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RESEARCH ARTICLE

Limiting factors and landscape connectivity: the American marten in the Rocky Mountains

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Abstract In mobile animals, movement behavior can maximize fitness by optimizing access to critical resources and minimizing risk of predation. We sought to evaluate several hypotheses regarding the effects of landscape structure on American marten foraging path selection in a landscape experiencing forest perforation by patchcut logging. We hypothesized that in the uncut pre-treatment landscape marten would choose foraging paths to maximize access to cover types that support the highest density of prey. In contrast, in the post-treatment landscapes we hypothesized marten would choose paths primarily to avoid crossing openings, and that this would limit their ability to optimally select paths to maximize foraging success. Our limiting factor analysis shows that different resistant models may be supported under changing landscape conditions due to threshold effects, even when a species' response to landscape variables is constant. Our results support previous work showing forest harvest strongly affects marten movement behavior. The most important result of our study, however, is that the influence of these features changes dramatically depending on the degree to which timber harvest limits available movement paths. Marten choose foraging paths in uncut landscapes to maximize time spent in cover types providing the highest density of prey species. In contrast, following landscape perforation by patchcuts, marten strongly select paths to avoid crossing unforested areas. This strong response to patch cutting reduces their ability to optimize foraging paths to vegetation type. Marten likely avoid non-forested areas in fragmented landscapes to reduce risk of predation and to benefit thermoregulation in winter, but in doing so they may suffer a secondary cost of decreased foraging efficiency.

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Introduction

Habitat loss and fragmentation are among the most important drivers of the global biodiversity crisis (Fahrig 2003), and there is a wide consensus that studies of the effects of habitat fragmentation are especially urgent and should receive special priority (Lubchenco et al. 1991; Cushman 2006). Indeed, hundreds of theoretical and empirical studies of the ecological effects of habitat fragmentation have been conducted over the past 20 years (Saunders et al. 1991; Andre′n 1994, Debinski and Holt 2000; McGarigal and Cushman 2002). The knowledge gained from these studies has come from a variety of approaches, including field observations and experiments as well as mathematical and spatial models. In spite of these efforts, very little is yet known about the mechanisms that link ecosystem population responses to changes in habitat patterns resulting from fragmentation.

A major limitation of past fragmentation research is that rarely have patterns and processes been directly associated at the landscape-level in replicated and controlled studies. The effects of habitat fragmentation on population structure and dynamics is a landscape-level process, and failure to exert experimental control and replication at the landscape level produces results of unknown generality and robustness (McGarigal and Cushman 2002; Cushman 2006). For example, in a review of several hundred studies of habitat fragmentation, McGarigal and Cushman (2002) found that a very small proportion of these studies were in fact conducted at the landscape-level, less than 5% of published papers reported replication of representative landscapes, and very few had sufficient sample size for statistical inference at the landscape-level.

In mobile animals, movement behavior is used to maximize fitness by increased access to critical resources and minimizing risk of predation. It is predicated that as organisms move through spatially complex landscapes, they respond to the conditions of multiple ecological attributes, expressing movement paths that optimize fitness benefits while minimizing fitness costs. Measurement of movement paths through complex landscapes provides data to associate movement behavior with ecological attributes, and allows direct assessment of the influences of landscape features on movement path selection. This enables the development of species-specific landscape resistance models in which the resistance of any location, or pixel, in a landscape is a function of multiple landscape features measured at one or several scales. As such, individual-based analysis of movement path selection is a particularly powerful means to quantify habitat fragmentation effects on population structure (e.g., Bruggeman et al. 2007; Coulon et al. 2008; Cushman and Lewis 2010). For example, such analyses may directly evaluate the relative support for multiple alternative models relating landscape composition, configuration and interspecific interactions to movement cost (e.g., Cushman et al. 2010).

The path-level randomization approach (Cushman et al. 2010; Cushman and Lewis 2010) provides a robust means to compare the landscape features an animal encounters in its utilized path with those that would be encountered in a large sample of available paths of identical length and topology. By holding length and topology constant and randomizing location in the landscape, the approach avoids pseudoreplication and autocorrelation of observations, as may be an issue with some analyses evaluating point data (Harris et al. 1990; Litvaitis et al. 1994; Cushman 2010).

The objectives of this study are to use path-level analysis of movement and case–control logistic regression (Hegel et al. 2010) to predict selection of movement paths by American marten (*Martes americana*) as a function of forest type, seral stage, roads and clear cuts in a study area that experienced intensive experimental fragmentation by clear cut logging. We have two specific objectives. First, we use case–control logistic regression in a multi-model framework to predict landscape resistance to marten movement in an unmanaged roadless landscape. Second, we predict changes in apparent landscape resistance in the same landscape following intensive fragmentation (perforation) of that landscape by roads and clearcuts. We have four hypotheses:

1. *Prior to timber harvest in the study area, marten will select movement paths to maximize foraging success*. Past work has indicated that prey density

and diversity is higher in mixed conifer and spruce-fir forest than in lodgepole pine cover types (Raphael 1988; Nordyke and Buskirk 1991). Therefore our first hypothesis is that we expect selection for mixed conifer and spruce-fir and avoidance of lodgepole pine and other forest types.

