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Using diffusion models to simulate the effects of land use on grizzly bear dispersal in the Rocky Mountains

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Abstract

Timber harvests proposed for Trail Creek Watershed, in southwestern Montana, U.S.A., have been opposed because grizzly bear (*Ursus arctos horribilis*) dispersal from northern Montana wildernesses into the Greater Yellowstone Ecosystem may be less likely. We used an individual-based model to simulate grizzly bear responses to: 1) region-level management practices represented by ownership patterns, and 2) watershed-level changes in habitat availability due to proposed harvests and road building. We assigned permeabilities (*i.e.*, values that represent how easily a bear can move through a patch) to ownership blocks (region-level) and habitat patches (watershed-level) based upon a literature review, and used a correlated random-walk diffusion model to simulate movements. Simulated bears were placed into rasterized landscapes in a stratified random manner. At the regional level, bears moved ≤ 1500 times (*i.e.*, ≈ 1530 km), and their destinations were tallied. At the watershed level, the number of moves required for bears to leave the watershed were tallied. Sensitivity analyses were used to determine the variability of the results with respect to changes in some parameters of interest (*i.e.*, permeabilities of private lands, harvest permeabilities, and disturbance indices).

With the permeability of private land set at 50 (range: 0 to 99), simulated grizzlies did not disperse from the Scapegoat and Bob Marshall Wildernesses into Yellowstone National Park (0 of 10000 simulated individuals). Under the assumptions of this model, a linkage between the wildernesses in northern Montana and Yellowstone does not appear to exist. However, a significant number of simulated grizzlies (41%) dispersed from Anaconda Pintler Wilderness, which is near Trail Creek Watershed, into the wilderness ES in eastern Idaho. A linkage may exist between these sites.

At the watershed-level, removal of forest habitat under proposed Harvest I (1.77% of the watershed cut) led to simulated grizzlies using slightly more moves (*i.e.*, ≤ 5.6%, P = 0.042) to exit the watershed than under existing conditions. Harvests of 3.5% of the watershed (planned Harvest 11) did not alter the number of moves required to exit the watershed (P = 0.068). When disturbances associated with roads and harvests were also examined, large increases in number of movements required to exit the watershed occurred (≤ 151%, P = 0.002). These analyses suggest that grizzly bears would be disturbed while timber harvests were ongoing, but that long-term changes in movement would not occur if roads were closed following harvests. The analyses demonstrate the utility of applying individual-based diffusion models to landscape-level movements of animals, and identifies the need for telemetry studies to determine movement rates through specific habitats.

1. Introduction

Grizzly bears (*Ursus arctos horribilis*) are listed as threatened in the contiguous U.S.A., and thus Federal law (U.S. Department of the Interior, Fish and Wildlife Service 1975) requires that populations be conserved. The population within the Greater Yellowstone Ecosystem appears in jeopardy, due in part to low genetic variability (Mattson and Reid 1991; Picton 1986). It has been hypothesized that dispersal of a few breeding grizzlies per generation from northern Montana populations into the Yellowstone population would improve the likelihood of the Yellowstone population persisting (Picton 1986). Plans made by the U.S. Department of Agriculture Forest Service (USDA FS) to harvest timber in Trail Creek Watershed, Montana, have been challenged by environmental groups (USDA FS 1991), in part because the harvests may alter the dispersal movements of grizzly bears across the watershed. Specifically, Trail Creek Watershed may be part of a landscape linkage joining grizzly bear populations in and around Glacier National Park and the Great Bear, Bob Marshall, and Scapegoat Wildernesses in northern Montana (Fig. 1), to Yellowstone National Park populations (Picton 1986; USDA **FS** 1991). However, such movements have not been documented to-date (Mattson and Reid 1991). Trail Creek Watershed also may be important in linking Yellowstone National Park and Montana wildernesses to the as-yet unpopulated (Davis *et al.* 1986; MacCracken *et al.* 1994) wilderness areas in eastern Idaho. Timber harvests within Trail Creek Watershed may alter rates of travel through the area by grizzly bears, because of reduced habitat quality (McLellan 1986), disturbance at harvest sites (McLellan and Shackleton 1989a, 1989b), or disturbances of bears along roads (Aune and Stivers 1983; Elgmork 1978; McLellan and Shackleton 1988). Presumably, reduced rates of travel across landscapes would decrease the likelihood of grizzly bears dispersing into (or out **of)** Yellowstone National Park (Buechner 1987).

We investigated the effects of proposed timber harvests in Trail Creek on grizzly bear dispersal by modelling landscape permeability, the corollary of landscape resistance (Forman and Godron 1986). In heterogenious landscapes, animals move more readily through some habitats than others, and these habitats are termed more permeable than habitats that restrict movement (Forman and Godron 1986). By assigning permeabilities to landscape patches based upon some attribute (*e.g.,* cover type), movements through landscapes may be modelled (Johnson *et al.* 1992).

Analytical methods using diffusion equations can model movements of animals in heterogeneous habitats (*e.g.,* Turchin 1991), but the models can be complex, and interpreting the results in ecological contexts can be difficult (Mange1 and Clark 1988). Incorporating specific habitat geometry, known to be important in determining rates of movements (Stamps *et al.* 1987) further increases model complexity. Instead, we used a simple individual-based model, specifically a correlated random-walk diffusion model, to simulate responses of grizzly bears to their habitats (Huston **et** *al.* 1988; Johnson **et** *al.* 1992). Rules for movements based upon permeabilities of nearby habitats were used to model responses to region-level management patterns, and changes in permeability due to timber harvest and road construction at the watershed-level. In the region-level analyses, dispersal (*i.e.,* potentially large movements by subadult bears) was modelled. At the watershed-level, the model could represent dispersal or more frequent movements (*e.g.,* seasonal migrations). We addressed the following questions: 1) is it likely that grizzly bears will disperse between the wilderness areas in northern Montana and Yellowstone National Park, during the period that harvests in Trail Creek might reduce habitat quality (say 20 to 50 years); 2) if dispersal does occur, is Trail Creek Watershed part of an important linkage; 3) would harvests and roads proposed for Trail Creek alter the frequency of movement across the watershed; and 4) would the mean direction of movement through the watershed be altered by proposed harvests and roads?

