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Bias in the use of broadscale vegetation data in the analysis of habitat selection

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Effective conservation efforts often depend on accurate identification of habitat requirements. Studies that identify habitat requirements for animals typically investigate use of structural habitat (vegetation) instead of functional habitat (conditions for biological fitness). The spatial scale of data could bias the match between functional and structural habitat because broadscale structural habitat maps exclude small habitat patches (inclusions) and broadscale location error can bias estimates of habitat use. To investigate how spatial scale affects the match between functional and structural habitat, we backtracked American marten (*Martes americana*) and fisher (*Pekania* [formerly *Martes*] *pennanti*) movement paths during winter and compared results from selection and tortuosity analyses conducted with broadscale (4 ha) and fine-scale (0.02 ha) structural habitat data. Functional habitat (rest sites and prey kill sites) occurred disproportionately in hemlock–cedar. Fine-scale structural habitat data detected greater selection and tortuosity within hemlock–cedar by traveling martens, but broadscale structural habitat data did not, which demonstrates that combining fine-scale location data with fine-scale structural habitat data improves the match between functional and structural habitat and understanding of habitat requirements. Selection and tortuosity indexes were poorly correlated, indicating that factors other than structural habitat influenced movement patterns. Within-stand structural habitat heterogeneity is important to martens and fishers, especially when heterogeneity includes mature conifer inclusions within primarily deciduous forests. Broadscale data may identify structural habitat associated with required types, rather than required habitat itself, when functional habitat corresponds with landscape features such as inclusions.

Key words: American marten, fisher, functional habitat, habitat selection, *Martes americana*, *Pekania pennanti*, spatial scale, structural habitat, tortuosity, Wisconsin

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The effectiveness of conservation efforts for many animals depends on accurately identifying habitat requirements. Species-specific habitat that is required for occupancy, survival, and reproduction can be classified as functional habitat (Dennis et al. 2003; Gaillard et al. 2010), whereas structural habitat is synonymous with vegetative communities that exist in an area independent of use by an organism (Hall et al. 1997; Garshelis 2000; Gaillard et al. 2010). Habitat selection studies typically investigate structural habitat instead of functional habitat because structural habitat maps for large areas are common, whereas similar maps for functional habitat are rare or nonexistent. When structural habitat is studied, the degree to which functional habitat corresponds with structural habitat will influence the accuracy with which habitat requirements are identified.

Structural habitat can be an incomplete match with functional habitat for multiple reasons. When functional habitat exists in multiple structural habitats, identification of a selected structural habitat will only partially correspond with functional habitat. Use of broadscale data also can cause mismatches between functional and structural habitat. Broadscale (coarse-grained, sensu Turner et al. [2001]) maps exclude structural habitat types that occur as small patches (Turner et al. 1989), which could result in a biased understanding of habitat needs if functional habitat is found in small patches. Broadscale telemetry location error can be hundreds of meters (Potvin et al. 2000; Poole et al. 2004; Dumyahn et al. 2007), which leads to incorrect assignment of animal locations to a structural habitat and biased estimates of its use (White and Garrott 1986; Nams 1989; Potvin et al. 2000). The combination of broadscale structural habitat and location data can create a disconnect between estimates of structural habitat use and actual use. Collecting location and structural habitat data simultaneously at fine spatial scales would improve the relationship between structural and functional habitat because fine-scale data can elucidate existing patterns of structural habitat use that cannot be detected at broader spatial scales but are relevant for associating habitat needs with behavior (Zollner et al. 2000; Proulx and O'Doherty 2006; Vigeant-Langlois and Desrochers 2011).

The importance of structural habitat can be evaluated using tortuosity (meandering—Nams and Bourgeois 2004) and selection (use relative to availability—Manly et al. 2010) indexes, which provide insight into animal behavior, including where animals conserve energy (Godbout and Ouellet 2010) and find prey (Phillips et al. 2004; Maletzke et al. 2008). Selection of a structural habitat to search for resting sites and foraging opportunities can correspond to where movement paths are most tortuous, indicating an area-restricted search for these resources (Karieva and Odell 1987; Valeix et al. 2010). Because selection and tortuosity can provide similar insights into mammalian predator space-use, Mayor et al. (2009) suggested that the concept of habitat selection can be extended to include tortuosity. The relationship between tortuosity and selection, however, is unclear and merits further investigation.

Fine-scale data may be necessary to identify habitat requirements for American martens (*Martes americana*; hereafter martens) and fishers (*Pekania* [formerly *Martes*] *pennanti*) because both species perceive structural habitat at scales that are finer than the forest stand (Weir and Harestad 2003; Nams and Bourgeois 2004; Godbout and Oullet 2010). Martens and fishers use multiple forest types (but avoid nonforested areas), which correspond with rest sites, prey availability, and structure provided by large-diameter trees, coarse woody debris (e.g., logs), forest floor complexity, and horizontal cover (Spencer 1987; Buskirk and Powell 1994; Payer and Harrison 2004). In areas where deciduous forests dominate, studies that followed marten and fisher tracks on the ground identified softwood islands (Steventon and Major 1982), old-growth pockets (Spencer et al. 1983), coniferous ridges (Raine 1983), and dense coniferous patches (Arthur et al. 1989) as selected structural habitat types that differed from the surrounding deciduous stand (hereafter, inclusions). Selection of inclusions is not detected when using broadscale location and structural habitat data (Potvin et al. 2001; Poole et al. 2004), suggesting that use of inclusions is underestimated. Underestimating use of inclusions that provide functional habitat such as prey and rest sites results in a biased understanding of habitat requirements for martens and fishers.

We investigated how the spatial scale of data affects the match between functional and structural habitat by backtracking marten and fisher movement paths during winter while collecting forest type and location data together at fine spatial scales. Using both fine-scale and broadscale data, we quantified patterns of functional and structural habitat selection and path tortuosity. We hypothesized that use of fine-scale structural habitat and location data would elucidate patterns of habitat use not detected with broadscale data and that tortuosity and selection indexes derived from the same movement paths would be statistically correlated.

Materials and Methods

Study area.—We studied martens and fishers on and near the Great Divide District of the Chequamegon-Nicolet National Forest in northern Wisconsin (Fig. 1). The region has cool summers and long winters. The mean temperature near the study area was –9.9°C during January and February, when we collected most data for this study (National Oceanic and Atmospheric Administration 2009–2010). Mean monthly liquid precipitation was 0.4 cm (National Oceanic and Atmospheric Administration 2009–2010), resulting in a mean snow depth of 34.8 cm during our study. Irregular topography and diverse geologic features, including moraine ridges composed of stony, red, and acidic sandy loams, outwash plains composed of sand and gravel, and deposits of windblown silt, are a result of multiple Pleistocene glaciations (Albert 1995).