2. *Prior to timber harvest, marten will not significantly avoid the few* non-forest *patches that perforate the landscape because they do not limit potential movement paths*. Marten have widely been found to avoid open-canopy and non-forest habitat types (Chapin et al. 1998; Hargis et al. 1999). Martens avoid clearcuts and areas with little or no canopy cover (Hawley and Newby 1957; Koehler et al. 1975; Hargis and McCullough 1984; Snyder and Bissonette 1987; Potvin et al. 1999). However, we hypothesize that avoidance of non-forest types will only be significant when non-forest patches limit path selection. In cases where the landscape is dominated by a well-connected matrix of closed canopy forest we hypothesize there will be no statistically significant avoidance of the few non-forest patches that perforate the landscape because they do not have sufficient area or fragmentation to limit movement path selection.
3. *After timber harvest, marten will significantly avoid* non-forest *patches because extensive perforation by* non-forest *patches will limit movement path selection*. After the experimental harvest, the landscape was highly perforated by many small patch cuts. Under this condition we expect that the extent and pattern of patch cuts will limit path selection, and that marten will significantly avoid cutover areas.
4. *After timber harvest, marten will not select movement paths to maximize foraging success*. By limiting marten path selection choices, we expect that the extensive clear cutting post-harvest will reduce the ability of marten to optimally select habitat resources while simultaneously selecting paths to avoid clear cuts. Specifically, we expect weaker selection of optimal foraging cover types after harvest. We expect post-harvest path selection will be dominated by avoidance of clear cuts, limiting the ability of marten to optimally choose paths to maximize foraging time in optimal cover types. This would result in non-significant selection for optimal foraging cover types in the post-harvest landscape.

Materials and methods

Study area

The study was conducted in two adjacent sub-basins in the Central Rocky Mountains of Wyoming, U.S.A, extending from 41°00′50″ to 41°03′52″N latitude and from 106°40′53″ to 106°46′00″W longitude during the years 1986–1996 (Fig. 1). Elevations ranged from 2670 to 3340 m (mean of 2957 m) above sea level, and the average annual precipitation was 84 cm, mostly from snowfall. Complete snow cover persisted from at least mid-October to early June, and yearly maximum snow depth ranged from 146 to 235 cm during the study. Snow depth reached a maximum of about 2 meters, usually in March of each year. Mean monthly air temperatures ranged from −11°C in January to 13°C in July.

Both basins were heavily forested by mature lodgepole pine (*Pinus contorta*) Engelmann spruce (*Picea engelmannii)* and subalpine fir (*Abies lasiocarpa*). Bailey (1995) describes the ecoregion as the

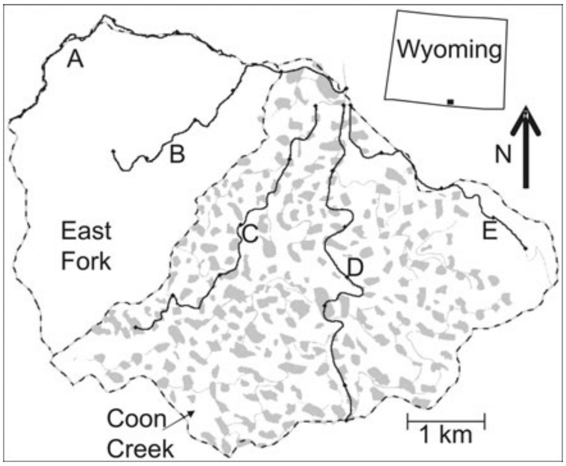

Fig. 1 The study area consisting of two watersheds (delineated by a *dashed line*): East Fork on the west side and Coon Creek on the east side. *Gray areas* indicate the small clearcuts and roads in the Coon Creek watershed post-harvest. Trails (labeled *A* and *B*) and roads (labeled *C*, *D*, and *E*) used for the snow track surveys are indicated by *black lines*. *Inset* indicates the location of the study area in south central Wyoming, USA

southern Rocky Mountain steppe—open woodland—coniferous forest—alpine meadow Province. Engelmann spruce, subalpine fir, and lodgepole pine were the only overstory tree species. Spruce-fir stands represented about 55% of the area of the combined watersheds and lodgepole pine stands comprised 40% (O'Doherty, unpublished data). The remaining area was in non-forested vegetation types including alpine tundra and riparian meadows.

