Movement paths reveal scale-dependent habitat decisions by Canada lynx

Authors: Fuller, Angela K., and Harrison, Daniel J.

Source: Journal of Mammalogy, 91(5) : 1269-1279

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/10-MAMM-A-005.1

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Mammalogy on 19 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Journal of Mammalogy, 91(5):1269–1279, 2010

Movement paths reveal scale-dependent habitat decisions by Canada lynx

ANGELA K. FULLER* AND DANIEL J. HARRISON

Department of Wildlife Ecology, University of Maine, Orono, ME 04469, USA (AKF, DJH)
Present address of AKF: United States Geological Survey, New York Cooperative Fish and Wildlife Research Unit and Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA

* *Correspondent: angela.fuller@cornell.edu*

We documented the relative grain at which Canada lynx (*Lynx canadensis*) perceive habitat heterogeneity using fractal dimension of foraging paths. We evaluated whether lynx expended greater foraging effort (i.e., greater fractal dimension of movement paths) in patches with the highest density of snowshoe hares (*Lepus americanus*), or in patches with intermediate densities of prey where lower stem densities and greater visibility promote increased mobility and access to prey. Lynx foraged within patches with intermediate to high hare density and intermediate cover for hares, and thus, attempted to maximize access to prey rather than exposure to habitats with highest prey density but optimal escape cover. Fractal dimension of movement paths was greater within preferred than in nonpreferred habitats and corresponded with higher foraging success in preferred habitats. Movement paths were more tortuous at broader than finer scales, suggesting that lynx were exhibiting stronger coarse-grained than fine-grained habitat preferences. Higher fractal dimension of movement paths reduced the number of transitions between patches of higher and lower foraging quality, resulting in individual movement patterns matching the scale of interpatch variation in hare abundance and accessibility within home ranges. Lynx made their strongest foraging decisions when exhibiting higher-order resource selection, so focusing conservation efforts to alter within-patch structure may be less effective than creating patch- and landscape-scale conditions that enhance foraging success. Coarse-grained resource selection by wide-ranging carnivores may reduce the importance of fine-scale conservation efforts and emphasizes the importance of focusing conservation for these coarse-grained species on factors influencing home-range quality and maintenance of viable landscapes. DOI: 10.1644/10-MAMM-A-005.1.

Key words: Canada lynx, fractal dimension, habitat, *Lepus americanus*, lynx, *Lynx canadensis*, movement, patch, snowshoe hare, tortuosity

Spatial processes in predator–prey systems can be influenced greatly by behaviors (Bergman et al. 2006) such as complex movement of predators while foraging and traveling within and between patches. Movement decisions are affected by availability, distribution, detectability, and vulnerability of prey; thus, quantification of spatial decision-making by predators can enhance understanding of habitat choices and predator–prey interactions (Swingland and Greenwood 1983). Evaluation of path tortuosity of individual animals has been used to interpret intraspecific perceptions of landscapes (Crist et al. 1992; With 1994), where the complexity of movement paths relates to the frequency of encountering resources (Sugihara and May 1990) and energy investment (Bascompte and Vilà 1997).

Fractal dimension quantifies path tortuousity for continuous movement paths and derives values of 1 when paths are straight to a maximum of 2 when a path is so tortuous as to completely cover a plane (Nams and Bourgeois 2004). Recent studies have used fractal dimension to provide unique insights into habitat (Newbury and Nelson 2007; Phillips et al. 2004; Saeki et al. 2007; Webb et al. 2009), gender (Webb et al. 2009), prey (Newbury and Nelson 2007), and scalar effects (Webb et al. 2009) on movement paths of wide-ranging mammals using consecutive telemetry fixes. However, these studies did not evaluate fine-scale movement behaviors because of imprecision caused by both time elapsed between consecutive fixes and inherent telemetry errors. Recent advances in spatial technologies (e.g., continuous-sampling global positioning systems [GPSs]) have aided quantification and have reduced the scale at which movement behaviors can be analyzed. However, collecting continuous movement data with the spatial precision needed to evaluate fine-scale movement decisions and interactions of movement paths with fine-scale vegetation and physical structures remains extremely time- and logistically intensive (e.g., documenting actual movement paths via backtracking on snow). Thus, such applications are uncommon for vagile species that interact with habitat and prey across multiple spatial scales.

Movement paths are influenced by the type and heterogeneity of habitat, and an analysis of path tortuosity in different habitat types can provide insights into fine-scale patterns of habitat choice (Phillips et al. 2004; Saeki et al. 2007; Webb et al. 2009; With 1994). Straight-line travel generally is associated with movement behaviors such as maintenance of territory, seeking mates, moving between patches within the home range, or dispersal, whereas tortuous paths are often indicative of active foraging (Arditi and Dacorogna 1988; Parker 1980). Therefore, area-restricted foraging (Tinbergen et al. 1967) for prey should increase foraging intensity in preferred habitats and result in higher path tortuosity (Nams and Bourgeois 2004; Phillips et al. 2004; Saeki et al. 2007).

Movement paths of animals have been evaluated with a variety of methods, including correlated random walks (Bergman et al. 2000; McCulloch and Cain 1989), tortuosity indices (Benhamou 2004; Wells et al. 2006), sinuosity indices (Maletzke et al. 2008), and fractal dimensions (Doerr and Doerr 2004; Mandelbrot 1967; Nams and Bourgeois 2004; Phillips et al. 2004; Saeki et al. 2007; With 1994). Those approaches have been used to characterize how animals perceive and respond to spatial heterogeneity. Specifically, fractal dimension can be an appropriate measure of path tortuosity when movement patterns deviate from the null model of a correlated random walk (Nams and Bourgeois 2004). Turchin (1996), however, criticized fractals as a scale-independent tool for analyzing tortuosity after rejecting the assumption that organisms are scale invariant with respect to their movement paths. Despite those published shortcomings, fractal dimensions have unique applications for defining transitions between domains of scale (Nams and Bourgeois 2004; Webb et al. 2009; Wiens 1989) and using those transitions to indicate that a different process (e.g., a change in movement decisions by a foraging animal in response to vegetation pattern) is predominant (Wiens 1989). Fractal dimension (D) of movement paths is expected to increase with scale, but a significant change in the slope of the relationship across a small change in scale can indicate the point at which movement behaviors transition from one scale to another (Nams and Bourgeois 2004). By combining the scale of transitions in D with information about the scale of changes in habitat quality (e.g., scale of changes in prey density or preferred versus avoided patches), unique insights into scale-specific movement decisions can be gained. Thus, the utility for determining the spatial scales where movement behaviors change is a unique advantage of fractals over other techniques for analyzing movement paths (Webb et al. 2009), and fractals have unique potential to enhance understanding of finer-scale processes in habitat selection for vagile species such as lynx that exhibit coarse-grained habitat selection at regional (Hoving et al. 2005), landscape (Hoving et al. 2004), and forest-stand scales (Fuller et al. 2007; Poole et al. 1996).