Sugar maple (*Acer saccharum*) and aspen (*Populus tremuloides*) were dominant forest types. Sugar maple stands often included a mix of yellow birch (*Betula alleghaniensis*) and basswood (*Tilia americana*) and occasionally included scattered white pines (*Pinus strobus*). Aspen stands were often mixed with paper birch (*Betula papyrifera*) and white spruce (*Picea glauca*). Several red pine (*Pinus resinosa*) plantations were distributed across the study area. Black spruce (*Picea mariana*), tamarack (*Larix laricina*), red maple (*Acer rubrum*), black ash (*Fraxinus nigra*), and white cedar (*Thuja occidentalis*) were present in lowland areas. Hemlock (*Tsuga canadensis*) was adjacent to white cedar when the land graded toward upland areas. Balsam fir (*Abies balsamea*) was found in scattered pockets within hardwood and white cedar understories. Shrubs found in forest subcanopies included hazelnut (*Corylus* spp.), ironwood (*Ostrya virginiana*), and serviceberry (*Amelanchier* spp.). Alder (*Alnus* spp.) was found in forest subcanopies or within openings and was often near water.

Capture and handling of martens and fishers.—We captured martens and fishers between October and February during 2008–2009 and 2009–2010 using single-door Tomahawk box-traps (models 106 and 108; National Live Trap Co., Hazelhurst, Wisconsin). Traps were placed where martens or fishers or their sign was observed. Very-high-frequency (VHF) transmitter collars containing activity switches (Gilbert et al. 2009) were fitted to each adult marten (model 080, 40 g; Telonics, Inc., Mesa, Arizona) and fisher (model 125, 55 g;

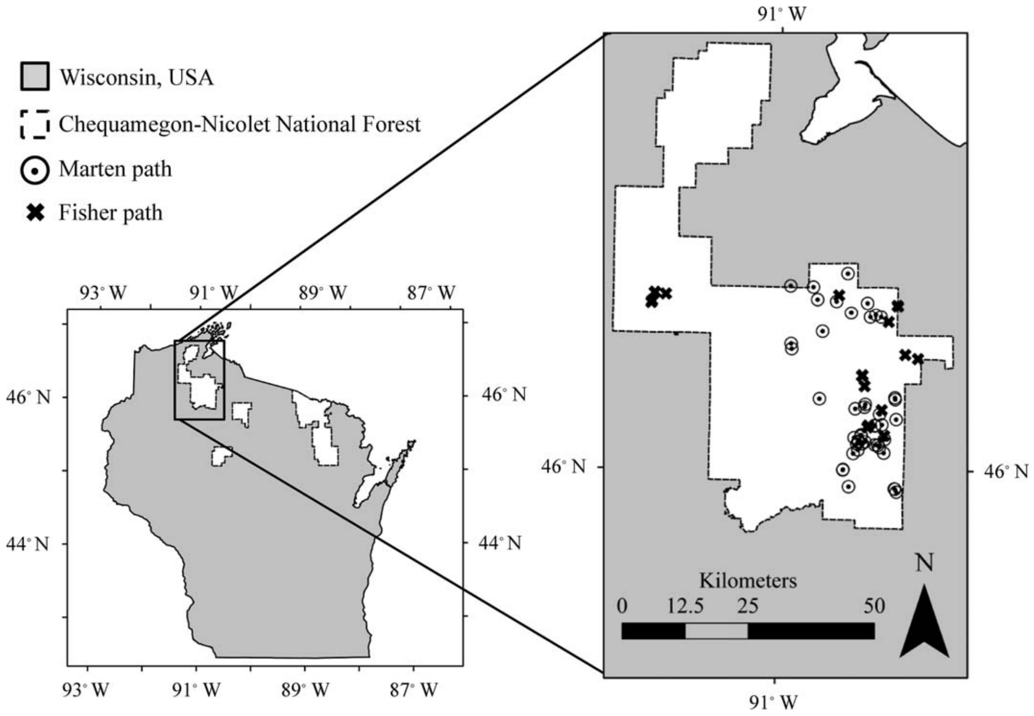

Fig. 1.—Study area in northern Wisconsin, where we studied the use of structural and functional habitat by American martens (*Martes americana*) and fishers (*Pekania pennanti*) during the winters of 2008–2009 and 2009–2010.

Telonics, Inc.). Adult martens were identified by well-developed sagittal crests and masses $>$ 680 g (females) or $>$ 900 g (males—J. H. Gilbert, Great Lakes Indian Fish and Wildlife Commission, pers. comm.). Adult fishers were identified by well-developed sagittal crests and masses $\geq$ 2,500 g (females) or $>$ 4,000 g (males—J. H. Gilbert, Great Lakes Indian Fish and Wildlife Commission, pers. comm.). Capture and handling procedures followed guidelines from the American Society of Mammalogists (Sikes et al. 2011) and Purdue University (Purdue Animal Care and Use Committee 07–032).

In addition to capturing residents, we studied martens that were outfitted with very-high-frequency transmitter collars and translocated to the study area from northeastern Minnesota by the Wisconsin Department of Natural Resources during the September that preceded each field season (15 females and 11 males—Woodford et al. 2013). Translocated martens received collars without activity switches (model MI-2M, 32 g; Holohil Systems, Carp, Ontario, Canada; model 080, 48 g; Telonics Inc.; or model LPM-2700 M, 28 g; Wildlife Materials Inc., Murphysboro, Illinois—Woodford et al. 2013) and were released in Wisconsin as part of a larger supplementation project developed by the Department of Natural Resources, the Great Lakes Indian Fish and Wildlife Commission, and the United States Forest Service (Woodford et al. 2013).

Snow-tracking.—We followed trails left by collared martens and fishers in snow between December and March of 2008–2009 and 2009–2010. In 2008–2009 we selected individuals to track using a random-stratified design without replacement until all individuals were sampled, where the strata were species and sex. In 2009–2010 we randomly sampled individuals to track each day without respect to species or sex and without replacement; individuals were resampled after all individuals were sampled 1 time.

We used telemetry signal characteristics to determine if collared martens and fishers were active or inactive. We navigated to inactive individuals, recorded the location of the rest site, and backtracked the path left in snow by the marten or fisher for $\geq$ 500 m. In 30% of backtracking attempts for martens and 50% for fishers, the focal animal was active or became active while we navigated to it. When this occurred, we determined the direction it was traveling from signal characteristics, navigated to a point behind its direction of travel, and located its path. We then followed the path backward $>$ 100 m before recording data.