2. Methods

2.1. Overview

Two types of analyses were conducted. First, to examine whether or not Trail Creek Watershed is important as part of a landscape linkage connecting northern Montana and eastern Idaho to Yellowstone National Park, we used an area that encompassed parts of three states (*i.e.,* Idaho, Montana, and Wyoming [Fig. 1]). These analyses reflected differences in region-level management practices, with permeabilities assigned based upon land ownership. The second set of analyses used Trail Creek Watershed as the study area (a small portion of the watershed is excluded from the study area, but we will use the term for convenience), and permeabilities were assigned to habitat types within a detailed vegetation map. Permeabilities were modified based on proposed harvests and roads. The individual-based models were similar for all analyses. Permeabilities for landscape patches of interest (*i.e.,* private land, harvested areas, and areas of disturbance) were varied in sensitivity analyses to determine the effects on results. Sensitivity analyses identify whether or not different parameter values affect results markedly, indicate nonlinear responses in models, and determine responses over broad ranges when specific parameters are unknown (Mangel and Clark 1988).

To develop the model, we used Microsoft BASIC 7.0 Professional Development System (Microsoft Corporation, Redmond, Washington), running on TRI-STAR 80486 50 and 66 Mhz computers. The

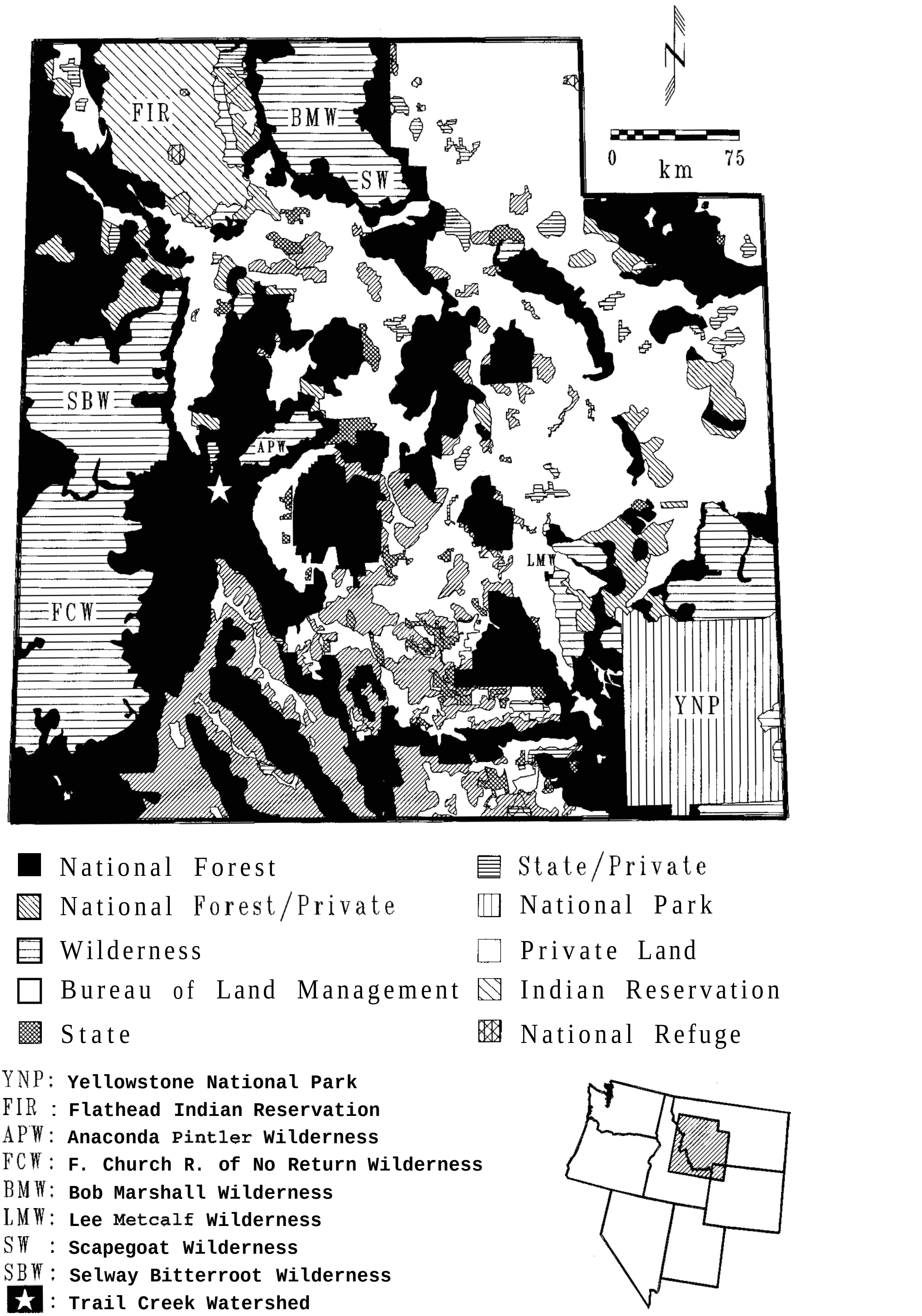

Fig. 1. **A** generalized ownership map of a three-state area, with 10 ownership categories. Selected areas are labeled and identified. (Digitized from a USDA FS map).