At the beginning of the study, less than 3% of the area of each watershed was non-forested, consisting of dispersed small wet and dry meadows, dry alpine areas, and rock outcrops. From 1990 to 1992, 240 patchcuts were created in the 1673-ha Coon Creek watershed as part of a water-yield augmentation study (Raphael 1987a; Troendle et al. 2001), while the adjacent watershed (Upper East Fork basin (908 ha) remained uncut (Fig. 1). The timber harvest and creation of service roads resulted in about 24% of the watershed being cleared. Clearcuts were uniformly distributed throughout the forested area, with the exception of riparian buffers (about approximately 330 m in width around all streams) and exposed ridge tops (Troendle et al. 2001). The mean size area of the clearcuts was 1.6 ha (SD = 1.0, n = 240) and mean nearest neighbor distance was 53 m (SD = 23.6). Prior to 1985, the only roads included one road along the northeastern edge of the Coon Creek basin and a narrow road into the northern part of East Fork basin from a small mining operation in the early 1940s. The only prior logging activity had been selective cutting of lodgepole pines for railroad ties from 1902 to 1912 in both basins.

GIS data

Maps of cover type and seral stage were produced for the study area through photo-interpretation of low elevation color-infrared aerial photography. The original landcover maps were in vector GIS form. The accuracy of the original landcover maps for cover type and seral stage were field validated, which indicated high accuracy with low omission and commission error rates (less than 15% for all classes). We converted these vector maps to raster form with 5 m pixel size through nearest neighbor reclassification in ArcGIS (ESRI 2009). There were two GIS maps produced for every year of the analysis (1986–1997). These include a map of cover type and a map of seral stage (Table 1). There were nine cover types in the original landcover maps. These were reclassified into eight for our analysis. No-canopy indicates portions of the landscape that had no forest cover. Patches dominated by pure stands of lodgepole pine were classified as "lodgepole". Stands dominated by a mix of Engelmann spruce (*Picea engelmannii*) or sub-alpine fir *(Abies lasiocarpa)* were classified as "spruce fir", stands in which a mix of conifer species were co-dominant were classified as "mixed conifer". Stands in which aspen and

Table 1 Description of the classes in the GIS maps used in the analysis

Cover class	Code	Description	Seral class	Code	Description
1	No-canopy	Clearcut	1	No-canopy	Rock_bare
2	No-canopy	Dry park	2	No-canopy	Clearcut, meadow
3	No-canopy	Wet meadow	3	l6 cm	<6 cm
4	lp	Lodgepole	4	6–22 cm	6–22 cm
5	sf	Spruce fir	5	23–35 cm	23–25 cm
6	mx	Mixed conifer	6	g35 cm	>35 cm
7	a	Aspen			
8	ac	Aspen-conifer			
9	w	Water			

There were two GIS maps produced for every year of the analysis (1986–1997). These include a map of cover type (left three columns) and a map of seral stage (right three columns). There were nine cover types in the original landcover maps. These were reclassified into eight for our analysis, including no-canopy, lodgepole pine, spruce-fir, mixed conifer, aspen, aspen-conifer and water. There were six seral classes in the original landcover maps. These were reclassified into five for our analysis, including no-canopy, forest less than 6 cm average dbh, forest between 6 and 22 cm average dbh, forest between 23 and 35 cm average dbh, and forest greater than 35 cm average dbh conifer were inter-mixed were classified as "aspen-conifer". There were six seral classes in the original landcover maps. These were reclassified into five for our analysis, including no-canopy, forest less than 6 cm average dbh, forest between 6 and 22 cm average dbh, forest between 23 and 35 cm average dbh, and forest greater than 35 cm average dbh. Landscape change resulting from road construction and timber harvest was burned onto these landcover maps by overlaying roads and clearcuts created each year. This enabled us to associate each snow track included in the analysis with the landscape conditions that were contemporary to it.

Marten paths

Throughout the snow-on periods from 1986 through 1996, roads and trails (Fig. 1) were systematically surveyed by snowmobile 1 to 4 days after snowfall. All marten track intercepts were marked on maps, and one to three tracks were randomly selected for further analysis. For each selected track, an observer followed the path for 30 m in a random direction, then established a plot and recorded vegetation and other data. The observer then continued along the path for a randomly determined distance between 50 and 150 m after which a new plot was established and the vegetation attributes were recorded for that point. In addition, the location of each sampling point was recorded on a map. This process was repeated until the observer completed 1500 m of survey along a particular track. Starting in 1990, the procedure was changed so that points were collected systematically every 100 m along a track, to a total of 1000 m. Once the observer returned to the lab, the track and sample points were digitized for later spatial analysis. All post-harvest paths utilized in this analysis were located fully within the bounding box defined by the extent of harvest treatments. Our analysis included 41 pre-harvest (1986–1992) paths and 50 post-harvest (1993–1996) paths.