We recorded all movement paths using a mapping-grade handheld global positioning system unit (GeoXT GeoExplorer 2005 Series; Trimble, Sunnyvale, California) that achieves submeter location accuracy in open and young forest conditions and $<$ 2-m accuracy in closed canopy conditions following differential correction (Serr et al. 2006; Wing et al. 2008). A point was recorded along the marten or fisher path where the animal changed its direction of travel, made a kill, rested, and changed structural habitat (described below). Changes in the direction of travel (hereafter, vertices) were defined as a $\geq$ 20-degree changes in direction along each path that continued for $\geq$ 0.75 m and at least 2 steps or bounds. Kill sites (hereafter, kills) were areas of disturbed snow with presence of blood, flesh, and feathers or fur. Rest sites were the structures within which the inactive animal was located by the

TABLE 1.—Descriptions of structural habitat types used by American martens (*Martes americana*) and fishers (*Pekania pennanti*) in northern Wisconsin during the winters of 2008–2009 and 2009–2010.

Structural habitat	Fine-scale description	Broadscale description
Aspen	Aspen and paper birch composed $> 30\%$ of basal area and had a larger diameter at breast height (DBH) than other hardwood tree species composing $> 30\%$ of basal area. Includes areas mixed with white spruce and balsam fir	Aspen and paper birch, and aspen containing white spruce and balsam fir
Balsam fir	Balsam fir and white spruce composed $> 30\%$ of basal area and deciduous species composed $\leq 30\%$ of basal area	Balsam fir dominates, but may contain a component of aspen or paper birch
Black ash	Black ash and red maple composed $> 30\%$ of basal area and had a larger DBH than other hardwood tree species composing $> 30\%$ of basal area. Typically found in lowlands	Black ash and red maple; also mixed lowland hardwoods
Black spruce	Black spruce and tamarack composed $> 30\%$ of basal area and deciduous species composed $\leq 30\%$ of basal area	Tamarack[a]
Hemlock–cedar	Eastern hemlock and white cedar composed $> 30\%$ of basal area and deciduous species composed $\leq 30\%$ of basal area	Northern white cedar and mixed swamp conifer
Nonforested	Areas without tree or shrub cover	Nonforested lowlands and uplands
Pine	White or red pine composed $> 30\%$ of basal area and deciduous species composed $\leq 30\%$ of basal area	White and red pine
Shrub	Shrubs composed $> 30\%$ of basal area and had a larger DBH than tree species that composed $> 30\%$ of basal area	Not classified in broadscale data set
Sugar maple	Sugar maple, basswood, and yellow birch composed $> 30\%$ of basal area and had a larger DBH than other hardwood tree species composing $> 30\%$ of basal area	Sugar maple; can be mixed with basswood (*Tilia americana*), white ash, birch, or 20–50% hemlock

[a] Black spruce is not structural habitat type in the broadscale data set. Tamarack was typically observed with black spruce.

researcher. These sites were typically within downed trees or root masses.

Fine-scale structural habitat data.—We recorded structural habitat data in the field by recording locations where movement paths changed forest type and size-class. The mean diameter at breast height (DBH) of trees and shrubs was visually estimated within a 0.02-ha semicircle. The centroid of the semicircle was on the path, 10-m radii were oriented perpendicular to the path, and the arc of the semicircle was oriented in the direction that the observer traveled while backtracking. We recorded structural habitats present within the semicircle (Table 1) and the DBH size-class (< 3 cm, 3–13 cm, 13–23 cm, and > 23 cm) for each structural habitat. At the end of each marten and fisher path, we walked a 500-m linear availability path that was oriented toward the location where we began homing to the marten or fisher from a forest road. If the location where we began homing was less than 500 m from the end of the use path, we continued past the start point to complete the availability path. We recorded fine-scale structural habitat type and DBH size-classes on each availability path using the methods described above.

Broadscale structural habitat data.—Broadscale structural habitat data were from a stand-level data set for the Chequamegon-Nicolet National Forest developed from field surveys and aerial photographs (USDA Forest Service 2001). Broadscale maps included 38 forest stand types and DBH estimates using a minimum mapping unit of 4 ha. The same maps were used for previous habitat selection studies in northern Wisconsin (Wright 1999; Dumyahn et al. 2007).

We matched broadscale structural habitat classifications to fine-scale classifications because definitions for fine-scale classifications were more precise (Table 1). Broadscale structural habitat classifications matched most fine-scale classifications made in the field. Broadscale aspen, balsam fir, nonforested, pine, and sugar maple classifications matched fine-scale classifications. Broadscale classifications that included hemlock–cedar, tamarack, black spruce, and shrub were imprecise or were not present in the broadscale and matched fine-scale classifications made in the field less well (Table 1). To improve the match between classifications we reclassified the broadscale mixed swamp conifer as hemlock–cedar and broadscale tamarack as black spruce. Path segments classified as mixed swamp conifer using broadscale data were typically classified as hemlock–cedar in the field and most areas classified as tamarack in the broadscale data set corresponded to areas that included both black spruce and tamarack (N. P. McCann, Conservation Department, Minnesota Zoological Garden, pers. comm.). Shrub was not a broadscale data set classification but was maintained as a fine-scale classification because it differed from nonforested areas that lacked shrub cover.

Path tortuosity in structural habitats where martens and fishers traveled.—We imported vertices, structural habitat, and DBH data into ArcMap (Environmental Systems Research Institute, Inc. 2008) after differential correction to improve accuracy (Trimble Pathfinder Office 2003; Wing et al. 2008) and divided each path into segments. We located boundaries for each segment at points where a change in dominant structural habitat or DBH occurred. We completed this process separately for structural habitat data that we collected in the field (fine-scale) and stand-level data (broadscale). For fine-scale data, we placed points at structural habitat boundaries located in the field. For broadscale data, we placed points at forest stand type (polygon) boundaries to define segments.

We calculated tortuosity (Benhamou 2004:214, equation 9) for each segment. The tortuosity metric we used describes the correlation of successive step angles and tortuosity values correlate positively with tortuous paths; tortuosity of 0 indicates linear movements and values > 0 indicate paths that are more tortuous (Benhamou 2004; Bodin et al. 2006). Tortuosity calculations required equally spaced vertices. To achieve equally spaced vertices we converted the set of vertices collected in the field to a line and then placed new vertices every 3 m along the new line (i.e., we rediscretized the path—sensu Benhamou 2004). Tortuosity calculations varied $< 5\%$ when rediscretized 3, 4, and 5 m, indicating that results would be consistent across these spatial scales. We used path segments with at least 20 rediscretized vertices from which to calculate tortuosity, resulting in segments that were at least 60 m in length.