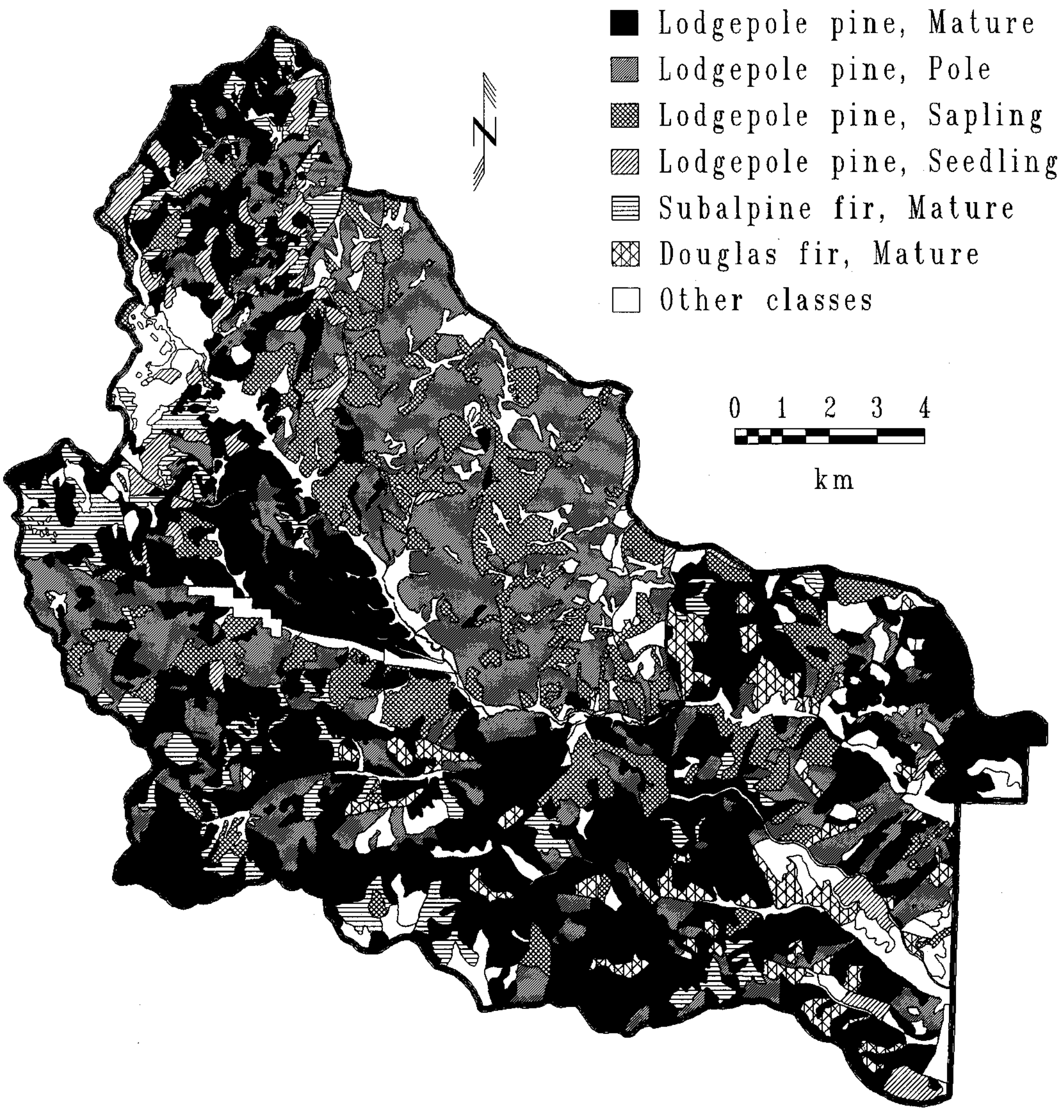

Fig. 2. Existing vegetation within Trail Creek Watershed, Montana. "Other classes" represents 20 categories that each comprise ≤ **3%** of the watershed area. (Digital data provided by USDA FS, Missoula, MT)

program included menu-driven selections that were used to conduct analyses, and individual paths of animals were plotted using real-time graphic displays.

2.2. *Study area*

Trail Creek Watershed (≈ 113°50' W, 45°40' N) is a 244 km^2 area in southwestern Montana, bordered on the west by the Continental Divide and Idaho, and to the east is Big Hole National Battlefield, Montana. The entire study area, excluding three small private inholdings, is part of the Beaverhead National Forest managed by the USDA FS (USDA FS 1990). State Highway 43 bisects the watershed into northern and southern sections. Elevations in the watershed range from about 1900 m to 2440 m.

We received from the USDA FS a series of geographic information system **(GIS)** files detailing the vegetation in Trail Creek. The vegetation was classified using aerial photographs, and compared with ground-truthed forest inventory data for accuracy (Dick Roulliex, USDA FS, Missoula, MT, pers. comm.). When compared to the inventory data, 75% ±

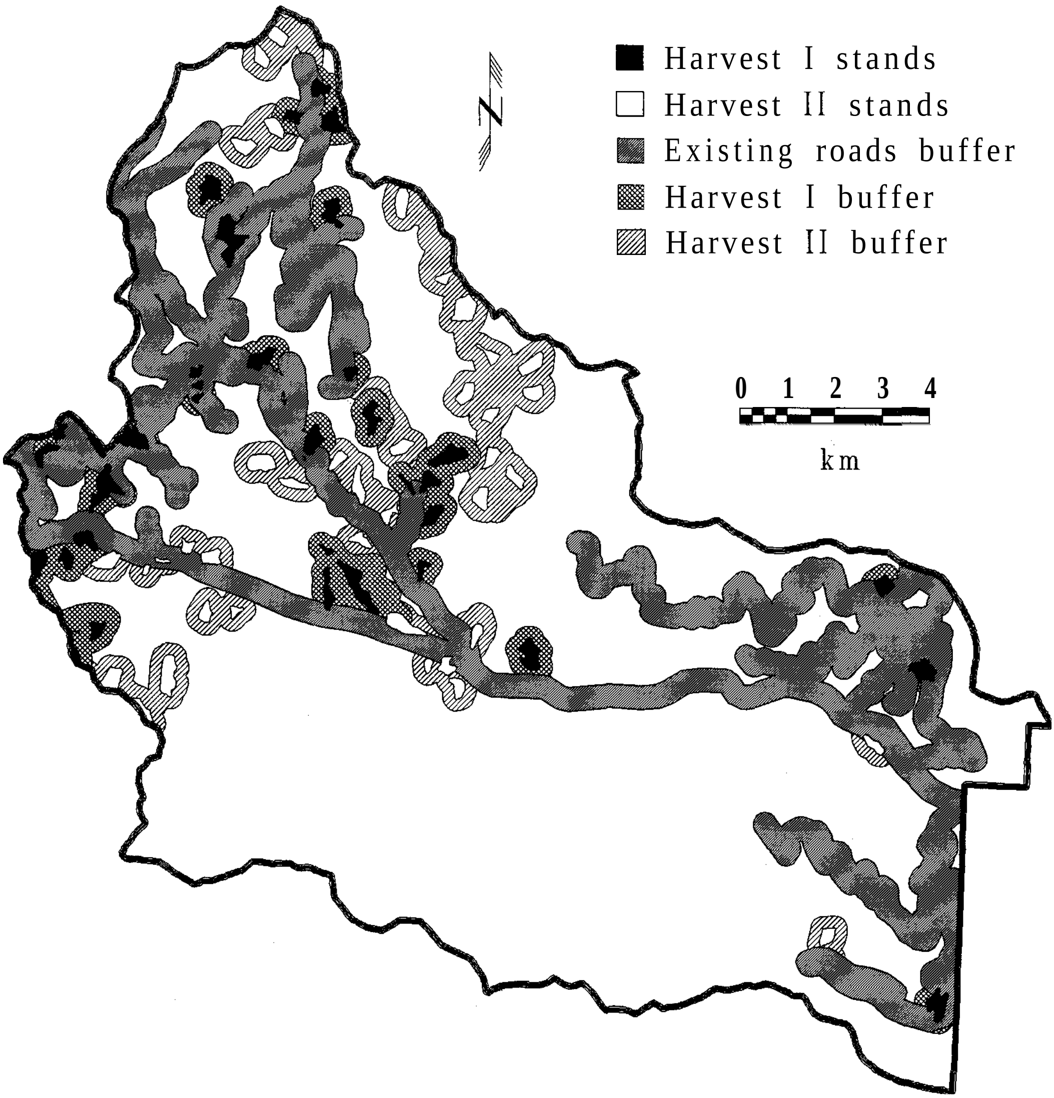

Fig. 3. **A** summary of timber harvests proposed for Trail Creek Watershed. Buffers *250* m from the centerline of roads were used **to** model disturbances **to** grizzly bears. (Digital data provided by USDA FS, Missoula, MT)