Documenting changes in the scale at which organisms perceive and respond to habitat heterogeneity (i.e., statistical transitions in D with scale) also reflects the grain (Kotliar and Wiens 1990) that is ecologically appropriate for species-level management. Finally, fractals have proven useful for comparing tortuosity across patch types within a standardized range of spatial scales (Doerr and Doerr 2004), and thus are useful for interpreting whether animals are attempting to minimize or maximize their exposure (as indexed by D) to a patch type relative to other types within a particular scale of consideration where statistical self-similarity of patterns (i.e., a constant slope of D versus scale) exists (Wiens 1989).

The foraging behavior of Canada lynx (*Lynx canadensis*) and their movement patterns are largely influenced by their strategies to pursue snowshoe hares, *Lepus americanus* (Mowat et al. 2000; Parker 1980) and are predicted to respond to the fine-scale habitat choices of hares (Mowat and Slough 2003). Lynx exhibit strong selection among forest stand types available within their territories, which are closely associated with patches that contain intermediate to high densities of hares (Fuller et al. 2007; Mowat et al. 2000). High densities of hares are associated with dense understories of woody saplings (Keith et al. 1984; Litvaitis et al. 1985), and Mowat and Slough (2003) reported that habitat quality for lynx is similarly dependent on dense understory woody vegetation. However, Fuller et al. (2007) presented evidence suggesting that lynx selected against stand types within home ranges where hare densities were highest. Areas of highest hare density were characterized by optimal escape and concealment cover provided by dense woody understory structure. Similarly, recent studies with African felids have reported higher preferences for habitats that provide greater access to prey relative to habitats with highest prey abundances (Balme et al. 2007; Hopcraft et al. 2005). Thus, we hypothesized that lynx would exhibit greater path tortuosity and foraging success in preferred patches (Fuller et al. 2007) across a standardized range of spatial scales encountered during a single day of foraging.

Our first objective was to evaluate whether fractal dimension of movement paths was indicative of within-stand scale habitat choices by lynx. We analyzed paths of lynx during the limiting winter season to evaluate differences in path tortuosity and foraging success among habitat types that were documented as preferred (i.e., selected positively) versus nonpreferred (i.e., avoided) during a companion study (Fuller et al. 2007). Our second objective was to evaluate whether solitary male lynx exhibited less tortuous paths than females traveling with dependent kittens resulting from reduced energy requirements, larger home-range area, and higher territorial maintenance costs of males (Sandell 1989). Our third objective was to determine whether a discontinuity in scale

Table 1.—Patch-type classification used in lynx movement analyses, northwestern Maine.

Patch type	Code	Description
Mature forest	Mature	Mature, >40 years postharvest, coniferous, deciduous, and mixed coniferous–deciduous forest, dense to closed canopy (>50%), dominant trees >12-m height
Recent partial harvest	RecentPH	1–10 years postharvest, deciduous (74%), mixed coniferous–deciduous (18%), and coniferous (8%) dominated overstory
Established partial harvest	EstablishedPH	11–21 years postharvest, deciduous (56%), mixed coniferous–deciduous (36%), and coniferous (8%) dominated overstory
Short regenerating clear-cut	RegenShort	3.4–4.3 m tall, 11–26 years postharvest, coniferous (71%), mixed coniferous–deciduous (29%), and deciduous (<1%) dominated regeneration
Tall regenerating clear-cut	RegenTall	4.4–7.3 m tall, 11–26 years postharvest, mixed coniferous–deciduous (58%), deciduous (22%), and coniferous (20%) dominated regeneration
Road and road edge	RoadEdge	30-m buffer on both sides of roads (unpaved and unplowed logging roads with only off-road vehicle access during winter)

existed in the fractal dimension of movement paths of lynx, and if this domain of scale coincided with transitions from within- to between-patch processes in our landscape. Our fourth objective was to evaluate which within-patch scale habitat variables best differentiated between lynx paths and randomly located paths within the home ranges of lynx.

Materials and Methods

Study area.—The study area included parts of 9 townships in northwestern Maine (T10 R10-11 WELS, T11 R10-13 WELS, T12 R11-13 WELS) with elevations of 244–536 m. Average snow depth measured during January–March was 45 cm in 2002 and 65 cm in 2003. The townships were managed intensively for pulpwood and saw timber, resulting in 81% of the forested area having been harvested in the 26 years before the study. The resulting landscape was a mosaic of regenerating stands characterized by complex understory structure and high hare densities, interspersed with mature, partially harvested, and recently cut stands with less understory structure and lower hare densities (Fuller and Harrison 2005; Fuller et al. 2007; Robinson 2006).

Dominant species in mature deciduous stands included red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), paper birch (*Betula papyrifera*), and yellow birch (*Betula alleghaniensis*). Mature coniferous forests were composed of balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and white pine (*Pinus strobus*). Forests regenerating from clear-cutting were composed primarily of dense stands of balsam fir, red spruce, red maple, and paper birch saplings, interspersed with raspberry (*Rubus* sp.) thickets.

Patch types on the study area included mature forest, short regenerating conifer-dominated clear-cuts (RegenShort), tall regenerating clear-cuts (RegenTall), recent partially harvested patches (RecentPH), established partially harvested patches (EstablishedPH), and road edge (30-m buffer on both sides of road; Table 1). Habitat selection by lynx among these 6 patch types was described by Fuller et al. (2007).

Snowtracking.—We first verified the location of a lynx using radiotelemetry, walked to its location on snowshoes until the track was intersected, began backtracking, and subsequently measured vegetation and continuously recorded the track location using continuous real-time GPS sampling (Trimble Pro XR®, Trimble Navigation Limited, Sunnyvale, California) with <1-m accuracy. The movement path was recorded directly over the snow tracks of the lynx, and a GPS point was recorded every 4 s and at every discernable turn. The maximum straight-line distance between any 2 GPS points on the lynx movement path was 4 m. The distance that lynx followed the trails of snowshoe hares also was recorded, and the location of snowshoe hares killed by lynx was spatially verified. We calculated the expected number of snowshoe hare kills in preferred and nonpreferred habitats (Fuller et al. 2007), on the basis of the total percentage of preferred and nonpreferred habitats in the home range of each lynx (i.e., total kills × percentage of a habitat type in home range = expected kills). We summed the observed and expected kills across all lynx and tested whether the observed distribution fit the expected distribution using a chi-square test with Yate's correction for continuity (Zar 1999). Following trails of snowshoe hares has been documented as a hunting technique for lynx because of its potential to increase encounter rates (Brand et al. 1976); therefore, we also recorded the total distance that lynx followed the trails of hares. Methods for lynx capture, radiocollaring, radiotelemetry, and home-range estimation are described in Fuller et al. (2007).

Vegetation sampling.—Vegetation was measured on random straight-line transects that were placed in a stratified random design within the 90% fixed kernel home ranges of each focal lynx. These measurements were compared with those collected along actual movement paths of lynx. The starting point and direction of each 1-km-long transect was chosen randomly, with the constraint that all patch types were sampled proportionally relative to the composition of forest stands occurring within home ranges of lynx. We sampled random transects either when it was snowing or when >48 h had elapsed since the last snowfall.