Selection of structural habitat where martens and fishers traveled.—Selection indexes can be used to assess disproportionate use of structural habitat by comparing distances traveled in a structural habitat to its availability (Manly et al. 2010). To assess selection of structural habitat by martens and fishers, we calculated a selection index by determining the fraction of each structural habitat on the path used by each marten or fisher, and subtracting the fraction of that structural habitat on its paired availability path (Strauss 1979; Potvin et al. 2000). Index values were calculated using fine-scale and broadscale structural habitat data separately.

Selection of functional habitat by martens and fishers.—To determine if functional habitat corresponded with structural habitat we compared the number of rest sites, kills, and the sum of rest sites and kills (hereafter, referred to as use sites) observed under each fine-scale structural habitat type to the number expected under each fine-scale structural habitat. Rest sites and kill sites were functional habitat because they were where martens and fishers conserved and obtained energy. We calculated the expected number of rest sites, kills, and use sites by multiplying the total number of each by the proportion of distance traveled under each structural habitat on paired availability paths. Expected values were calculated only from availability paths paired to paths containing rest sites, kills, or use sites.

Detection of inclusions in areas used by martens and fishers.—We were interested in determining the degree to which broadscale structural habitat data detected substand heterogeneity and whether classification accuracy was affected by inclusion area. For each path segment on each marten and fisher path, we determined if broadscale classifications matched those made using fine-scale structural habitat data collected in the field. We also measured segment length and used it to index the area of each forested inclusion. We did this because other fine-scale data describing forested inclusions do not exist for our study area and because path segment length corresponded roughly to the size of inclusions. Short segments (< 50 m) typically occurred in small (< 0.5 ha) inclusions and longer segments (> 100 m) typically occurred in large (> 1 ha) inclusions and stands.

Statistical analyses.—We compared tortuosity and selection of structural habitats used by martens and fishers while traveling with linear mixed models in SAS (MIXED procedure—SAS Institute Inc. 2002). Each species and structural habitat data set (fine-scale and broadscale) was analyzed separately. Linear mixed models are appropriate when residuals are not independent or do not have constant variance (West et al. 2007). We fit a priori linear statistical models for structural habitat and its 2- and 3-way interactions with DBH and sex for each species. We also modeled interactions with residency status as a fixed effect for martens; nonresident martens were released on the study area < 1 year before we tracked them and resident martens were present for > 1 year. We treated individuals as random effects and paths as repeated measures.

We used Akaike's information criterion values adjusted for small sample sizes (AIC_c) to determine which repeated measures covariance structure yielded the best fit for each model. We fit each model using the variance components and autoregressive (AR1) covariance structures to model repeated measures. The covariance structure that yielded the lowest AIC_c was used for subsequent modeling. For analyses using fine-scale structural habitat data, the autoregressive (AR1) covariance structure was used for marten selection and tortuosity models and the variance component covariance structure was used for fisher tortuosity and selection. For broadscale structural habitat data, the variance component structure was used for all analyses except fisher tortuosity.

After fitting each a priori model using the covariance structure that yielded the best fit, we compared AIC_c values for each model while holding the covariance structure constant. Models with $\Delta AIC_c < 2$ had the best relative fit (Burnham and Anderson 2002) and their significance was evaluated using P-values from type 3 F-statistics. Pairwise comparisons followed each significant F-test. We used F-tests to compare relative selection (Johnson 1980) because some structural habitats were commonly used but received negative selection values because of high availability. Thus, we chose not to categorize structural habitats as avoided when they were not identified as selected. We used Fisher's exact tests in SAS (FREQ procedure) to determine selection of structural habitats at rest sites, kill sites, and the sum of rest sites and kill sites (hereafter, referred to as use sites). The number of rest, kill, and use sites observed under each structural habitat was compared to the number expected under each structural habitat.

We explored the relationship between selection and tortuosity for each species and structural habitat scale separately using simple linear regressions in SAS (GLM procedure), yielding 4 regressions. The mean tortuosity for each structural habitat on each path was the dependent variable for each regression and selection was the independent variable. Mean tortuosity for each structural habitat on each path was used during analysis because each marten and fisher path yielded ≥ 1 value for tortuosity for each structural habitat but only 1 selection index.

TABLE 2.—Percentage of structural habitats measured at fine and broad spatial scales near American marten (*Martes americana*) and fisher (*Pekania pennanti*) paths and paired availability paths in Wisconsin, during the winters of 2008–2009 and 2009–2010. Nonforested and shrub composed < 2% of total use and availability and are excluded.

	Fine scale		Broad scale	
Structural habitat	Use	Available	Use	Available
Martens				
Aspen	14	10	7	11
Balsam fir	5	4	5	4
Black ash	6	5	10	6
Black spruce	4	4	6	6
Hemlock–cedar	22	12	12	10
Pine	4	3	2	4
Sugar maple	44	59	55	56
Fishers				
Aspen	23	18	18	26
Balsam fir	6	10	5	5
Black ash	12	7	0	5
Black spruce	2	1	5	2
Hemlock–cedar	13	9	14	15
Pine	2	1	4	4
Sugar maple	40	51	53	43

We used a generalized linear mixed model (GLIMMIX procedure in SAS version 9.1) to determine if fine-scale structural habitat data improved our ability to detect forested inclusions that martens and fishers used. We predicted that use of broadscale structural habitat data would more accurately identify large, contiguous areas of structural habitat but would misidentify smaller patches (inclusions). To test this, we determined if the likelihood that a broadscale structural habitat assignment matched a fine-scale structural habitat assignment made in the field varied due to segment length, fine-scale structural habitat, and the interaction of segment length and fine-scale structural habitat. Random effects for individuals were modeled using the variance component covariance structure.

We square-root transformed selection values (after adding 1) calculated using fine-scale structural habitat data to improve normality and homoscedasticity (Ott and Longnecker 2001). We also square-root transformed tortuosity values calculated using both fine-scale and broadscale structural habitat data. Mixed model fit was improved by only including fine-scale structural habitat data from structural habitats with sample sizes $\geq$ 5 segments. For broadscale structural habitat data, we lowered this threshold to include data from structural habitats with sample sizes $\geq$ 3 segments because we wanted to include fisher data that would have otherwise been excluded. The experimentwise error rate (α) was set to 0.05. We controlled for inflation of α when > 1 comparison was made using the same data using Tukey and Bonferroni adjustments, and by following significant Fisher's exact tests with permutation-based post hoc tests (SAS MULTTEST procedure).