We plotted all marten snow-track paths and habitat plot locations on a topographic map. Several features aided orienteering, including roads, streams, small meadows, streams, ridge tops, and 180 small mammal sample stations and four bird survey grids marked with survey tape throughout the two watersheds. The field crew had two or more years experience navigating through these watersheds from previous wildlife studies. Global Positioning System (GPS) technology was not available at the beginning of the study, but in 1996 we used GPS to compare points marked by the technician on the map and those derived from GPS (90 fixes for each location). For six habitat points along one snow-track, the difference between the map and GPS locations ranged from 11 to 52 m. Comparing three track vectors created using GPS instruments and those drawn on topographic maps, we found close correspondence in shape and geographic position (within 2–50 m).

Path-level analysis

Our movement analysis is based on contrasting the frequency that the utilized movement path crosses various landscape features with the frequency at which these features would be crossed in a large sample of available movement paths of the same length and topology (e.g., Cushman et al. 2010; Cushman and Lewis 2010). First, the utilized paths were created by converting the series of sequential point locations for each path into a line in ArcInfo workstation (ESRI 2009). Second, for each utilized path, nine available paths with identical topology were created by randomly shifting and rotating the utilized path, with the constraint that they lie entirely within the extent of the landscape in which timber harvest occurred. The available paths were randomly shifted a distance between 0 and 10 km in x and y, and randomly rotated between 0 and 360°.

A priori selection of variables

A priori, we proposed four landscape features that we believe may influence marten movement. Marten have been shown to avoid non-forest and open canopy conditions (Buskirk and Powell 1994; Chapin et al. 1998; Hargis et al. 1999). We combined roads, wet meadows, dry parks and clearcuts into a single non-forest class (no-canopy), for analysis. Marten are known to select for late-seral, closed canopy forest conditions. Therefore, we included three seral stage variables based on average tree diameter and breast height: 6–22, 22–35, and >35 cm. Finally, Raphael (1988) and Nordyke and Buskirk (1991) both found differences in prey density and diversity, and marten habitat selection, among different forest cover types in the study area. We included three forest cover types as variables to evaluate this: mixed conifer, spruce-fir, lodgepole pine.

Conditional logistic regression

In this analysis we used a matched case–control design with 1 utilized path matched with nine available paths. In such circumstances conditional logistic-regression is an appropriate modeling approach (Hegel et al. 2010). Such models are known as discrete choice models (DCM; Manly et al. 2002), conditional fixed-effects logistic regression (CFE; Johnson and Omland 2004), or case–control models (Pearce and Boyce 2006). Conditional logistic regression models use data in which a used (presence) location is specifically matched to a number of unused, or available, locations to create a group (stratum), and results of the model are conditional upon each group. These approaches have been used to deal with situations in which habitat availability changes during the course of a study (Arthur et al. 1996), and to deal with potential temporal autocorrelation arising from data collected from GPS radio-telemetry data (Johnson and Omland 2004). This approach is particularly useful when there is a lack of independence in the data, such as this case involving GPS radio-telemetry data (e.g., Cushman et al. 2010; Cushman and Lewis 2010). Interpretation of model coefficients is the same as for ordinary logistic regression, yet may be viewed as more reliable given that the natural clustering in the data is accounted for (Hegel et al. 2010). There is no intercept estimated since the model is conditioned on each stratum.

We proposed a suite of candidate models for pre- and post-harvest constructed from combinations of the predictor variables. Following our hypotheses, we proposed 19 pre-harvest models and 19 post-harvest models (Table 2). All statistical analyses were conducted in r (R Core Development Team 2009). We ranked pre- and post-harvest models by AIC value and used model averaging across all candidate models based on AIC weights to produce a final model with associated parameter estimates, and measures of variable importance across models. The final averaged model was used to create maps of landscape resistance to movement for both pre- and post-harvest landscapes by calculating e^b1v1 + b2v2… + bnvn, where bi is the coefficient for variable i (e.g., Cushman and Lewis 2010).

Results

Track data

Road track surveys were conducted on 62 non-consecutive days. A total of 615 marten track intercepts were detected from 775.7 km of roads or trails surveyed in the two watersheds. Most marten tracks did not enter clearcuts, and on the few occasions when tracks entered clearcuts they remained close to the forest edge. The deepest recorded incursion into a clear cut was 17 m from the forest edge.

Pre-harvest logistic regression

All 19 pre-harvest models had non-zero AIC weights (Table 2). Model averaging indicated that mixed conifer was the most influential variable, followed by no-canopy (Table 3). Consistent with our pre-harvest hypothesis, the averaged model indicates that marten selected paths that traversed higher than expected proportion of mixed conifer and lower than expected proportion no-canopy cells (Table 5).