5% of the sites within each vegetation class were mapped correctly in the files (Wendel Hann, USDA FS, Missoula, MT, pers. comm.). We converted the files into PC ARC/INFO 3.4 D Plus (Environmental Systems Research Institute, Inc., Redlands, California) coverages and summarized cover types. Habitats were classified by USDA FS into 26 categories, including 5 forest types with 4 size-classes (Fig. 2). The primary tree species was lodgepole pine (*Pinus contorta* var. *latifolia*), covering 77.1% of Trail Creek Watershed (percent of cover by size-class: greater than pole – 37.2%; pole – 24.0%; sapling – 12.4%; and seedling – 3.5%). Other habitat types included subalpine fir *(Abies lasiocarpa*), greater than pole size (5.2%), and Douglas fir (*Pseudotsuga menziesii* var. *glauca*), greater than pole size (3.5%). The remaining habitat types each comprised ≤ **3%** of the area of Trail Creek Watershed, and included Engelmann spruce *(Picea engelmannii*) and whitebark pine *(Pinus albicaulis*).

The USDA FS has proposed to harvest timber at Trail Creek Watershed in two phases under the preferred plan (*i.e.*, plan G in USDA FS 1990; USDA FS 1991). In the initial harvest (Harvest I), 1.77% of the

Table 1. Permeabilities of ownership blocks to grizzly bear movements, assigned to land ownership types based upon a literature review and our opinion.

Land owner or classification	Permeability
National Forest	85
National Forest/Private	70
Wilderness	99
Bureau of Land Management	80
State	75
State/Private	55
National Park	90
Private	Variable
Indian	85
National Wildlife Refuge	95

watershed would be cut in 38 patches (Fig. 3), with cut trees primarily consisting of 120 to 180 year-old lodgepole pines. About half of Harvest I would be clearcuts, and the remainder would use other silvicultural methods (*e.g.,* shelterwood cuts, individual tree selection). Similar stands would be harvested in the second phase (Harvest II), which would include cuts in 1.73% of the watershed (Fig. 3) in 39 patches (USDA FS 1991). New roads constructed for Harvest I would total 12.8 km, including 3.8 km of snow roads, which do not disrupt vegetation or soil (USDA FS 1990). Harvest II would add 34.2 km of new roads (Fig. 3).

2.3. *The individual-based models*

The model we developed uses a map in raster format, with habitat patches (or ownership blocks) represented by multiple cells (Johnson *et al.* 1992). Each cell in a patch is assigned a permeability, ranging from 0 to 99, based upon a patch attribute (*i.e.,* habitat type or land owner), and information from a literature review. In a simulation, an individual is placed in a cell of a patch, and an adjacent cell is selected randomly from the eight primary directions (N, NE, E, SE, S, SW, W, and NW), or the cell currently occupied may be selected. The permeability of the cell selected is queried, and compared to a uniform random number (≥ 0 and < 100). If the random number is less than the permeability, the animal moves into the cell (or stays in place if the occupied cell was selected). For example, if the permeability of a cell is 50 the odds of an animal proceeding into it are 50%; if the permeability is 90 the odds are 90%. If the animal does not move, another direction (or perhaps the same direction; direction was selected "with replacement") is selected at random, and the process repeats. After the initial move of an individual, successive moves are correlated (Johnson *et al.* 1992), because the current direction of travel is favored. If an animal is moving north, for example, during a move the first cell that will be queried will be to the north. If the individual "decides" to move into the cell, the move is completed. Otherwise, a new direction is selected randomly, that permeability is queried, and the process repeats.

In a second set of analyses at the landscape scale, we used a "without replacement" selection of direction. If an individual had tried to move into a cell and failed, another direction was selected from the remaining seven. Otherwise, the model was the same as that described above.

In simulations, the model led to long displacements and straight paths for individuals moving through highly permeable patches, and short displacements and convoluted paths in patches with low permeability – in essence, increased searching behavior was displayed. For a summary of the history of diffusion models see Johnson *et al.* (1992).

2.4. *Region-level analyses*

The map of ownership patterns (Fig. 1) was digitized using ARC/INFO software, from an original paper map produced by the USDA FS. Complex ownerships (*e.g.,* checkerboard patterns and many small holdings) in the region were generalized while digitizing. Checkerboard ownerships were represented by mixed categories (*i.e.,* National Forest/Private and State/Private). The GIS coverage was converted to a raster-based map, with a grid of 440 x 440 cells. Each cell represented 1.02 km^2 of land.

Permeabilities were assigned to ownership types based upon our opinions, derived in part from a review of the literature described below. Actual permeabilities were not cited in literature, so we made conservative estimates based upon the review (Table 1). For example, wildernesses were assigned the highest permeability of 99, because they are our most natural area (Wilderness Act of 1964), and human access is restricted; in the model, if a simulated grizzly bear considers moving into a cell classed as wilderness, it will do so 99% of the time. National parks are not undisturbed, but are managed considering the conservation of wildlife (Bean 1983; National Park Service

Table 2. Permeabilities of Trail Creek Watershed habitat types to grizzly bear movements, based upon a literature review. The percent cover of each habitat type follows the permeability value. Table 2a includes forested habitats classified by tree species and age, and Table 2b includes habitats without age classes.

a.

Cover type	Size-class Seedling	Sapling	Pole	Greater than pole
Lodgepole pine	50 (3.5)	60 (12.4)	70 (24.0)	85 (37.2)
Subalpine fir	55 (0.2)	65 (0.4)	75 (1.8)	90 (5.2)
Douglas fir	45 (0.5)	55 (0.1)	70 (1.2)	80 (3.5)
Engelmann spruce	50 (> 0.1)	65 (> 0.1)	75 (1.1)	90 (0.2)
Whitebark pine/Lodgepole pine	– (0)	– (0)	99 (0.2)	– (0)
Undetermined spp.	30 (> 0.1)	– (0)	60 (> 0.1)	65 (0.1)

b.