RESULTS

Martens.—We captured, collared, and followed paths from 7 (4 females and 3 males) adult resident martens during 2008–2009 and 8 (3 females and 5 males) adult resident martens during 2009–2010. Three resident martens (1 female and 2 males) were studied both seasons. We followed paths from 8 (4 females and 4 males) translocated martens during 2008–2009 and 9 (5 females and 4 males) translocated martens during 2009–2010. One male adult marten was studied after it was translocated in 2008–2009 and as a resident during 2009–2010. We followed marten paths a total of 27,059 m, including 15,891 m on 27 paths (15 females and 12 males) in 2008–2009 and 11,168 m on 20 paths (8 females and 12 males) in 2009–2010. Mean path length was 588 m ($SE \pm 31$ m, $n = 27$) in 2008–2009 and 558 m ($SE \pm 66$ m, $n = 20$) in 2009–2010.

Examination of fine-scale and broadscale structural habitat data indicated that martens used similar amounts of sugar maple, and that sugar maple was used more than other structural habitats (Table 2). Broadscale structural habitat data underestimated use of hemlock–cedar, aspen, and pine. Martens used hemlock–cedar, aspen, and pine about 2 times more often than was detected by using broadscale structural habitat data. Structural habitats other than sugar maple and hemlock–cedar each composed < 15% of the distance we followed martens at either spatial scale.

Fine-scale and broadscale structural habitat data best explained variation in tortuosity and selection when candidate models were evaluated using $\mathrm{AIC_c}$ (Table 3). Fine-scale structural habitat data yielded mean tortuosity and selection indexes that were highest in hemlock–cedar (Figs. 2 and 3). Tortuosity differed by fine-scale structural habitat ($F_{6,96} = 2.60$, $P = 0.022$) and paths were more tortuous in hemlock–cedar than in sugar maple ($t_{96} = -3.20$, Tukey test, $P = 0.030$). Selection also differed by fine-scale structural habitat ($F_{8,137} = 3.11$, $P = 0.003$) and was greater for hemlock–cedar ($t_{137} = 4.46$, Tukey test, $P = 0.001$) and aspen ($t_{137} = 3.34$, Tukey test, $P = 0.029$) than for sugar maple.

TABLE 3.—Results for linear mixed models of tortuosity within structural habitats and selection of structural habitats for American martens (*Martes americana*) in Wisconsin, during the winters of 2008–2009 and 2009–2010. Structural habitats were characterized using fine-scale and broadscale data. AIC_c = Akaike's information criterion values adjusted for small sample sizes; DBH = diameter at breast height.

Model	AIC_c	ΔAIC_c	AIC_c weight
Tortuosity			
Fine scale			
Structural habitat	−197.4	0.0	0.8
Structural habitat × Status[a]	−194.1	3.3	0.2
Structural habitat × Sex × Status	−188.1	9.3	0.0
Structural habitat × Sex	−187.7	9.7	0.0
Structural habitat × DBH × Status	−179.7	17.7	0.0
Structural habitat × DBH	−179.3	18.1	0.0
Structural habitat × DBH × Sex	−160.4	37.0	0.0
Broad scale			
Structural habitat	−109.3	0.0	1.0
Structural habitat × DBH	−98.5	10.8	0.0
Structural habitat × Status	−95.2	14.1	0.0
Structural habitat × Sex	−92.2	17.1	0.0
Structural habitat × DBH × Status	−77.5	31.8	0.0
Structural habitat × Sex × Status	−76.8	32.5	0.0
Selection			
Fine scale			
Structural habitat	−162.2	0.0	1.0
Structural habitat × Status	−150.6	11.6	0.0
Structural habitat × Sex	−140.8	21.4	0.0
Structural habitat × Sex × Status	−117.0	45.2	0.0
Broad scale			
Structural habitat	36.6	0.0	0.6
Structural habitat × Sex × Status	38.5	1.9	0.2
Structural habitat × Status	38.7	2.1	0.2
Structural habitat × Sex	41.7	5.1	0.0

[a] Martens were translocated to the study area the fall prior to the study or were residents that had been present > 1 year.

Broadscale structural habitat data yielded mean tortuosity and selection that was highest in black ash. Tortuosity differed by broadscale structural habitat ($F_{6,40} = 2.44$, $P = 0.042$) but differences were not significant when we accounted for inflation of alpha due to multiple comparisons (Tukey test, $P > 0.05$ for all tests; Fig. 2). Although broadscale structural habitat best explained variation in selection indexes when evaluated using AIC_c, selection did not differ by structural habitat for martens at broad scales ($F_{5,31} = 1.47$, $P = 0.228$). The 3-term interaction model for selection that included broadscale structural habitat, sex, and status was ranked 1.9 AIC_c units lower than the single-factor structural habitat model. Selection did not differ by this interaction when evaluated with F-statistics ($F_{1,3} = 0.54$, $P = 0.516$). All other models for marten selection and tortuosity at either structural habitat scale achieved ΔAIC_c scores > 2 and were not evaluated using F-statistics.

Selection and tortuosity indexes were poorly correlated for martens. Selection explained < 10% of variation in tortuosity when fine-scale structural habitat data were used for analysis ($R^2 = 0.07$, $P = 0.022$, $y = 0.502 + 0.149x$). Correlation between selection and tortuosity also was poor for broadscale structural habitat data ($R^2 = 0.07$, $P = 0.080$, $y = 0.489 + 0.157x$).

We located 38 rest sites and 8 kill sites while following marten paths (Table 4). Kills included 5 small mammals, 1 woodpecker (family Picidae), and 2 ruffed grouse (*Bonasa umbellus*). The number of use sites relative to the expected number differed due to structural habitat (Fisher's exact test, $P = 0.031$). The difference between the number of use sites relative to the expected number was greater in hemlock–cedar than in sugar maple (permutation test, $P = 0.001$), but did not differ between hemlock–cedar and aspen, balsam fir, black spruce, pine, or red maple (permutation test for each comparison, $P > 0.05$). About 4 times more use sites occurred in hemlock–cedar than was expected, whereas 2 times fewer sites occurred in sugar maple. The number of rest sites (Fisher's exact test, $P = 0.130$) or kills (Fisher's exact test, $P = 0.300$) did not differ from expected.