Habitat variables measured along actual lynx trails and along random transects were chosen to represent the within-patch scale vegetation structure that we hypothesized would influence local abundance of snowshoe hares and lynx. We measured density of deciduous and coniferous saplings and used those values to calculate stem cover units (SCU = 3 × coniferous saplings + deciduous saplings), which is a measure of understory structure that accounts for greater visual obstruction and protection from convective and radiational heat loss provided by softwood stems; thus, high values indicate greater thermal and predator escape cover for hares (Litvaitis et al. 1985). We also measured basal area (BA; m^2/ha) of trees >7.6 cm diameter at breast height (dbh), overhead canopy closure (CC), and the percentage of the surveyed lynx path or random transect that occurred within skid trails (SKID) from previous logging operations. SCU and CC were the 2 variables that best predicted within-stand indices of abundances (i.e., pellet densities) for snowshoe hares in Maine (Fuller 2006). BA was measured because it indexes the level of stand maturity. SKID was used to index the ease at which lynx could travel through a stand without encountering dense understory vegetation structure. We measured vegetation in 2-m × 6-m plots spaced every 100 m along lynx paths and at 100-m intervals along randomly oriented 1-km transects distributed throughout the home range of each lynx. We measured CC with a spherical densitometer and averaged readings from the 4 cardinal compass directions. We measured BA of live coniferous and deciduous trees (m^2/ha) using a 2-factor wedge prism. We counted all deciduous and coniferous saplings (<7.6 cm in diameter, stems protruding through snowpack), which were used in calculating SCU. We also measured snow depth at the center of each plot and calculated relative snow depth (SNOWR) by subtracting the snow depth measured on random transects from the average snow depth calculated on lynx paths during 2-week intervals beginning 10–23 January and ending 21 March–3 April. Positive SNOWR indicates that snow depth on lynx paths exceeded depth on random transects. The 2-week averages were calculated separately for lynx monitored in 2002 and 2003.

Fractal analysis.—Movement paths were first tested for their fit to a correlated random walk (CRW) model (Kareiva and Shigesada 1983). We used program FRACTAL 5.00 (V. O. Nams, pers. comm.) to calculate $\mathrm{CRW}_{\mathrm{diff}}$ (Nams 2006) for males and females separately. We tested for a significant deviation from a CRW as the mean difference between observed and expected net distance squared, and conducted fractal analyses only when the null hypothesis of a CRW was rejected. We calculated fractal dimensions along continuous movement paths of lynx using a modification (Nams 2005) of the divider method (Sugihara and May 1990) and using the fractal mean estimator in the program FRACTAL 4.00 (V. O. Nams, pers. comm.).

Does fractal analysis reflect habitat selection decisions?—Following the methods of Phillips et al. (2004), we compared tortuosity of lynx movement paths between patch types that were preferred and nonpreferred by lynx at the stand scale. We calculated D for each path segment by analyzing D over the same range (4–50 m) of spatial scales (Doerr and Doerr 2004). The minimum scale represented the lowest resolution of the data, which was the maximum distance between any 2 GPS points along the movement paths (4 m). The upper limit of scale was set by finding the distance that represented approximately 75% of all path lengths in each patch type, so as to not overrepresent the longest path lengths. We then used one-third of that distance (With 1994) to arrive at the maximum scale of 50 m for our analyses of D in relation to patch type. Minimum segment length used to calculate D within a patch type was 100 m. We analyzed the influence of sex, patch type, and a sex-by-patch-type interaction term on fractal dimension values with an analysis of variance (ANOVA) using a log $(D - 1)$ transformation to meet assumptions of normality. Patch types used in the ANOVA were those preferred within home ranges (RegenTall and EstablishedPH) and types nonpreferred (D pooled across types) by lynx (RegenShort, RecentPH, Mature, and RoadEdge) during a companion study (Fuller et al. 2007). Previous papers (Nams and Bourgeois 2004; Phillips et al. 2004) have used the path segment as the unit of replication for comparing fractals across patch types, despite potential inflation of type I errors if tortuosity is autocorrelated spatially across patches. To reduce potential effects of spatial autocorrelation we used the mean D across all path segments that occurred within a particular patch type traversed by a lynx during a single sampling day as the unit of replication.

Gender differences in fractal dimension and habitat selection.—To test our prediction that males would exhibit less tortuous movement paths than females, we compared D across all 60 daily movement paths using a 2-way ANOVA (Zar 1999) that evaluated effects of gender, habitat (preferred versus nonpreferred), and a habitat × gender interaction. We were also interested in whether larger-bodied males and smaller females (Quinn and Parker 1987) responded differently to snow depth by comparing the snow depths along lynx paths to the snow depths observed along random transects (SNOWR). We evaluated if SNOWR differed from zero for males and females using Wilcoxon signed-rank tests (Zar 1999) using the daily foraging path as the unit of replication and evaluated sex-specific differences in SNOWR using a Mann–Whitney U-test (Zar 1999). Finally, we compared whether females exhibited greater foraging investment than males by devoting a greater percentage of their movement paths to foraging within the trails of snowshoe hares (HARETRAIL) using a Mann–Whitney U-test (Zar 1999).

Domains of scale.—To analyze whether lynx perceived habitat at 2 different domains of scale coinciding with within-patch (i.e., 4th-order) and among-patch (3rd-order) patterns of habitat selection (Johnson 1980), we analyzed plots of D versus spatial scale (Doerr and Doerr 2004; Nams and Bourgeois 2004; Westcott and Graham 2000). Nams and Bourgeois (2004) indicated that identifying a discrete break in a plot of D versus spatial scale represents a transition between domains of scale. If lynx were responding to finer-grained structural features within patches, we predicted that a change in the slope of D with spatial scale would occur at scales smaller than the average distance between preferred and

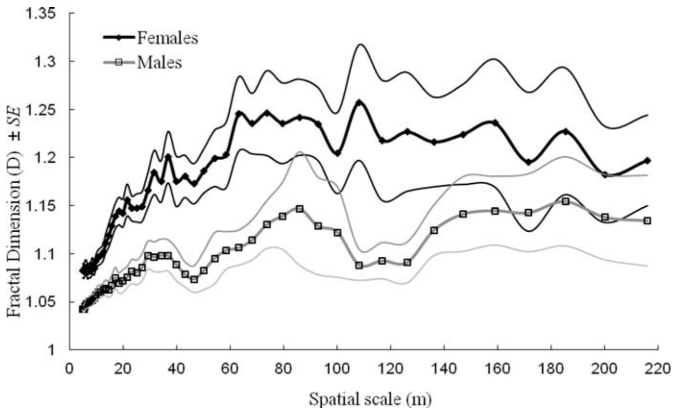

FIG. 1.—Fractal dimension (*D*) ± *SE* of movement paths during winter for female ($n = 30$ paths) and male ($n = 30$ paths) Canada lynx across a range of spatial scales.

nonpreferred patch types (Fuller et al. 2007) within lynx home ranges. To the contrary, if lynx were exhibiting coarser-grained selection for different patch (e.g., forest stands) types within their home ranges, we predicted that a change in *D* would occur at broader scales associated with average distances between preferred and nonpreferred patches. Our rationale was similar to that of Webb et al. (2009), who observed that movement patterns of white-tailed deer (*Odocoileus virginianus*) changed as path lengths approximated the size of habitat patches. We calculated the distance between preferred and nonpreferred patches by averaging the distance between random points (100/ha) in preferred patches (established partial harvests and tall regenerating clear-cuts) within home ranges to the nearest edge of nonpreferred patches (mature stands, short regenerating clear-cuts, recent partial harvests, road edge) and compared those distances with the scale of transitions in behavioral decisions as indicated by significant changes in the slope of *D* versus scale (Nams and Bourgeois 2004).