Other classes	Permeability
Private	35 (0.7)
Riparian	70 (0.6)
Previously harvested areas still unvegetated	50 (3.0)
Undetermined	30 (0.2)
Proposed harvests — Harvest I	Variable (1.8)
Proposed harvests — Harvest II	Variable (1.7)

Organic Act of 1916), so they were assigned a somewhat lower permeability (90). We examined the effect of permeability of private land on results using sensitivity analyses, assigning a range of permeabilities (0, 10, 20, ..., 90, 99) to that parameter. Evidence is strong that grizzly bears that venture onto private lands are at high risk of being shot (Craighead 1980; Knight *et al.* 1988), and therefore we believe that biologically reasonable permeabilities for private land are ≤ 50.

Dispersal of 10000 grizzly bears was simulated in each of three analyses. In the first analysis, individuals were placed randomly within the Scapegoat Wilderness, and allowed to make 1500 moves (≈ 1530 km, or more than 3.4 times the width of the 440 x 440 grid). The numbers of individuals reaching Yellowstone National Park, Anaconda Pintler Wilderness, and the eastern Idaho wildernesses (Frank Church River of No Return and Selway Bitterroot Wildernesses), were tallied. A second, analogous test was conducted, with 10000 individuals dispersing from Yellowstone National Park. The third analysis placed grizzly bears within the Anaconda Pintler Wilderness, tracked their paths, and tallied their destinations. The final broad-scale analysis placed grizzly bears within the eastern Idaho wildernesses and tallied how many reached the other three destinations.

2.5. *Watershed-level analyses*

Permeability values were assigned to the 26 habitat types (Table 2) based upon a review of literature (Agee *et al.* 1989; Almack 1986; Aune and Stivers 1982; Bratkovich 1986; Butterfield and Key 1986; Craighead *et al.* 1982; Despain 1986; Hillis 1986; Knight 1980; Knight *et al.* 1987; Mattson *et al.* 1991; Mattson and Knight 1986; McLellan 1986; Servheen 1983; Servheen **and** Sandstrom 1993; Young 1986; Zager 1980). We were reluctant to assign specific permeabilities to harvested areas, based upon evidence that harvests can be beneficial or detrimental to grizzly bears (Bratkovich 1986; Hillis 1986; McLellan 1986; Zager 1980). We therefore used sensitivity analyses to determine the effect of the range of permeabilities (*i.e.,* 0, 10, *20,* **...,** 90, 99). To simplify the model, permeabilities of harvest patches were the same for any given analysis; we did not differentiate patches by silvicultural practice. Because the USDA FS proposed Harvest II as a second entry into the watershed, we modelled the effects of Harvest II by summing the cuts and roads from Harvest I and Harvest 11. So, in our analyses Harvest II refers to all harvests and roads proposed for Harvest I plus Harvest II.

Grizzly bears have been reported to avoid roads from a distance of 100 m (McLellan and Shackleton

1988) up to 1 km (Aune and Stivers 1983; Servheen *et al.* 1995; Young 1986). Similarly, grizzlies may avoid areas within 800 m of ongoing timber harvests (Young 1986). We are unable to predict when timber harvests would be ongoing in individual patches, but < 15% of the sites would be active at any one time (USDA FS 1991). To keep the model simple, but incorporate these avoidance observations, we chose to create *250* m buffers around roads and all harvested areas, and assigned disturbance indices to them. These disturbance indices were subtracted from the permeability values of the habitat types within the buffer, and the indices were varied in sensitivity analyses. For example, a patch of pole-size lodgepole pine (assigned permeability 70) within *250* m of a road or harvest, would have a permeability of 50 if the disturbance index was 20. In these analyses, harvest patches were assigned permeabilities of *50.*

The GIS coverage of existing vegetation for Trail Creek Watershed was converted to a 440 x 440 cell grid. Each cell represents a block of land *52.5* m^2. Other GIS coverages containing proposed harvest areas, and buffers around roads and harvests, were converted into a raster format with the same dimensions, and merged with the vegetation map.

A series of analyses were conducted that allowed comparisons of movements of bears with: 1) existing vegetation, and with proposed harvests in place; *2)* existing vegetation, and existing vegetation with current roads considered, and 3) existing vegetation and roads, and proposed harvests and roads in place. Each analysis entailed placing 10000 individuals into Trail Creek Watershed. The bears were placed in a stratified random manner, so that the probability of placement within any cell was determined by that cell's permeability *(i.e.,* a cell was selected randomly, then a random value [≥ 0, < 100] was generated and compared to the permeability to determine if a bear was placed at that cell). Simulated grizzlies were allowed to move up to 10000 times, or until they reached an edge of the watershed. If simulated bears reached the edge of the watershed or moved the maximum number of times, they stopped, and their destinations and the number of moves made were recorded. Wilcoxon signed ranks tests ($\alpha = 0.05$) were used (using SYSTAT, from SYSTAT, Inc., Evanston, IL) to identify significant differences between scenarios in the number of movements bears made exiting the watershed.

To determine if the general direction of dispersal was varying in response to harvests or new roads, we calculated the centroid of Trail Creek Watershed, then determined the eight quadrants (NNE, ENE, ESE, SSE, SSW, WSW, WNW, and NNW) from the centroid. In each analysis, the quadrant from which each simulated grizzly left Trail Creek Watershed (for those that had) was determined. MANOVA techniques were used to test the effect of harvest scenario and permeability on the number of grizzlies leaving the watershed in the eight directions.

3. Results

3.1. Region-level analyses

In the regional analyses, with the permeability assigned to private lands at 50 or less, 0 of 10000 individuals moved between Yellowstone National Park and the Scapegoat and Bob Marshall Wildernesses (Table *3).* With the permeability of private land at its highest (99), 0.1% of the bears beginning in Scapegoat Wilderness reached Yellowstone, and 5.3% from Anaconda Pintler Wilderness reached Yellowstone. Counts of bears reaching wilderness areas and Yellowstone were consistently lower when using the modified, "without replacement" turning algorithm (Table 3). These counts were lower because of the algorithm's tendency to increase turning behavior, but otherwise patterns appear to be similar to the "with replacement" results. Contrary to Picton (1986), in these simulations a significant landscape linkage between Yellowstone National Park and northern wildernesses did not exist. If this is correct, resource extraction within Trail Creek Watershed (9.6 km SW of Anaconda Pintler Wilderness) would not disrupt the frequency of grizzly bear movements to or from Yellowstone National Park because, under current conditions, the probability of these movements is already exceedingly small. This supports the view that any link that may have existed has been severed (Mattson and Reid 1991). Under the assumptions of the model, dispersal between the northern wildernesses and Yellowstone will be rare under any foreseeable circumstance.