Fishers.—We captured and collared 3 (1 females and 2 males) fishers during 2008–2009 and 7 (4 females and 3 males) during 2009–2010, including 1 male juvenile fisher. We followed paths from 2 fishers (1 female and 1 male) during 2008–2009 and 8 fishers (4 females and 4 males) during 2009–2010, including 1 male fisher collared in 2008–2009. We followed fisher paths for a total of 9,791 m, including 4,291 m on 10 paths (6 females and 4 males) in 2008–2009 and 5,500 m on 9 paths (5 females and 4 males) in 2009–2010. Mean path

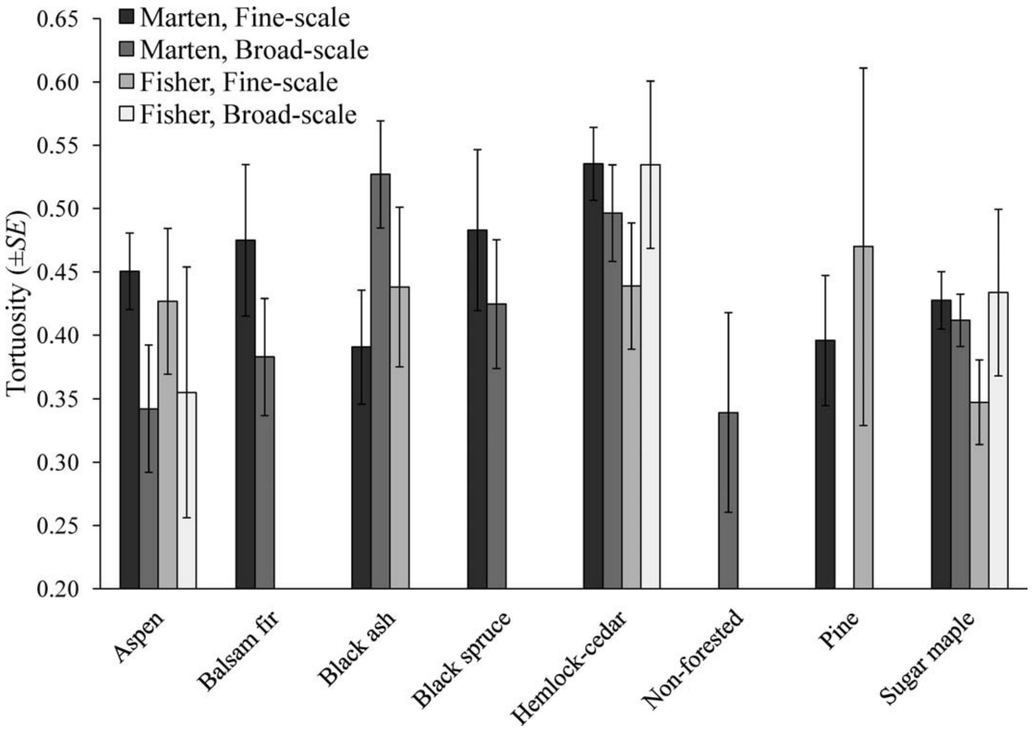

FIG. 2.—Tortuosity of movement paths left by American martens (*Martes americana*) and fishers (*Pekania pennanti*) under structural habitats measured at 2 spatial scales in northern Wisconsin, during the winters of 2008–2009 and 2009–2010. Marten path tortuosity was highest in fine-scale hemlock–cedar, but did not differ between broadscale structural habitats. Fisher path tortuosity did not differ for fine-scale and broadscale structural habitats.

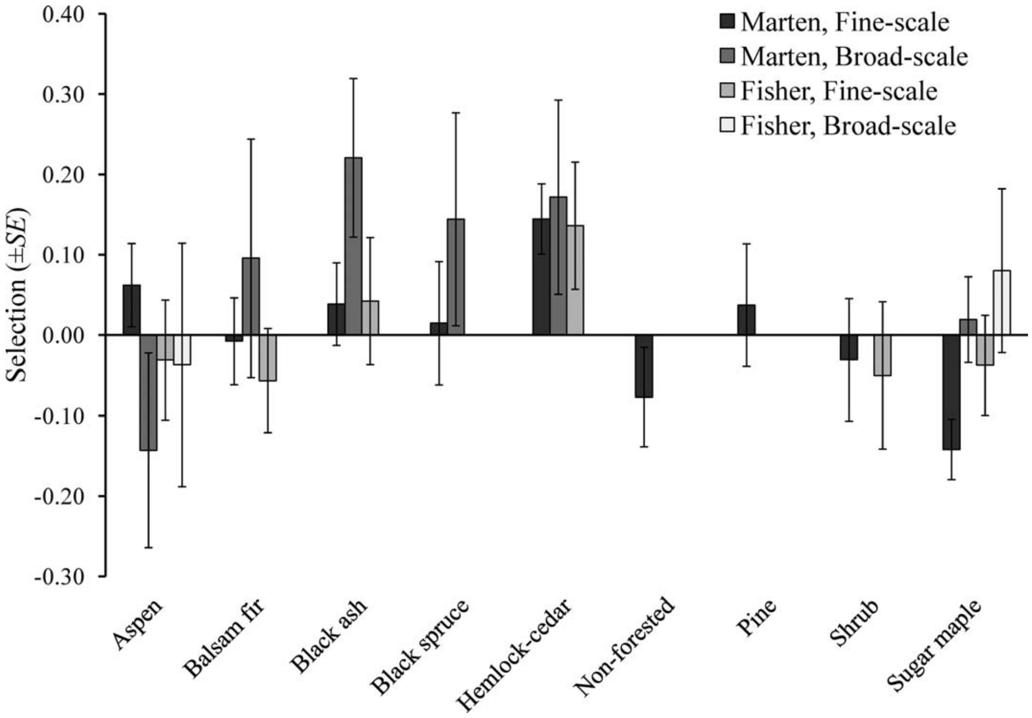

FIG. 3.—Selection of structural habitats by American martens (*Martes americana*) and fishers (*Pekania pennanti*) measured at 2 spatial scales in northern Wisconsin, during the winters of 2008–2009 and 2009–2010. Higher selection values indicate greater use relative to availability. Marten structural habitat selection was highest in fine-scale hemlock–cedar, but did not differ between broadscale structural habitats. Fisher structural habitat selection did not differ for fine-scale and broadscale structural habitats.

Table 4.—Observed and expected number of use sites (sum of rest and kill sites) on American marten (*Martes americana*) and fisher (*Pekania pennanti*) paths in Wisconsin, during the winters of 2008–2009 and 2009–2010.

	Marten use sites		Fisher use sites	
Structural habitat	Observed	Expected	Observed	Expected
Aspen	4	5	1	5
Balsam fir	2	2	1	3
Black ash	4	2	3	2
Black spruce	2	2	0	0
Hemlock–cedar	18	5	10	2
Nonforested	0	1	0	0
Pine	2	2	0	0
Shrub	0	0	0	1
Sugar maple	14	27	8	10

length was 429 m (*SE* ± 75 m, $n = 10$) in 2008–2009 and 611 m (*SE* ± 99 m, $n = 9$) in 2009–2010.