Post-harvest logistic regression

In the post-harvest analysis, 13 of 19 models had non-zero AIC weights (Table 4). Model averaging indicated that no-canopy was by far the most influential variable. The averaged model indicates that following extensive timber harvest in the study area martens select paths that strongly avoid crossing non-forested cells, with very weak response to any other landscape variables (Table 5).

The pre-harvest and post-harvest averaged models predict very different patterns and degree of landscape resistance to marten movement (Fig. 2). In the pre-harvest condition, there is relatively low contrast in predicted resistance to marten movement path selection, with modest selection for mixed conifer forest and relatively weak avoidance of non-forest areas (Fig. 2a). Conversely, the post-harvest resistance map shows reveals very strong avoidance of non-forest areas (Fig. 2b). In the post-harvest landscape martens avoid paths crossing non-forest cells approximately 16 times more strongly than in the pre-harvest landscape, based on model averaging coefficients (Table 5). In addition, in the pre-harvest

Table 2 List of pre- and post-harvest candidate models for relationship between landscape features and marten movement path selection

Pre-harvest models	Post-harvest models
Mixedcon	Mixedcon
Spruce-fir	Spruce-fir
Lodgepole	Lodgepole
No-canopy	No-canopy
6–22 cm	6–22 cm
22–35 cm	22–35 cm
>35 cm	>35 cm
Mixedcon + spruce-fir	No-canopy + mixedcon
Mixedcon + lodgepole	No-canopy + spruce-fir
Mixedcon + no-canopy	No-canopy + lodgepole
Mixedcon + 6–22 cm	No-canopy + 6–22 cm
Mixedcon + 22–35 cm	No-canopy + 22–35 cm
Mixedcon + > 35 cm	No-canopy + >35 cm
Mixedcon + no-canopy + spruce-fir	Mixedcon + no-canopy + spruce-fir
Mixedcon + no-canopy + lodgepole	Mixedcon + no-canopy + lodgepole
Mixedcon + no-canopy + >35 cm	Mixedcon + no-canopy + >35 cm
Mixedcon + no-canopy + 22–35 cm	Mixedcon + no-canopy + 22–35 cm
Mixedcon + no-canopy + 6–22 cm	Mixedcon + no-canopy + 6–22 cm
Mixedcon + spruce-fir + lodgepole + no-canopy + 6–22 cm + 22–35 cm + >35 cm	Mixedcon + spruce-fir + lodgepole + no-canopy + 6–22 cm + 22–35 cm + >35 cm

Mixedcon mixed conifer forest cover type, *Spruce-fir* Subalpine fir—Engelmann spruce cover type, *Lodgepole* lodgepole pine cover type; 6–22 cm—average within-stand tree diameter between 6 and 22 cm; 22 and 35 cm—average within-stand tree diameter between 22 and 35 cm; >35 cm—average within-stand tree diameter greater than 35 cm; no-canopy—open canopy conditions associated with clearcuts, roads, wet meadows and dry parks

landscape marten select paths crossing mixed conifer forest approximately 27 times more strongly than in the post-harvest landscape (Table 5).

Discussion

Our analysis indicates that in unharvested landscapes marten actively choose foraging paths to maximize time spent in mixed conifer cover types with large average basal area, which have the highest density of prey species (Raphael 1988; Nordyke and Buskirk 1991). Prior to timber harvest, non-forest cover in the study area was low and likely provided very little constraint on the ability of martens to choose optimal foraging paths while avoiding non-forest habitat. Therefore, as we expected, there was relatively weak statistical avoidance of non-forest in the pre-treatment landscape, not because martens were more inclined to utilize unforested areas, but because unforested areas were so limited in extent that available marten paths rarely included non-forest habitat. A statistical model based on use versus availability cannot identify avoidance of a feature that does not limit habitat use or movement because it is very limited in extent within the study area. This, however, could easily be misinterpreted as the lack of an ecological relationship when in fact it reflects an undetectable relationship (e.g., Cushman et al. 2006; Short Bull et al. 2011).

Our post-treatment results clearly show this would be an error. In the pre-treatment study area, where forest is extensive and unfragmented, we posited that there would be a weak relationship between movement path selection and forest cover. Forest cover would not limit movement path selection of a forest-dependent species in landscapes that are continuously forested. In contrast, in landscapes where forests are

Table 3 Pre-harvest model ranking for effects of landscape composition on marten movement path selection