Patterns of fractal dimension with spatial scale were relatively consistent among individuals (Fig. 1) but varied between sexes (see ''Results''). Given that we were not interested in how individuals perceived scale but rather how *D* varied across spatial scales for male and female lynx, we evaluated sex-specific break points in the slope of *D* by pooling across all lynx in each gender. We estimated *D* at 50 equally (log) spaced spatial scales ranging from 4 to 272 m, representing a range that was greater than the sampling precision of our data and less than one-third the maximum path length. The resulting minimum path length used in our analyses was 500 m. We used piecewise regression (Neter et al. 1996) to fit 2 lines to different portions of the data, with a break point that resulted in the best fit for both lines. We chose to fit 2 lines because we were interested in determining if lynx respond to spatial structure of vegetation at finer scales within patches or across coarser scales while moving between different patch types. A linear *x*-axis was used because we assumed that energy expenditure and distance required to travel between adjacent patches would scale linearly.

Vegetation and structure: lynx movement paths versus random transects.—To evaluate how habitat and physical structure within stands could be influencing selection along actual movement paths, we used an information theoretic approach based on Kullback–Leibler (K-L) information to rank 6 a priori logistic regression models that considered understory stem density, CC, BA, and SKID on movement paths versus straight random transects distributed representatively throughout the home ranges of each lynx. Models were structured on the basis of variables hypothesized to influence either prey density or ease of mobility and access to prey to provide additional insights into how lynx were selecting movement paths within their home ranges.

We computed Akaike information criterion (AIC) values and Akaike weights (w_i), and inferences were made from these models following the guidelines of Burnham and Anderson (2002). We calculated the second-order AIC for small sample size, $\mathrm{AIC_c}$, using the residual sum of squares from least-squares models (Burnham and Anderson 2002). Values of $\Delta\mathrm{AIC_c}$ from 0–2 were considered to have substantial support as being the K-L best model (Burnham and Anderson 2002). We also calculated the likelihood of the model $[\exp(-\frac{1}{2}\Delta_i)]$ to determine the relative strength of evidence for each model. All variables were examined for pairwise correlation and were retained if $r < |0.95|$ (Burnham and Anderson 2002).

Models that supported the prey density hypothesis included variables associated with abundance of snowshoe hares. Variables (Tables 2 and 3) included SCU (positively associated with hare density—Litvaitis et al. 1985) and CC (negatively associated with SCU and with hare density—Fuller 2006). For the lynx mobility and prey access hypothesis we considered models (Table 3) hypothesized to influence the ability of lynx to move through habitat patches and to enhance visibility and ease of pursuit of hares by lynx. Variables (Table 2) included SCU (we assumed that high understory stem densities would interfere with the ability of a lynx to detect and pursue hares), SKID (we predicted that lynx traveling a disproportionately greater percentage of their movement distance on skid trails would expend less energy per distance traveled), and BA (we assumed that lynx traveling disproportionately in areas with high BA of stems above the small sapling stage, >7.6 cm dbh, would encounter less understory structure and fewer understory stems—Fuller 2006). We considered 2 models to evaluate whether vegetation variables associated with prey density (SCU: positive relationship; CC: negative relationship) best described differences between foraging paths of lynx and random transects. Those models were evaluated relative to 4 additional models considered to evaluate whether lynx mobility and prey access (SCU: negative relationship; SKID: positive relationship; BA: positive relationship) best described those differences. We evaluated fit of our top-ranking model using McFadden's ρ^2 to indicate whether our best suite of descriptor variables meaningfully described differences in vegetation and structure between observed movement paths and the availability of those features within home ranges of lynx. We performed all

TABLE 2.—Mean (*SE*) values of subpatch scale variables measured on 60 lynx movement paths and on 64 straight-line transects (1 km) that were sampled randomly within the home ranges of male ($n = 27$ transects) and female ($n = 37$ transects) lynx.

	Female movement paths	Male movement paths	Random transects in female ranges	Random transects in male ranges
BA[a]	15.36 (1.35)	10.80 (1.20)	16.47 (1.10)	14.64 (1.22)
CC[b]	46.85 (2.69)	33.19 (2.92)	48.13 (2.57)	45.15 (3.73)
SCU[c]	23,733 (3,068)	17,712 (1,710)	48,722 (4,226)	39,626 (2,675)
SKID (%)[d]	14.17 (2.12)	20.74 (3.24)	9.69 (1.45)	8.29 (1.21)

[a] BA = basal area (m^2/ha) of trees (>7.6 cm diameter at breast height [dbh]).

[b] CC = percentage canopy closure.

[c] SCU = stem cover units/ha = 3 × coniferous saplings + deciduous saplings (<7.6 cm dbh).

[d] SKID = percentage of lynx movement path that was on skid trails.

statistical analyses with SYSTAT 11 (SYSTAT Software, Inc., Chicago, IL) unless noted otherwise.

RESULTS

Snow tracking.—We snow tracked radiocollared adult lynx (3 females [F], 3 males [M]) for 65.50 km (median = 10.77 km/lynx, range = 9.64–12.34) during January–March, 2002 and 2003; 74 individual movement paths (median = 12 snow tracks/lynx, range = 11–14) were traversed and measured. Sixty (30 M, 30 F) movement paths were >500 m in length (i.e., complete length for substand scale analyses: median F = 1,050 m, range = 526–1,673 m; median M = 1,159 m, range = 611–2,878 m). The remaining 14 movement paths (<500 m) were omitted from subsequent analyses. All adult females were accompanied by 1, 2, or 3 kittens that traveled with adult females on all occasions when snow tracking occurred.

Vegetation sampling.—We sampled vegetation on 641 plots along the 60 complete lynx paths and averaged values across each path ($\bar{X} \pm SD = 10.7 \pm 3.6$ plots/path). We also sampled vegetation in 684 vegetation plots along 64 random straight-line transects ($\bar{X} \pm SD = 10.7 \pm 1.5$ plots/transect) that were distributed within lynx home ranges. Our objective to representatively sample the home range of each lynx was achieved; the mean percentage availability of our 5 patch types within home ranges ranged from 6% to 24%, which corroborated the 7–21% of random vegetation plots sampled in those types.

CRW null model.—Movement paths differed from those described by a CRW for both males ($\mathrm{CRW_{diff}}$: 0.569, $SE = 0.172$, $P = 0.003$) and females ($\mathrm{CRW_{diff}}$: 0.514, $SE = 0.029$, $P = 0.000$). The positive value of $\mathrm{CRW_{diff}}$ for both sexes indicates that movement paths covered a greater straight-line distance than a CRW and were more directional than random walks. Thus, we concluded that fractal dimension was an appropriate tool for evaluating movement path tortuosity across that same range of spatial scales.