Examination of both fine-scale and broadscale structural habitat data indicated that fishers used sugar maple more than other structural habitats (Table 2). About 20% of the distance traveled by fishers was in aspen when measured using fine-scale and broadscale structural habitat data. Other structural habitats each composed < 15% of paths used by fishers.

Fine-scale and broadscale structural habitat data best explained variation in tortuosity and selection when candidate models were evaluated using $\mathrm{AIC_c}$ (Table 5). Structural habitat, however, did not explain variation in tortuosity or selection at either scale (tortuosity, fine-scale: $F_{4,26} = 1.06$, $P = 0.394$, and tortuosity, broadscale: $F_{2,2} = 3.66$, $P = 0.215$; Fig. 2; selection, fine-scale: $F_{5,42} = 0.86$, $P = 0.519$, and selection, broadscale, $F_{1,3} = 0.54$, $P = 0.516$; Fig. 3). Four of 6, and 3 of 5, structural habitats present at fine scales were not detected when using broadscale data for selection and tortuosity analyses, precluding computations for those structural habitats at broad scales (Figs. 2 and 3). All other models for fisher selection and tortuosity at either spatial scale yielded $\Delta\mathrm{AIC_c}$ scores ≥ 4.2 and were not evaluated using F-statistics.

Selection and tortuosity indexes were poorly correlated for fishers. Selection explained < 10% of variation in tortuosity when fine-scale structural habitat data were used during analysis ($R^2 = 0.07$, $P = 0.181$, $y = 0.358 + 0.260x$). Less than 20% of variation in tortuosity was explained by broadscale structural habitat selection ($R^2 = 0.17$, $P = 0.591$, $y = 0.203 + 0.419x$), although small sample size (4 points used to develop the regression) limits inference from broadscale linear regression analysis for fishers.

We located 15 rest sites and 8 kills while following fisher paths (Table 4). Prey items included 6 small mammals, 1 snowshoe hare (*Lepus americanus*), and 1 woodpecker. The number of use sites relative to the expected number differed due to structural habitat (Fisher's exact test, $P = 0.045$). The difference between the number of use sites and the expected number of use sites was greater in hemlock–cedar than in sugar

Table 5.—Results for mixed models of tortuosity within structural habitats and selection of structural habitats for fishers (*Pekania pennanti*) in northern Wisconsin, during the winters of 2008–2009 and 2009–2010. Structural habitats were characterized using fine-scale and broadscale data. $\mathrm{AIC_c}$ = Akaike's information criterion values adjusted for small sample sizes; DBH = diameter at breast height.

Model	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	$\mathrm{AIC_c}$ weight
Tortuosity			
Fine scale			
Structural habitat	−41.7	0.0	0.9
Structural habitat × Sex	−36.0	5.7	0.1
Structural habitat × DBH	−30.0	11.7	0.0
Structural habitat × DBH × Sex	−24.9	16.8	0.0
Broad scale			
Structural habitat	−6.7	0.0	1.0
Structural habitat × DBH	9.9	16.6	0.0
Structural habitat × Sex	20.4	27.1	0.0
Selection			
Fine scale			
Structural habitat	−67.5	0.0	1.0
Structural habitat × Sex	−52.5	15.0	0.0
Broad scale			
Structural habitat	8.2	0	1.0
Structural habitat × Sex	41.7	33.5	0.0

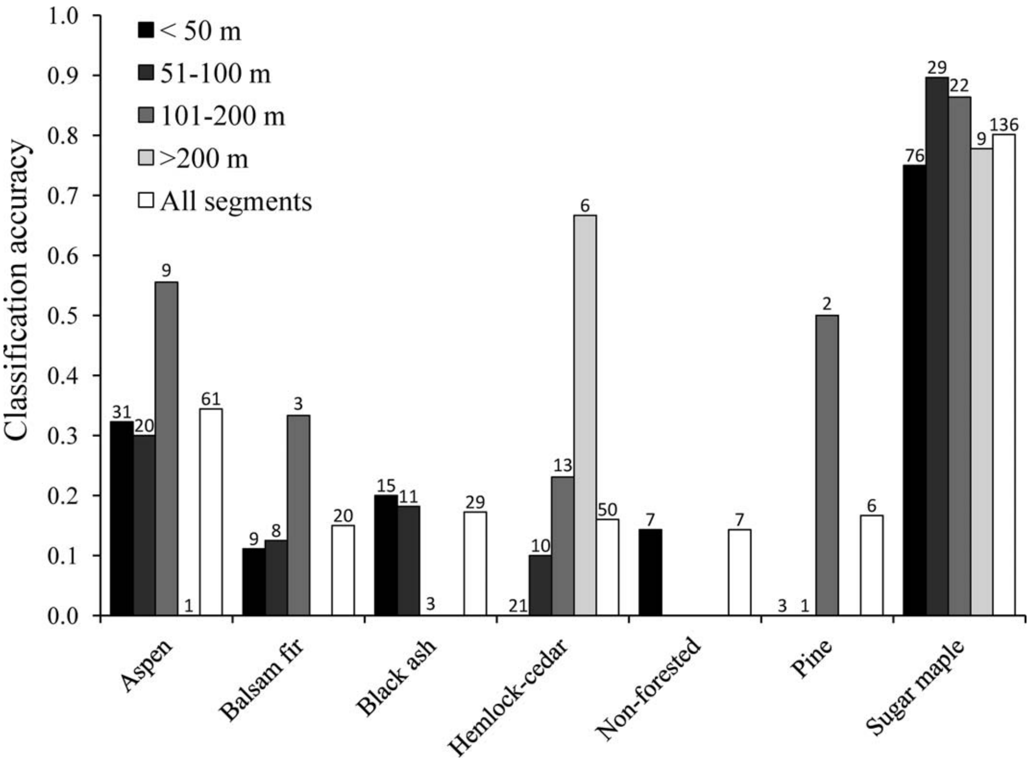

FIG. 4.—Accuracy with which broadscale structural habitat data identified forest types present along American marten (*Martes americana*) and fisher (*Pekania pennanti*) paths in northern Wisconsin, during the winters of 2008–2009 and 2009–2010. Accuracy was determined by comparing broadscale classifications to those recorded in the field. Numbers above bars equal the number of path segments of each length, and of all lengths combined.

maple (permutation test, $P = 0.040$) and aspen ($P = 0.012$), but did not differ between hemlock–cedar and balsam fir or red maple (permutation test, $P > 0.05$ for each comparison). We detected about 6 times more use sites in hemlock–cedar than was expected and 5 times fewer in aspen than was expected. The proportion of use sites that we detected in sugar maple was similar to expected. The number of rest sites (Fisher's exact test, $P = 0.124$) or kills (Fisher's exact test, $P = 0.334$) did not differ from the number expected.