Plotting the paths of individuals (Fig. 4 is an example with a subsample of 100 individuals), we determined that the Trail Creek area would be frequently used in movements from Anaconda Pintler Wilderness into the Selway Bitterroot Wilderness and Frank Church River of No Return Wilderness in eastern Idaho. For example, when private land was assigned a permeability of 50, 41.4% of 10000 individuals

***Table** 3.* The number of simulated grizzly bears (n = 10000 in each analysis) moving between Yellowstone National Park (YNP), Anaconda Pintler Wilderness (APW), the Scapegoat and Bob Marshall Wildernesses (SW), and the eastern Idaho wildernesses (EIW) (*i.e.,* Frank Church River of No Return Wilderness and Selway Bitterroot Wilderness). Results from analyses that included individuals selecting directions "with replacement" (see Methods) are shown in standard type, and those that were "without replacement" are shown in italics.

		Permeability index of private lands										
Source of individuals	Destination	0	10	20	30	40	50	60	70	80	90	99
Yellowstone National Park	APW	0	0	0	1	0	2	8	14	29	43	61
		0	*1*	0	*0*	*1*	*3*	*I*	*3*	*7*	*24*	*43*
	EIW	3	1	4	1	2	5	8	*8*	13	18	44
		2	2	*4*	1	2	*5*	I	5	*5*	*6*	*20*
	SW	0	0	0	0	0	*0*	1	1	2	17	42
		0	*0*	0	0	0	0	0	0	0	*7*	*23*
Anaconda Pintler Wilderness	EIW	3360	3529	3551	3705	3860	4114	4243	4410	4550	4444	4266
		2773	*2789*	*2976*	*3153*	*3222*	*3481*	*3539*	*3750*	*3883*	*3979*	*3800*
	SW	0	6	29	82	183	258	391	582	756	1018	1421
		0	0	*7*	*17*	*49*	*120*	*162*	*357*	*501*	*738*	*1151*
	YNP	332	265	259	251	257	211	268	*300*	357	428	529
		275	*226*	*204*	*241*	*215*	*236*	*234*	*274*	*274*	*314*	*418*
Scapegoat and Bob Marshall Wildernesses	APW	0	0	4	5	9	24	32	49	50	74	103
		0	0	0	*3*	*3*	*7*	*15*	*17*	*26*	*44*	*91*
	EIW	3	2	9	9	26	24	45	77	94	144	176
		I	*1*	*2*	*8*	*6*	18	*29*	*48*	*64*	*83*	*145*
	YNP	0	0	0	0	0	*0*	0	0	5	5	18
		0	0	0	0	0	0	*0*	0	*0*	*2*	*10*
Eastern Idaho Wildernesses	APW	168	199	239	251	318	322	350	397	416	542	581
		I62	*158*	*183*	*184*	*205*	*245*	*273*	*317*	*375*	*411*	*493*
	SW	4	7	21	28	61	86	118	129	218	291	420
		3	*3*	8	*11*	*20*	*35*	*57*	*85*	*I20*	*177*	*235*
	YNP	39	43	46	42	43	42	44	46	38	60	89
		43	*30*	*45*	*38*	*28*	*48*	*43*	*38*	*31*	*47*	*47*

moved from Anaconda into the wildernesses in eastern Idaho. The Selway Bitterroot Wilderness does not contain a viable population of grizzlies (MacCracken *et al.* 1986), but has been identified as an area with potential for recovery of grizzlies (Davis *et al.* 1986; U.S. Department of the Interior, Fish and Wildlife Service 1982). This result prompted us to evaluate how management of Trail Creek might affect the movement of grizzlies between the wildernesses of central and northern Montana, and wildernesses in eastern Idaho.

3.2. Watershed-level analyses

In our analyses of grizzly bear movements across Trail Creek Watershed, simulated grizzlies were allowed to move about, responding to proposed harvest patches. Few grizzlies (< 0.2%) failed to exit the watershed in 10000 moves; these individuals were assigned scores of 10000 in analyses. There was a small increase [illegible].6% for all permeabilities, P = 0.042) in the mean number of moves used to exit the watershed with 1.77% of the cover harvested (Harvest I), compared with existing conditions (Fig. 5). With 3.5% of the watershed harvested (Harvest II, 1.77% + 1.73%), the difference in number of movements was not significant (P = 0.068), nor was the difference between Harvest I and Harvest II (P = 0.343). In addition, the mean number of animals exiting from the eight sections of the watershed was independent of harvest level (Existing cover vs. Harvest I, P = 0.955; Existing cover vs. Harvest II, P = 0.921; Harvest I vs. Harvest II, P = 0.067), and thus the proposed harvests did not change the mean direction of movement of grizzlies.