Patch-scale fractal dimension.—We calculated fractal dimension for 121 (n = 60 F, 61 M) path segments (mean length = 334 m) in patch types that were preferred ($n = 54$) and nonpreferred ($n = 67$) by lynx during a companion study (Fuller et al. 2007). Fractal dimension of combined paths of both male and female lynx were greater ($F_{1,117} = 8.34$, $P = 0.00$) in preferred ($\bar{X} \pm SE = 1.12 \pm 0.01$) than in nonpreferred ($\bar{X} \pm SE = 1.08 \pm 0.01$) patch types, indicating that lynx were attempting to increase their exposure to preferred patches relative to nonpreferred patches. These results were not confounded by gender of lynx because we observed no significant effect of sex × patch type (i.e., preferred or nonpreferred) interaction ($F_{1,117} = 0.06$, $P = 0.81$) on fractal dimension. Small differences in D can result in substantial changes in path tortuousity because D represents an exponent in a scaling relationship. Thus, the magnitude of differences in D that we observed between preferred and nonpreferred patches resulted in visibly different movement paths (Fig. 2) that indicate substantial differences in behaviors of lynx across habitats with different foraging benefits.

We observed 15 snowshoe hare kills along trails of lynx. Consistent with our finding of greater fractal dimension within preferred habitat types, we observed that lynx within preferred and nonpreferred habitat killed hares disproportionately to expected ($\chi^2_1 = 2.77$, $P = 0.098$). Within preferred habitats (RegenTall, EstablishedPH; Table 1) lynx killed more hares ($n = 9$) than expected (5.0), whereas in nonpreferred habitats (Mature, RegenShort, RoadEdge, RecentPH; Table 1) lynx killed fewer hares ($n = 6$) than expected (8.1).

Gender-specific trends in fractal dimension.—Female lynx had a greater ($F_{1,117} = 15.58$, $P = 0.00$) mean fractal dimension ($\bar{X} \pm SE = 1.12 \pm 0.01$) than males ($\bar{X} \pm SE = 1.08 \pm 0.01$), indicating more tortuous paths by females (Fig. 1). Additionally, female home ranges contained 23% denser understory structure (Table 2) relative to home ranges of males (mean SCU = 48,722/ha along 30 random transects in female home ranges and 39,626 along 30 random transects within male home ranges). Movement paths of females traversed areas with average snow depths that were 2.58 cm shallower than random transects (SNOWR), whereas paths of males averaged 3.91 cm shallower than random; however, neither difference was significantly different from zero (M: $Z = 0.689$, $P = 0.491$; F: $Z = 0.710$, $P = 0.478$), and SNOWR was not significantly different between sexes ($U = 461$, $n_1 = 30$, $n_2 = 30$, P = 0.870). Combined, 9.7% of the movement paths of males and females followed hare trails. We observed no sex-specific differences between sexes in mean percentage of movement paths along hare trails ($U = 504$, $n_1 = 30$, $n_2 = 30$, $P = 0.424$).

TABLE 3.—Akaike's information criterion (AIC_c)[a] for the a priori set of logistic regression models related to prey density and prey access for male and female Canada lynx. Models were structured to evaluate which subpatch scale variables[b] best differentiated between areas used by Canada lynx and random straight-line transects (availability) within the home ranges of lynx in winters 2002 and 2003 in northwestern Maine. Bold fonts indicate models where the observed direction (positive or negative) of the parameter estimates matched the expected directions, as predicted by the respective prey-density or prey-access hypothesis.

Model	Expected direction[c]	Observed direction[d]	Rank	K[e]	Log (L)[f]	AIC_c	ΔAIC_c	Model likelihood	w_i[g]
Males									
Prey density[h]									
SCU	+	−	4[i]						
SCU, CC	+, −	−, −	3	3	−17.519	41.49	5.007	0.082	0.056
Mobility & prey access[j]									
SCU	**−**	**−**	4	2	−19.832	43.887	7.404	0.025	0.017
SCU, SKID	**−, +**	**−, +**	1	3	−15.015	36.483	0	1	0.690
SCU, BA	−,+	−, −	5	3	−18.790	44.033	7.550	0.023	0.016
SCU, BA, SKID	−,+,+	−, − , +	2	4	−14.998	38.765	2.282	0.319	0.220
Females									
Prey density[h]									
SCU	+	−	2[i]						
SCU, CC	+, −	−, +	5	3	−34.932	76.246	2.798	0.247	0.078
Mobility & prey access[j]									
SCU	**−**	**−**	2	2	−34.933	74.053	0.605	0.739	0.233
SCU, SKID	**−, +**	**−, +**	1	3	−33.533	73.448	0	1.00	0.315
SCU, BA	−,+	−, −	3	3	−33.974	74.328	0.880	0.644	0.203
SCU, BA, SKID	−,+,+	−, − , +	4	4	−33.011	74.667	1.220	0.543	0.171

[a] Akaike's information criterion adjusted for small sample size.

[b] See Table 2 for a description of variables.

[c] Expected direction (positive or negative) of each parameter estimate in the model, given the hypothesis. See Materials and Methods for an explanation of each model.

[d] Observed direction (positive or negative) of each parameter estimate in the model, given the hypothesis. See Materials and Methods section for an explanation of each model.

[e] K = number of estimable parameters.

[f] Log (L) = maximized log-likelihood.

[g] w_i = Akaike weight.

[h] Prey-density hypothesis = lynx forage in areas with the greatest density of understory cover, which corresponds to the highest densities of snowshoe hares.

[i] The model SCU did not match predictions of the prey-density model (i.e., SCU was predicted to have a positive association with hare density and was expected to be higher along lynx movement paths if prey density was driving lynx movement decisions; however, the observed relationship with SCU was negative).

[j] Prey-access hypothesis = lynx forage in areas with intermediate densities of snowshoe hares where lower stem densities and greater visibility during winter promote increased access to hares.

Domains of scale.—Movement paths were straighter (i.e., D was lower) at the finer range of spatial scales than at broader scales for both males and females (Figs. 1 and 2). A piecewise regression model with 2 line segments (females $AIC_c = -413.31$, $w_i = 1.00$, $r^2 = 0.94$; males $AIC_c = -419.96$, $w_i = 1.00$, $r^2 = 0.83$) better described the relationship between fractal dimension and spatial scale than a single linear regression model (females $AIC_c = -201.69$, $\Delta AIC_c = 211.61$, $w_i = 0.00$, $r^2 = 0.50$; males $AIC_c = -284.36$, $\Delta AIC_c = 135.60$, $w_i = 0.00$, $r^2 = 0.71$; Fig. 3). This indicated that both female and male lynx exhibited 2 different movement behaviors in response to changes in habitat–behavior processes as scale changed. For females, fractal dimension at a scale of 4 m was 1.09 but increased to 1.19 at a scale of 220 m (Fig. 3). For males, fractal dimension at 4 m was 1.04 but increased to 1.14 at 220 m (Fig. 3). The magnitude of differences in observed D between scales and sexes resulted in very different movement trajectories (Fig. 2) that likely are biologically and statistically meaningful. As indicated by significant break points in the regression of fractal dimension on spatial scale (Fig. 3), males and females transitioned from within-patch to between-patch responses to habitat heterogeneity at similar domains of scale. The scale at which males transitioned from within-stand to between-stand decisions occurred at 50 m and the observed transition for females occurred at 65 m (Fig. 3).

We generated 500,150 random points (100/ha) in preferred patch types. The average distance between random points in preferred patches within home ranges of lynx to the nearest edge of nonpreferred patches was 57.87 m (95% *CI* = 57.73–58.01 m), which closely coincided with the transition between domains of scale (50 m and 65 m for males and females, respectively), and further corresponded with changes in lynx behavior from less tortuous to more complex paths near the break point in the D versus scale regression (Fig. 3).