Rank	Model	AIC	Delta	wi
1	Mixedcon	525.502	0	0.10363
2	No-canopy mixedcon	525.96	0.458	0.08242
3	Mixedcon 22–35 cm	526.426	0.924	0.065289
4	Mixedcon g25 cm	526.522	1.02	0.062229
5	Mixedcon nocaopy 22–35 cm	526.649	1.147	0.0584
6	No-canopy	526.673	1.171	0.057704
7	Mixedcon nocaopy g35 cm	526.759	1.257	0.055275
8	Mixedcon 6–22 cm	526.926	1.424	0.050847
9	Mixedcon no-canopy 6–22 cm	527.076	1.574	0.047173
10	Mixedcon sprucefir	527.358	1.856	0.040969
11	22–35 cm	527.415	1.913	0.039818
12	Mixedcon lodgepole	527.491	1.989	0.038333
13	g35 cm	527.511	2.009	0.037952
14	Mixedcon no-canopy sprucefir	527.719	2.217	0.034203
15	Mixedcon no-canopy lodgepole	527.922	2.42	0.030902
16	Lodgepole	528.444	2.942	0.023803
17	Sprucefir	528.536	3.034	0.022733
18	Global	528.57	3.068	0.02235
19	6–22 cm	528.571	3.069	0.022339

Table 4 Post-harvest model ranking for effects of landscape composition on marten movement path selection

Rank	Model	AIC	Delta	wi
1	No-canopy	369.518	0	0.209100765
2	6–22 cm no-canopy	370.522	1.004	0.126572626
3	22–35 cm no-canopy	370.84	1.322	0.107965989
4	g35 cm no-canopy	370.92	1.402	0.103732582
5	No-canopy mixedcon	371.357	1.839	0.083372312
6	Sprucefir no-canopy	371.389	1.871	0.08204897
7	Lodgepole no-canopy	371.47	1.952	0.078792378
8	6–22 cm mixedcon no-canopy	372.416	2.898	0.0490979
9	22–35 cm mixedcon no-canopy	372.747	3.229	0.041608991
10	g35 cm mixedcon no-canopy	372.849	3.331	0.039540136
11	Sprucefir mixedcon no-canopy	373.301	3.783	0.031541882
12	Lodgepole mixedcon no-canopy	373.355	3.837	0.030701646
13	Global	374.668	5.15	0.015923823
14	6–22 cm	416.717	47.199	0
15	22–35 cm	416.791	47.273	0
16	g35 cm	417.389	47.871	0
17	Mixedcon	417.416	47.898	0
18	Sprucefir	418.143	48.625	0
19	Lodgepole	418.655	49.137	0

fragmented we would expect the movement path selection of a forest dependent organism to be highly related to forest cover as a limiting factor. In the post-treatment landscape marten very strongly avoid non-forest habitat, with an effects size approximately 16 times larger than in the pre-treatment landscape. This

Table 5 Model averaging parameter estimates, standard errors and variable AIC importance values for pre- and post-harvest models

	Pre Harvest			Post Harvest		
	Parameter Estimate	SE	AIC import Value	Parameter Estimate	SE	AIC import Value
No-canopy	−0.46517	1.169	0.358149	*−8.157*	*1.39*	1
6–22 cm dbh	−0.01621	0.149	0.100266	−0.043	0.1517	0.191594
22–25 cm dbh	*−0.19932*	*0.181*	0.195059	−0.004	0.166	0.165499
>35 cm dbh	0.112971	0.180	0.186609	0.011	0.166	0.119656
Mixed-conifer	*0.521693*	*0.455*	0.568013	0.020	0.500	0.220705
Spruce-fir	0.015239	0.924	0.126209	−0.004	0.844	0.129515
Lodgepole	0.018511	0.516	0.121101	0.050	0.860	0.125418

Parameters in italics have standard errors that do not overlap zero. The AIC importance value is the sum of AIC weights of models that include the variable. Pre-harvest marten actively select fo mixed-conifer forest of the largest size class, while after harvest marten very strongly avoid no-canopy conditions