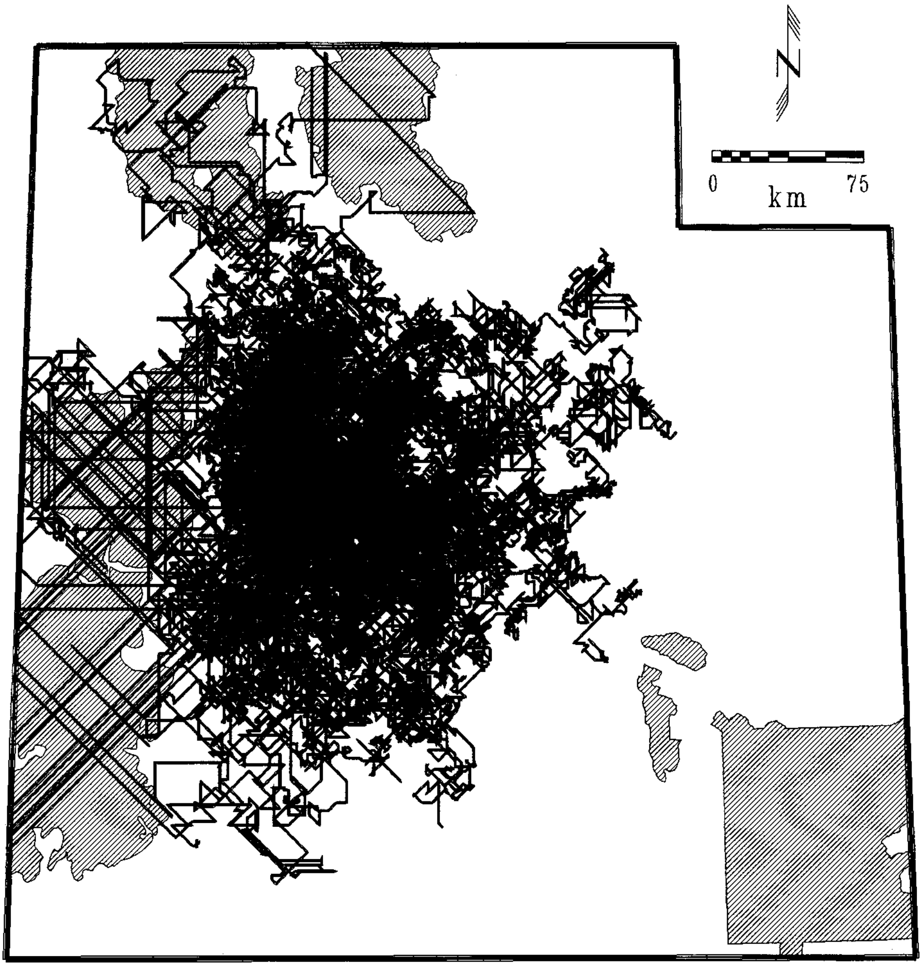

Fig. 4. Simulated movements of 100 grizzly bears originating in Anaconda Pintler Wilderness are mapped, using a permeability assigned to private lands of 50. None **of** the bears reached Yellowstone National Park, and three reached the Scapegoat and Bob Marshall Wildernesses (selected sites are identified on Fig. 1). One approached the Lee Metcalf Wilderness NW of Yellowstone, and several reached the Flathead Indian Reservation near Bob Marshall Wilderness. Many individuals moved through Trail Creek Watershed and reached the wildernesses in eastern Idaho.

When the effect of disturbance within 250 m of roads was included in the model, grizzlies required significantly more moves to exit the watershed (Existing road buffer vs. Existing cover, P = 0.001). For example, a mean of 1072 moves were required to exit the watershed if disturbance was excluded (Fig. *5* and Fig. 6, disturbance index = 0), but with a disturbance index of 50, 1711 moves were required (Fig. 6). The direction of movement out of the watershed was not altered by including disturbance (without harvests) in the model (Existing cover vs. Existing roads, P = 0.538).

Most of the 38 patches planned in Harvest I were positioned near existing roads (Fig. 3), so including disturbance buffers around new roads and harvests removed relatively little available cover. Including Harvest I in the model did not alter the number of moves grizzlies made while leaving the watershed (Harvest I vs. Existing roads buffer, P = 0.101), (Fig. 6). However, the direction animals exited the watershed was altered ($P < 0.001$).

Harvest II includes 10 cuts along a new road near Elk Creek, in the northcentral portion of Trail Creek Watershed (Fig. 3). **A** significant portion of available cover was removed when disturbance around these harvests was modelled. When Harvest II was included, grizzly bears made more moves while exiting the watershed (Harvest II vs. Existing roads buffer, P =

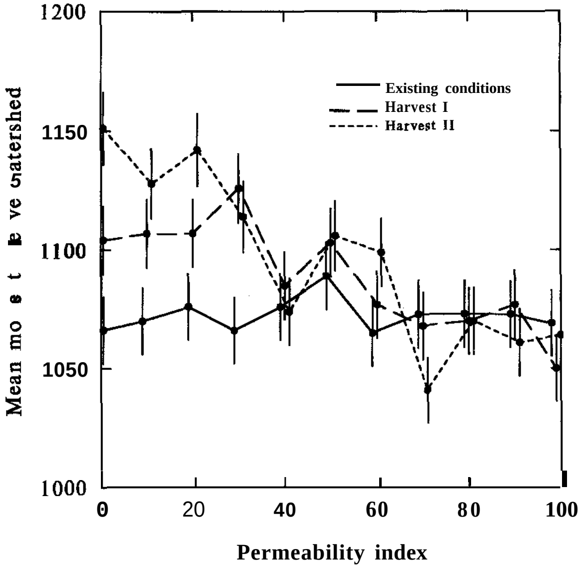

Fig. 5. Results of sensitivity analyses that varied the permeability assigned to harvested areas under three scenarios.

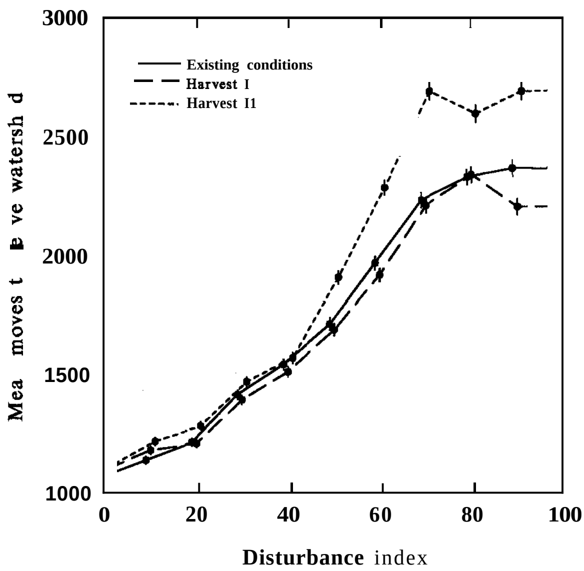

Fig. 6. Results **of** sensitivity analyses that varied the disturbances index associated with a *250* m buffer around roads and harvested areas.

0.002, Harvest II vs. Harvest I, P = 0.003) (Fig. **6).** The mean direction of travel was also altered, compared to the mean direction under existing conditions and that of Harvest I (Existing roads buffer vs. Harvest I, $P < 0.001$; Harvest I vs. Harvest II, $P < 0.001$).

4. Discussion

4.1. Applicability of the results

Picton (1986) developed his hypothesis of a link between Yellowstone and Glacier National Parks considering multiple generations of dispersals; populations may move long distances through each generation making relatively short movements. Simulations in our region-level analyses can represent both individual dispersals, or combined dispersals of individuals from several generations (assuming that habitat is available to support intermediate generations). Watershed-level analyses, however, represent movements of individuals because the periods of harvest and presence of clearcuts are relatively brief.

Allowing grizzlies to move about Trail Creek Watershed until they exited is realistic biologically; Trail Creek is much smaller than a typical grizzly bear home range. For example, four male grizzlies in Yellowstone had a mean home range of 3757 km^2 (Blanchard and Knight 1991), 15 times the size of Trail Creek Watershed. Blanchard and Knight (1991) recorded a male moving 105 km from its maternal range (Trail Creek Watershed is 28.5 km along the longest axis), and transplanted brown bears returned successfully from an average distance of 198 km (Miller and Ballard 1982). Almack (1986) notes an individual moving 45.7 km in a day, and a transplant grizzly bear in the Cabinet Mountains made daily movements of from 1.2 km to 5.8 km (Servheen *et al.* 1995).