Selection of vegetation and structure: movement paths versus random transects.—The top logistic regression model for males ($w_i = 0.69$) and females ($w_i = 0.32$) differentiated lynx movement paths from random straight-line transects and included the variables SCU (− association) and SKID (+; Table 3). For males, no other plausible ($\Delta AIC_c < 2.0$) models existed. For females, 4 models were plausible ($\Delta AIC_c = 0.0$–1.2), but all contained the variable SCU (− association), and each was consistent with the lynx mobility and prey access hypothesis. The top-ranked models supporting the lynx mobility and prey access hypothesis all exhibited good fit to

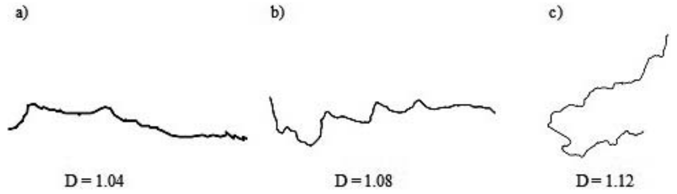

FIG. 2.—Examples of observed continuously sampled lynx movement paths with indicated fractal dimensions (*D*). Trajectory of a) 1.04, b) 1.08, and c) 1.12. Trajectory a) resembles the most linear movement paths observed among males at the finest spatial scale of 4 m. Paths in nonpreferred patch types resembled the trajectory in b), as did the movement paths of males across all patch types combined. Movement paths in preferred path types resembled the trajectory in c), as did the movement paths of females across all patch types combined.

the data for both males and females (McFadden's $\rho^2 = 0.619$ and 0.272, respectively). In contrast, the 2 competing models consistent with the prey-density hypothesis (i.e., positive association with SCU and negative association with CC) were not supported by our results. Our observed SCU was lower on movement paths of both sexes than on random transects, which was opposite the predictions of the prey-density hypothesis.

For males, average understory stem structure (SCU) and percentage of the movement path on skid trails (SKID) were the explanatory variables driving the top model for differentiating observed movement paths from random straight-line transects (Table 3). Movement paths of males traversed through areas with only 45% of the density of understory stem structure encountered on random transects, and use of skid trails was 2.5 times what was expected on the basis of random straight-line movements throughout male home ranges (Table 2). BA also was included with SCU and SKID in the second-ranked model for males (Table 3), whose movement paths traversed through stands with BA of live trees that were 26% lower than observed along random transects (Table 2). Correspondingly, males also traversed through areas with 26% lower CC than observed along random transects (Table 2).

For females, SCU and SKID were similarly included in the top model differentiating movement paths from random transects (Table 3). Understory stem structure (SCU) along movement paths of females was only 49% as dense as the understory along random transects, whereas use of skid trails exceeded randomly expected use by 46% (Table 2). BA was 7% lower on movement paths than on random transects within female home ranges. BA was included in 2 of the 4 top competing models (Table 3); however, the 95% *CI* on the odds ratio included 1, suggesting that BA was an ineffective predictor of *D* for females. Correspondingly, females also traversed through areas with slightly lower CC (3%) than expected (Table 2); however, CC was not supported in any of the top competing ($\Delta \mathrm{AIC_c}$ of top model with CC = 2.80) models (Table 3).

DISCUSSION

Lynx focused their movements within a restricted area (Tinbergen et al. 1967) around preferred habitats, exhibited more tortuous paths within those preferred patches, and exhibited higher foraging success in preferred patches relative to nonpreferred patches. Thus, increased foraging success was associated with greater path complexity, which is consistent with an expectation of greater foraging efficiency within high-resource areas and more directed movements between high-resource areas (Nolet and Mooij 2002). A more tortuous path suggests that lynx invested more time hunting in areas with greater foraging success (Arditi and Dacorogna 1988; Parker 1980) but does not necessarily indicate higher prey abundance because greater fractal dimension also can indicate areas of higher prey availability (Edwards et al. 2001) and accessibility. Prey densities in tall regenerating clear-cuts and established partial harvests, which had higher fractal dimension of foraging paths (this study) and were preferred by lynx (Fuller et al. 2007), were intermediate relative to short regenerating clear-cuts (Fuller and Harrison 2005; Homyack et al. 2007; Robinson 2006). Despite higher prey densities, short regenerating clear-cuts were nonpreferred by lynx (Fuller et al. 2007). Further, understory cover was suboptimal for hares in established (>10 years since cut) partially harvested patches, which were preferred by lynx (Fuller et al. 2007; Robinson 2006). Our results of more tortuous paths in preferred patches that had intermediate densities of

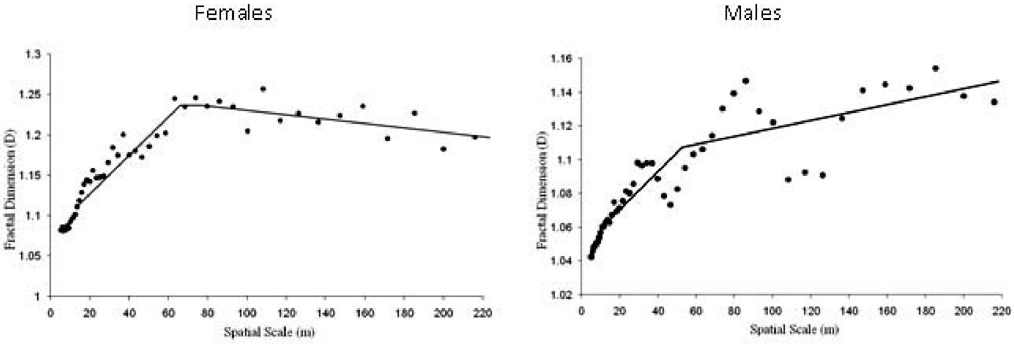

FIG. 3.—Piecewise regression models of fractal dimension (*D*) across a range of spatial scales for female and male Canada lynx in northern Maine, 2002–2003. Note the breaks in spatial scale at 65 m and 50 m for females and males, respectively, which indicate that the grain at which lynx recognize and respond to habitat heterogeneity changes at a scale of 50–65 m.

snowshoe hares was not explained by differences in structural complexity of the understory because models containing understory structure (SCU) did not explain differences in fractal dimension for movement paths of male or female lynx (Fuller 2006). We suggest that lynx preferred stands that provided intermediate prey density and easier access and visibility to hares. This finding is consistent with Mowat et al. (2000) and Fuller et al. (2007), who hypothesized that lynx trade off prey density to forage in areas with highest access to prey.