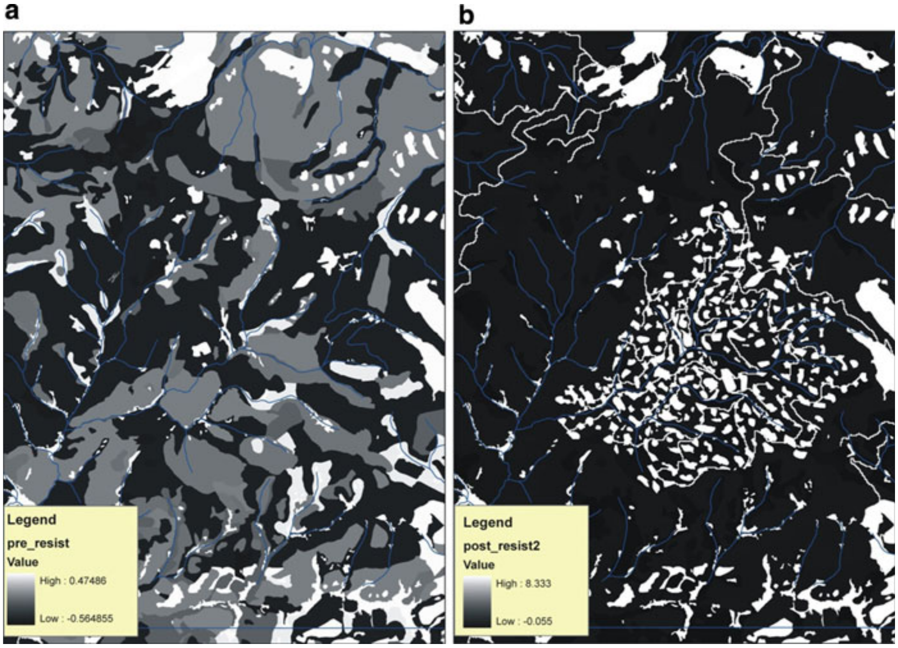

Fig. 2 Resistance surfaces predicted for pre- and post-treatment using model averaging. **a** Resistance map predicted pre-harvest; **b** resistance map predicted post-harvest

shows that marten strongly avoid non-forest areas, but that the effect is only detectable when there is a sufficient degree of fragmentation by non-forest cover to limit available movement paths. Application of the pre-treatment model to the post-treatment landscape would enormously under-represent the true impact of habitat fragmentation. Inferences about habitat relationships taken before a large landscape perturbation may not predict the pattern-process relationships that operate after perturbation.

Consistent with our hypotheses, strong avoidance of open canopy conditions following timber harvest acts to constrain the foraging paths available to marten such that they are unable to optimally select cover types that offer the highest density of prey species. Mixed conifer forest types have a substantially higher diversity and biomass of small mammal prey utilized by American marten in the central Rocky Mountains than other forest types (Raphael 1987b; Nordyke and Buskirk 1991). In the pre-harvest landscape, mixed conifer forest was the landscape variable with the strongest influence on movement path selection, indicating that martens chose paths to optimize foraging in this cover type. In contrast, following harvest, marten very strongly avoid paths that cross non-forest cells. Marten are known to suffer increased rates of predation by avian and mammalian predators in open canopy and non-forest conditions (Ruggiero et al. 1994). It is very likely that in the post-harvest landscape, marten actively choose foraging paths that avoid clearcuts to minimize risk of predation. However, in doing so their ability to simultaneously optimize movement path selection for foraging is reduced. The effects size for selection for mixed conifer forest is approximately 27 times greater in the pre-harvest landscape than the post-harvest landscape. This indicates that in the post-harvest landscape marten are much less actively selecting mixed conifer forest. There appears to be a tradeoff between marten's ability to avoid landscape features presenting high predation risk and their ability to select landscape features providing high foraging success. The large decrease in the degree of selection of mixed conifer forest post-harvest suggests that it was not possible for marten to both avoid risky landscape conditions and simultaneously maximize foraging time in late seral mixed conifer stands.

It is widely known that forest cover is an essential component of habitat for American marten. Several studies have concluded that martens avoid areas with little or no canopy cover and that marten establish home ranges in landscapes with a high proportion (over 70%) of preferred habitat (Hawley and Newby 1957; Koehler et al. 1975, Snyder and Bissonette 1987; Hargis et al. 1999; Potvin et al. 1999; Heinemeyer 2002). However, our results indicate that landscape analyses in unharvested landscapes would fail to detect this relationship. Where forest cover is high and forest fragmentation is low it is likely that movement behavior will not be related to patterns in forest cover, as forest extent and fragmentation are not limiting to movement and dispersal. This does not mean that forest cover is not important, only that it is not limiting. This is an important case of where a relationship with a necessary resource is not detectible because it is not limiting and therefore does not structure the response variable. From this it would be tempting to incorrectly conclude that forest cover is not important to American marten foraging path selection. This would be a logical error of denying the antecedent (Cushman and Huettmann 2010). We were only able to identify this in our study through the use of a controlled landscape-level experiment involving pre-treatment control and experimental landscape fragmentation treatments (McGarigal and Cushman 2002). This highlights the importance of landscape-level experiments to rigorously evaluate pattern-process relationships.

Our results in the post-treatment landscape confirm the findings of Hargis et al. (1999) who found that marten occupancy decreases greatly in landscapes that are perforated by relatively low area (20–25%) of nonforested openings. Specifically, our results offer an explanation for this observation for threshold effects at relatively low degrees of habitat loss. Specifically, we found marked change in foraging behavior and movement path selection in the post-harvest landscape, after only loss of 24% of habitat area. In the post-harvest landscape marten expressed paths that were much more tortuous as a result of actively avoiding crossing patch cuts. This reduced their ability to select preferred cover types for foraging. As a result we can speculate that marten likely had reduced foraging efficiency and likely higher risk of predation in the post-harvest landscape.