Detection of inclusions along marten and fisher paths.—Broadscale structural habitat data matched fine-scale classifications poorly. Structural habitat segments that we identified in the field along marten and fisher paths only matched broadscale classifications on 148 (48%) of 309 occasions (Fig. 4). Our ability to identify structural habitats correctly using broadscale structural habitat data depended on the habitat type and area. The interaction of structural habitat type and path segment length (an index for area) affected the likelihood that broadscale data classifications matched those made in the field ($F_{6,278} = 2.61$, $P = 0.018$; Fig. 4). Classification accuracy was positively correlated with segment length for hemlock–cedar (odds ratio for a 1-m increase of segment length in hemlock–cedar: 1.020, 95% confidence limits 1.008, 1.032), but classification accuracy for other structural habitats was independent of segment length (odds ratio 95% confidence limits bounded 0 for all other structural habitats).

Hemlock–cedar inclusions used by martens and fishers were typically small and omitted by broadscale data. Of the 50 segments in hemlock–cedar, 31 (62%) were ≤ 100 m, and all but 1 were misclassified using broadscale data, including all 21 segments that were < 50 m. Classification of hemlock–cedar was more accurate for segments > 200 m, where 4 (67%) of 6 segments were classified correctly. Broadscale data misclassified 27 (64%) hemlock–cedar segments as sugar maple, 8 (19%) as black ash, 4 (10%) as aspen, 2 (5%) as black spruce, and 1 (2%) as nonforested.

DISCUSSION

Our results indicate that caution should be used when employing broadscale data to identify required habitat for mammalian predators because broadscale data can bias the match between functional and structural habitat. Broadscale structural habitat data were a poor match with functional habitat for martens because broadscale maps reduced map complexity, which caused omission of hemlock–cedar inclusions (often < 0.5 ha) that martens used for rest sites and hunting. Broadscale data are often the only type of data available to researchers and managers, are valuable for identifying structural habitat selection and predicting the location of suitable habitat (Guissan and Thuiller 2005; McCann and Moen 2011), and accurately detected the dominant structural habitat type (sugar maple) that martens and fishers did not select. Our results demonstrate, however, that broadscale data will identify structural habitat associated with required types rather than required habitat itself when functional habitat corresponds with landscape features such as inclusions that broadscale maps omit.

Associations between functional and structural habitat that we did not detect using broadscale data were identified using fine-scale data. Although we did not detect structural habitat selection for martens using broadscale data, we detected selection of hemlock–cedar as structural habitat by pairing fine-scale location and structural habitat data that better represented structural habitat heterogeneity. Hemlock-cedar also was where martens located functional habitat disproportionately, which demonstrates that fine-scale data improve the match between structural and functional habitat. Other marten studies in Wisconsin that used broadscale structural habitat and telemetry location data did not detect selection of hemlock and cedar (Wright 1999; Dumyahn et al. 2007). Although selection order differed between studies, telemetry location error was up to 40 times larger than many inclusions used by martens (20 ha—Dumyahn et al. 2007), making it unlikely that telemetry locations would have been plotted within hemlock–cedar inclusions regardless of the spatial scale of structural habitat data. Detection of hemlock–cedar was improved by fine-scale data, which likely explains why we detected selection of hemlock–cedar whereas other studies did not.

Structural habitat selection was an incomplete match with functional habitat. Hemlock–cedar was functional habitat for martens and fishers, but we detected about 60% of marten and fisher use sites in other structural habitats and we did not detect selection of hemlock–cedar as structural habitat by fishers. For fishers, small sample size (19 paths) could explain why we did not detect selection of structural habitats and thus the mismatch between structural and functional habitat. Fishers hunt porcupines in open hardwood forests during winter (Powell 1979, 1994) and porcupine quills were attached to fishers we captured, but we did not detect porcupine kills along fisher paths, indicating that our kill data underestimated the importance of hardwoods for hunting porcupines. For martens and fishers, the mismatch between structural and functional habitat can be explained by supplementation (sensu Dunning et al. 1992); use of hemlock–cedar was supplemented by use of other structural habitats. Lastly, the mismatch can be explained by how we defined functional habitat. We restricted the definition of functional habitat to areas where we detected rest and kill sites. Areas used for traveling would be functional habitat if they provided cover from predators, reduced the cost of locomotion through snow, and increased occupancy (irrespective of the presence of kill and rest sites). Our definition of functional habitat was biased if functional habitat included areas where martens and fishers traveled but did not kill prey and rest.

Further consideration should be given to extending the concept of habitat selection to include tortuosity. Martens and fishers moved along both tortuous and linear paths in selected structural habitat, indicating that cues other than structural habitat influenced movement behavior. Patterns of movement can be affected by multiple factors. Past experience can lead predators to move linearly toward areas where they have detected prey (Powell 1994) and to leave an area where resources have been depressed (Charnov et al. 1976; Amano and Katayama 2009). Movement patterns also are influenced by resource distribution (Wiens et al. 1997; Zollner and Lima 1999) and predators (Fortin et al. 2005), and by nonvegetative habitat features that improve hunting success (Andruskiw et al. 2008). These factors and others may explain why structural habitat selection did not correspond well with path tortuosity for martens and fishers and could influence the relationship between selection and tortuosity for other animals.

Within-stand structural habitat heterogeneity is important to martens and fishers, especially when heterogeneity includes pockets of mature conifers within primarily deciduous forests. Mature forest conditions are important to martens and fishers because large-diameter trees and dead and down woody material provide access to prey and rest sites (Sherburne and Bissonette 1994; Gilbert et al. 1997) and offer thermoregulatory benefits during winter (Taylor and Buskirk 1994; Weir et al. 2005). Martens and fishers located mature conditions in hemlock–cedar areas, which have been typically left uncut during logging in Wisconsin. Nearly closed canopies also occurred in hemlock–cedar, which provided protection from raptors that kill martens (Hargis and McCullough 1984; McCann et al. 2010). Managers should retain pockets of $>$ 23-cm-DBH hemlock–cedar and manage areas surrounding them for mature forest conditions in Wisconsin. In primarily deciduous forests outside of Wisconsin and the range of hemlock and cedar, fine-scale data will be needed to determine if inclusions composed of other coniferous species are required habitat for martens and fishers.

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