The greater fractal dimension values for female versus male lynx suggest that females might respond to landscape complexity within their home ranges to a greater extent than males (Westcott and Graham 2000), or they might invest greater foraging effort per linear distance traveled than males. Female raccoon dogs (*Nyctereutes procyonoides*) also had a greater fractal dimension than males, which was attributed to restricted mobility of females with young (Saeki et al. 2007). Relative to solitary male lynx, females must encounter more prey to meet their energy demands and those of their kittens, which accompanied them on 100% of movement paths. Thus, movements of females likely represented a greater emphasis on foraging than on other activities such as searching for mates or territorial defense (Sandell 1989). Males are not responsible for the foraging success of kittens and could be balancing foraging and breeding opportunities during the winter period. Therefore, motivations unrelated to foraging could account for less tortuous movement paths of males. Conflicting motivations to maximize foraging efficiency, territorial defense, and access to mates can confound interpretations of movement paths of male lynx during the winter season. Our results were restricted to the winter period when movement paths could be verified on snow; however, we speculate that fractal dimension of movement paths could be affected differently across sexes during the summer period when reproductive females are constrained by central place foraging from dens while provisioning kittens. Webb et al. (2009) also reported that female white-tailed deer moved more tortuously than males, suggesting that in polygynous mammals, males may exhibit more straight-line movements to increase exposure to potential mates, whereas movements of females who are attending offspring may be more focused on maximizing exposure to high-quality foraging patches.

Similar to observations of Webb et al. (2009) with white-tailed deer, and Nams and Bourgeois (2004) with martens (*Martes americana*), we observed a discontinuity in the relationship between fractal dimension and spatial scale. These changes indicate different domains of scale where process changes (Wiens 1989), coinciding with behavioral responses by lynx. The scale at which lynx responded to habitat heterogeneity changed at approximately 50 m for males and 65 m for females. Thus, the 50–65-m scale represents the finest grain at which lynx responded to habitat heterogeneity or spatial organization of habitat (Kotliar and Wiens 1990). However, our instrumentation could not measure changes in fractal dimension at scales finer than 4 m. Similar to the findings of Webb et al. (2009) with white-tailed deer, the break in spatial scale that we observed for male and female lynx coincided with the average distance between preferred and nonpreferred habitat patches. This suggests that lynx altered the tortuosity of their movement paths to avoid moving from higher- to lower-quality stands and to concentrate foraging investment within stands with highest accessibility to prey (i.e., intermediate densities of understory stem cover and hare abundances). Within habitat patches (i.e., at scales <50–65 m), movements by lynx were less tortuous and lynx did not exhibit strong fine-grained responses to subpatch scale habitat features. Strong coarse-grained selection for patch types within home ranges of lynx (Fuller et al. 2007) could have precluded the importance of finer-grained changes in response to habitat heterogeneity.

The large home-range areas traversed by lynx in our population (Vashon et al. 2008) might influence their perceptive scale because smaller species can exhibit greater path tortuosity than larger species (With 1994). Lynx might perceive and respond to habitat heterogeneity at a coarse grain because of their mobility, large stride length, and large home ranges. Lynx in eastern North America exhibit strong patterns of geographic (Hoving et al. 2005) and landscape-scale (Hoving et al. 2004) habitat selection. Additionally, lynx show strong habitat selection by selecting for patch types within home ranges that enhance foraging opportunities (Fuller et al. 2007; Poole et al. 1996).

Overall, mobility and prey access were more important than prey density in determining patch (Fuller et al. 2007) and within-patch scale resource selection by lynx. Similarly, lions (*Panthera leo*) and leopards (*Panthera pardus*) also preferred hunting in areas with increased prey catchability relative to areas with the highest prey density (Balme et al. 2007; Hopcraft et al. 2005). Lynx on our study area selected areas within their home ranges that had lower stem densities relative to random straight-line transects and also used more skid trails. Those conditions likely provided greater visibility and mobility (i.e., increased access to prey) when hunting hares and correspond with the hunting behaviors observed for leopards in South Africa (Balme et al. 2007). We conclude that the morphological and behavioral adaptations of felids that promote visual prey recognition and short, quick pursuits (Kleiman and Eisenberg 1973) constrain their foraging choices to areas of intermediate cover where prey are at relatively great risk and where the felid could have competitive advantages over more cursorial, sympatric canids.

In conclusion, our approach exemplifies some unique applications of fractal analysis to questions of ecological grain and resource selection. These approaches can be generalized across taxa and used to investigate the responses of organisms to environmental heterogeneity. For lynx, these analyses indicate that habitat conservation should be focused at the scales where strongest evidence of resource preference is expressed, which corresponded to patch (Fuller et al. 2007) and landscape scales (Hoving et al. 2004). Within-patch selection was expressed via a discontinuity in fractal dimension versus spatial scale and increases in movement tortuosity that allowed lynx to avoid moving from preferred to nonpreferred patches. Fractal analyses indicated that conservation of lynx via manipulation of within-patch scale structure might be ineffective on the basis of evidence of stronger patterns of resource selection at coarser grains. Resource selection (including selection of microhabitats) is a multilevel hierarchical process, both in space and time (Kotliar and Wiens 1990; Orians and Wittenberger 1991), and can provide contradictory results across relevant scales (Wiens 1989). We suggest that fine-scale characteristics associated with high prey densities will not necessarily reflect habitat quality for lynx because accessibility to prey also influences resource selection. Our results highlight that if the scale of study and analysis is inappropriate, key influences on habitat selection can be overlooked (Orians and Wittenberger 1991) or overstated. Further, our results indicate that coarse-grained resource selection (i.e., landscape and home-range scale) by mobile carnivores can reduce the importance of finer-scale conservation efforts. Our findings emphasize the importance of focusing conservation for coarse-grained species on home-range quality and maintenance of viable landscapes.

Acknowledgments

We gratefully acknowledge the Maine Cooperative Forestry Research Unit, the Maine Department of Inland Fisheries and Wildlife, the Maine Agricultural and Forest Experiment Station at the University of Maine, United States Fish and Wildlife Service, Nexfor Fraser Papers, the Department of Wildlife Ecology at the University of Maine, and The Nature Conservancy for funding. Irving Woodlands, Clayton Lake Woodlands, and 7 Islands Land Company provided geographic information system coverages and access to their lands. We thank field technicians J. Benson, K. Berger, A. Crook, T. Gorman, V. Green, T. Irvin, J. Tilden, and telemetry pilot J. McPhee (deceased). We also thank J. Vashon and S. Crowley for supervising the lynx capture effort and K. Pelletier and S. Pelletier for providing housing and logistical support. V. O. Nams graciously provided assistance with use and interpretation of the FRACTAL program. This is publication number 3120 of the Maine Agricultural and Forest Experiment Station.

Literature Cited

Arditi, R., and B. Dacorogna. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. American Naturalist 131:837–846.

Balme, G., L. Hunter, and R. Slotow. 2007. Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. Animal Behaviour 74:589–598.

Bascompte, J., and C. Vilà. 1997. Fractals and search paths in mammals. Landscape Ecology 12:213–221.

Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? Journal of Theoretical Biology 229:209–220.

Bergman, C. M., J. A. Schaefer, and S. N. Luttich. 2000. Caribou movement as a correlated random walk. Oecologia 123:364–374.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications 16:273–284.

Brand, C. J., L. B. Keith, and C. A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. Journal of Wildlife Management 40:416–428.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. 2nd ed. Springer-Verlag, New York.

Crist, T. O., D. S. Guertin, J. A. Wiens, and B. T. Milne. 1992. Animal movement in heterogeneous landscapes: an experiment with *Elodes* beetles in shortgrass prairie. Functional Ecology 6:536–544.