The amount of habitat required for species persistence depends on species-specific behavioral and life-history characteristics (Gibbs 1998; Vance et al. 2003), and the effects of habitat loss on each species will depend on the interaction of its ecological requirements and capabilities with the degree of habitat loss in the surrounding landscape (McGarigal and Cushman 2002; Schmiegelow and Monkkonen 2002; Fahrig 2003). Our results indicate that the spatial configuration of habitat and non-habitat has important effects of marten foraging behavior, even in landscapes with over 75% cover by suitable habitat. This is an interesting contrast to research that suggests that populations may generally not be strongly affected until a relatively high proportion of habitat is lost. Some theoretical and empirical work suggests that major population declines will occur due to habitat loss when habitat area drops below 10–30% (With and Crist 1995; Hill and Caswell 1999; Jansson and Angelstam 1999; Fahrig 2001; Flather and Bevers 2002). High trophic level species, such as the American marten, appear to be particularly vulnerable to local extinction due to habitat loss (Gibbs and Stanton 2001), and our results are consistent with others that suggest that American marten is particularly vulnerable to loss even of relatively low proportions of habitat (Hargis et al. 1999).

The majority of theoretical studies suggest that the effect of habitat fragmentation is weak relative to the effect of habitat loss (Fahring 1997; Henein et al. 1998; Collingham and Huntley 2000; Flather and Bevers 2002), although some predict larger effects (Boswell et al. 1998; Burkey 1999; Hill and Caswell 1999; Urban and Keitt 2001). In addition, some theoretical studies suggest that the effects of fragmentation per se should become apparent only at low levels of habitat amount, for example below approximately 20–30% of the landscape (Fahring 1997; Flather and Bevers 2002), although there is little empirical evidence available to test this prediction (Fahrig 2003).

Our results strongly suggest that relatively limited habitat loss associated with high perforation of the habitat matrix by non-habitat has large impacts on American marten foraging path selection. Our study, however, was not able to formally separate the effects of habitat area vs. habitat configuration, as we did not have a study landscape in which the harvested areas were aggregated into large patches. This would be an interesting opportunity for future experimental landscape-level research, and would provide a strong inferential design for evaluating the effects of habitat area vs. habitat fragmentation on American marten (McGarigal and Cushman 2002). However, our results do suggest large impacts of habitat configuration at relatively low levels of habitat loss for this species.

The path-based approach used in this paper is a powerful, general method to evaluate species-specific landscape resistance. It has been used successfully for several species of very different life-history characteristics, including African elephant (*Loxodonta africana;* Cushman et al. 2010) and American black-bear (*Ursus americanus*; Cushman and Lewis 2010). The approach used in this study focuses on association between selected movement paths and landscape features, providing a powerful means to evaluate effects of habitat composition and configuration on movement behavior. However, habitat is not the only attribute of the environment that may affect organism movement. In territorial animals, such as American marten, the locations of home ranges of other territorial individuals may also affect movement. With knowledge of this information one could readily incorporate such interspecific data into this analysis. This would be done by overlaying homeranges of competitors on the map and including path intersection with them as a predictor variable in the case–control modeling of landscape resistance. This would provide a strong means to evaluate the relative effects of habitat vs. social interactions. We feel this would be a very valuable addition to the work presented here. However, we lacked detailed information about the specific identity of marten paths which made it impossible to determine which marten home ranges would be likely competitors. Ongoing research that has such information (as provided by GPS) will be able to evaluate this question. In our analysis, we generated random paths by shifting a distance that on average will be within the home range of the study animal, so that exclusion by adjacent territories should not have had a major effect on our results.

Conclusions

Marten choose foraging paths in unfragmented landscapes to maximize time spent in late seral mixed conifer forest patches which provide the highest density of prey species. In contrast, following landscape fragmentation by clearcuts, marten strongly select paths to avoid crossing unforested areas. This strong response to fragmentation reduces their ability to optimize foraging paths to vegetation type. Marten likely avoid non-forested areas in fragmented landscapes to reduce risk of predation and to benefit thermoregulation in winter, but in doing so they may suffer a secondary cost of decreased foraging efficiency. The strong differences between the pre- and post-harvest resistance models have several important implications for predicting ecological effects of landscape change. For example, consider a species that is dependent upon forest and will not move outside of forested patches. Suppose you study relationships between movement path selection and landscape structure in a landscape that is completely covered in forest. In this situation forest is a necessary element of the species' habitat and its occurrence and movement are totally dependent upon it. However, forest would not appear in a model predicting movement because forest is not limiting in a landscape that is completely covered in forest.

Thus, it is possible for a critical dependence upon certain landscape features to be invisible to analysis depending upon whether this landscape element limits movement.

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