecosystem association
SR6	1	Coniferous cover
SR7	1	Young forest and mature forest deciduous ecosystems
SR8	1	Riparian forests
SR9	1	Overhead cover
SR10	1	Mean DBH
SR11	1	Stand age
SR12	2	Density of snags and vertical diversity
SR13	1	Location within non-denning home range
SR14	2	Riparian forest and location within non-denning home range
SR15	2	Mean DBH and location within non-denning home range
SR16	2	Density of den-sized deciduous trees and location within non-denning home range
SR17	2	Vertical diversity and location within non-denning home range
SR18	2	Shrub cover and location within non-denning home range
SR19	2	Density of declining or dead trees and location within non-denning home range
S-Null	0	No selection (null model)

^a Indicates that 2 or more variables were combined to function as a single interaction term (Hosmer and Lemeshow, 2000, p. 70).

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