Doerr, V. A. J., and E. D. Doerr. 2004. Fractal analysis can explain individual variation in dispersal search paths. Ecology 85:1428–1438.

Edwards, M. A., G. J. Forbes, and J. Bowman. 2001. Fractal dimension of ermine, *Mustela erminea* (Carnivora: Mustelidae), movement patterns as an indicator of resource use. Mammalia 65:220–225.

Fuller, A. K. 2006. Multi-scalar responses of forest carnivores to habitat and spatial pattern: case studies with Canada lynx and American martens. Ph.D. dissertation, University of Maine, Orono.

Fuller, A. K., and D. J. Harrison. 2005. Influence of partial timber harvesting on American martens in northcentral Maine. Journal of Wildlife Management 69:710–722.

Fuller, A. K., D. J. Harrison, and J. H. Vashon. 2007. Winter habitat selection by Canada lynx in Maine: prey abundance or accessibility? Journal of Wildlife Management 71:1980–1986.

Homyack, J. A., D. J. Harrison, and W. B. Krohn. 2007. Effects of precommercial thinning on snowshoe hares in Maine. Journal of Wildlife Management 71:4–13.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74:559–566.

Hoving, C. L., D. J. Harrison, W B Krohn, W. J. Jakubas, and M. A. McCollough. 2004. Canada lynx *Lynx canadensis* habitat and forest succession in northern Maine, USA. Wildlife Biology 10:285–294.

Hoving, C. L., D. J. Harrison, W. B. Krohn, R. A. Joseph, and M. O'Brien. 2005. Broad-scale predictors of Canada lynx occurrence in eastern North America. Journal of Wildlife Management 69:739–751.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Kareiva, P. M., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. Oecologia 56:234–238.

Keith, L. B., J. R. Cary, O. J. Rongstad, and M. C. Brittingham. 1984. Demography and ecology of a declining snowshoe hare population. Wildlife Monographs 90:1–43.

Kleiman, D. G., and J. F. Eisenberg. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Animal Behaviour 21:637–659.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253–260.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1985. Influence of understory characteristics on snowshoe hare habitat use and density. Journal of Wildlife Management 49:866–873.

Maletzke, B. T., G. M. Koehler, R. B. Wielgus, K. B. Aubry, and M. A. Evans. 2008. Habitat conditions associated with lynx hunting behavior during winter in northern Washington. Journal of Wildlife Management 72:1473–1478.

Mandelbrot, B. B. 1967. How long is the coast of Britain? Statistical self-similarity and fractional dimension. Science 155:636–638.

McCulloch, C. E., and M. L. Cain. 1989. Analyzing discrete movement data as a correlated random walk. Ecology 70:383–388.

Mowat, G., K. G. Poole, and M. O'Donoghue. 2000. Ecology of lynx in northern Canada and Alaska. Pp. 265–306 in Ecology and conservation of lynx in the United States (L. F. Ruggiero et al., eds.). University Press of Colorado, Boulder.

Mowat, G., and B. Slough. 2003. Habitat preference of Canada lynx through a cycle in snowshoe hare abundance. Canadian Journal of Zoology 81:1736–1745.

Nams, V. O. 2005. Using animal movement paths to measure response to spatial scale. Oecologia 143:179–188.

Nams V. O. 2006. Detecting oriented movement of animals. Animal Behaviour 72:1197–1203.

Nams, V. O., and M. Bourgeois. 2004. Fractal analysis measures habitat use at different spatial scales: an example with American marten. Canadian Journal of Zoology 82:1738–1747.

Neter, J., M. H. Kutner, C. J. Nachtesheim, and W. Wasserman. 1996. Applied linear statistical models. 4th ed. Irwin, Chicago, Illinois.

Newbury, R. K., and T. A. Nelson. 2007. Habitat selection and movements of raccoons on a grassland reserve managed for imperiled birds. Journal of Mammalogy 88:1082–1089.

Nolet, B. A., and W. M. Mooij. 2002. Search paths of swans foraging on spatially autocorrelated tubers. Journal of Animal Ecology 71:451–462.

Orians, G., and J. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:829–849.

Parker, G. R. 1980. Winter habitat use and hunting activities of lynx (*Lynx canadensis*) on Cape Breton Island, Nova Scotia. Pp. 221–248 in Worldwide furbearer conference proceedings, August 3–11, 1980, Frostburg, Maryland (J. A. Chapman and D. Pursley, eds.). Worldwide Furbearer Conference, Inc.

Phillips, M. L., W. R. Clark, S. M. Nusser, M. A. Sovada, and R. J. Greenwood. 2004. Analysis of predator movement in prairie landscapes with contrasting grassland composition. Journal of Mammalogy 85:187–195.

Poole, K. G., L. A. Wakelyn, and P. N. Nicklen. 1996. Habitat selection by lynx in the Northwest Territories. Canadian Journal of Zoology 74:845–850.

Quinn, N. W., and G. Parker. 1987. Lynx. Pp. 638–694 in Wild furbearer management and conservation in North America (M. Novak, J. A. Baker, M. E. Obbard and B. Malloch, eds.). Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

Robinson, L. 2006. Ecological relationships among partial harvesting, vegetation, snowshoe hares, and Canada lynx in Maine. M.S. thesis, University of Maine, Orono.

Saeki, M., P. J. Johnson, and D. W. Macdonald. 2007. Movements and habitat selection of raccoon dogs (*Nyctereutes procyonoides*) in a mosaic landscape. Journal of Mammalogy 88:1098–1111.

Sandell, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pp. 164–182 in Carnivore behavior, ecology and evolution. Vol. 1 (J. L. Gittleman, ed.). Chapman and Hall, London, United Kingdom.

Sugihara, G., and R. M. May. 1990. Applications of fractals in ecology. Trends in Ecology and Evolution 3:79–86.

Swingland, I. R., and P. J. Greenwood. 1983. The ecology of animal movement. Clarendon Press, Oxford, United Kingdom.

Tinbergen, N., M. Impekoven, and D. Frank. 1967. An experiment on spacing out as defense against predation. Behavior 28:307–321.

Turchin, P. 1996. Fractal analyses of animal movement: a critique. Ecology 77:2086–2090.

Vashon, J. H., et al. 2008. Spatial ecology of a Canada lynx population in northern Maine. Journal of Wildlife Management 72:1479–1487.

Webb, S. L., S. K. Riffell, K. L. Gee, and S. Demaris. 2009. Using fractal analyses to characterize movement paths of white-tailed deer and response to spatial scale. Journal of Mammalogy 90:1210–1217.

Wells, K., M. Pfeiffer, M. B. Lakim, and E. K. V. Kalko. 2006. Movement trajectories and habitat partitioning of small mammals in logged and unlogged rain forests on Borneo. Journal of Animal Ecology 75:1212–1223.

Westcott, D. A., and D. L. Graham. 2000. Patterns of movement and seed dispersal of a tropical frugivore. Oecologia 122:249–257.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

With, K. A. 1994. Using fractal analysis to assess how species perceive landscape structure. Landscape Ecology 9:25–36.

Zar, J. H. 1999. Biostatistical analysis. 4th ed. Prentice Hall, Inc., Englewood Cliffs, New Jersey.

Submitted 5 January 2010. Accepted 4 April 2010.

Associate Editor was Madan K. Oli.