4.2. Implications for management

When interpreting the results of this exercise, one must remember that it is an untested model, and that landscape permeabilities are not directly reported in the literature, and were inferred by us. Different permeabilities, and different movement algorithms, may alter the results. Considering this, our results indicate that Trail Creek Watershed may be part of a landscape linkage between the wilderness habitat in central and northern Montana and wilderness habitat in eastern Idaho, but not, under current conditions, to Yellowstone National Park. Under this model, to allow interbreeding within the region, grizzly bears may need to be transplanted (MacCracken *et al.* 1994; Servheen *et al.* 1995). For the parties debating harvests in Trail Creek, the absence of a landscape linkage may be both positive and negative. For those wanting to harvest wood, this research supports their belief that harvests in Trail Creek would not affect the Yellowstone grizzly bear population. Those opposing harvests in Trail Creek lose a politically strong position of conserving Yellowstone wildlife, but can still argue that timber harvesting in Trail Creek may affect movements of grizzlies between the wildernesses of the region. Similarly, the results indicate that the proposed roads and harvests (especially at the level of Harvest 11) could affect the watershed's permeability to grizzlies. This supports the concerns of opponents of harvesting in Trail Creek.

Our results indicate that the most important question regarding the effect of harvests on grizzly bear movements is whether or not bears are disturbed by harvesting activities and roads. Loss of 3.5% of cover, due to harvests in the planned configuration (Fig. 3), did not cause appreciable changes in the number of movements simulated grizzlies used to exit Trail Creek Watershed, or changes in direction of movement. However, including a disturbance index altered the mean direction of escapes, and a disturbance index $\geq$ 10 significantly increased the number of movements grizzlies needed to leave the watershed (Fig. 6).

Given that disturbances associated with resource extraction altered simulated grizzly bear movements markedly, and removal of 3.5% of the habitat did not, grizzlies should be affected by harvests in Trail Creek only during active cutting when roads are passable [roads would be blocked with logs upon completion of harvests, and closed to traffic (USDA FS 1991)]. Under the assumptions of the model, the watershed-level analyses indicate that, considering both existing and proposed manipulations, the greatest change to potential grizzly bear movements has been the construction of permanent roads prior to 1990 (Fig. 5, Fig. 6). This result, and the significant increase in moves used by grizzlies when exiting Trail Creek under Harvest II (with 34.2 km of roads modelled for disturbance) emphasizes that road building can be detrimental to movements of wildlife (Servheen and Sandstrom 1993). Harvesting in winter, when bears are in dens, would limit the disturbance, as would the use of snow roads (USDA FS 1991).

*4.3. **Comments** on **the modelling approach***

As with most modelling exercises, the models we used could be made more complex, and presumably more refined. For example grizzly bears may select streams and other riparian areas while traveling (Servheen 1983; Zager 1980). These features may be too small to be represented in the 52.5 m^2 cells of the model. Streams could be overlaid on the existing cover map, represented as lines of 52.5 m^2 cells, or a smaller cell size could be used. Ridge tops also may be used for travel (Zager 1980). Such relations could be modelled by including raster-based elevation maps (*e.g.,* digital elevation models). Individuals could also be made to be sensitive to habitats beyond the neighboring cells (the effects of this change will be explored in future models). In general however, we believe that modelers should be parsimonious in selecting variables for inclusion in analyses because a truly realistic model would be too complex to be understood (Mange1 and Clark 1988).

The specific results of our analyses are dependent upon the permeabilities we assigned to habitat types and other assumptions of the model, and the model itself has not been tested. Perhaps more noteworthy is our application of a diffusion model to a current, real-world, landscape-level management question. There are many questions in landscape ecology that concern the movement of animals through space, and individually-based diffusion models allow identification of key variables (Huston ***et al.*** 1988; Johnson ***et** al.* 1992). Once key variables are identified, other researchers, such as those using radio-telemetry, can focus on measuring these variables. With cooperation and feedback, modelers and field researchers can work towards a more complete understanding of how land use affects wildlife.

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References

Agee, J.K., Stitt, S.C.F., Nyquist, M. and Root, R. 1989. A geographic analysis of historical grizzly bear sightings in the North Cascades. Photo. Eng. and Remote Sense. 55: 1637–1642.

Almack, J.A. 1986. Grizzly bear habitat use, food habits, and movements in the Selkirk Mountains, northern Idaho. *In* Proceedings – Grizzly Bear Habitat Symposium. pp. 150–157. Compiled by G.P. Contreras and K.E. Evans, U.S.D.A. Forest Service General Technical Report INT-207.

Aune, K. and Stivers, T. 1983. Rocky Mountain Front grizzly bear monitoring and investigation. Montana Dept. of Fish and Wildlife, Helena, Montana.

Bean, M.J. 1983. The evolution of national wildlife law. Praeger Publishers, New York.

Blanchard, B.M. and Knight, R.R. 1991. Movements of Yellowstone grizzly bears. Biol. Conserv. 58: 41–67.

Bratkovich, A.A. 1986. Grizzly bear habitat components associated with past logging practices on the Libby Ranger District, Kootenai National Forest. *In* Proceedings – Grizzly Bear Habitat Symposium. pp. 180–184. Compiled by G.P. Contreras and K.E. Evans, U.S.D.A. Forest Service General Technical Report INT-207.

Buechner, M. 1987. Conservation in insular parks: simulation models of factors affecting the movement of animals across park boundaries. Biol. Conserv. 41: 57–76.

Butterfield, B.R. and Key, C.H. 1986. Mapping grizzly bear habitat in Glacier National Park using a stratified Landsat classification: a pilot study. *In* Proceedings – Grizzly Bear Habitat Symposium. pp. 58–66. Compiled by G.P. Contreras and K.E. Evans, U.S.D.A. Forest Service General Technical Report INT-207.

Craighead, J.J. 1980. A proposed delineation of critical grizzly bear habitat in the Yellowstone region. Int. Conf. Bear Res. and Manage. Monogr. No. 1.

Craighead, J.J., Sumner, J.S. and Scaggs, G.B. 1982. A definitive system for analysis of grizzly bear habitat and other wilderness resources. Wildlife-Wildlands Institute Monogr. No. 1, University of Montana, Missoula.

Davis, D.L., Melquist, W.E. and Graham, D. 1986. The Selway-Bitterroot ecosystem as grizzly bear habitat. *In* Proceedings – Grizzly Bear Habitat Symposium. pp. 158–162. Compiled by G.P. Contreras and K.E. Evans, U.S.D.A. Forest Service General Technical Report INT-207.

Despain, D.G. 1986. Habitat type and cover type as a base for grizzly bear habitat mapping and evaluation. *In* Proceedings – Grizzly Bear Habitat Symposium. pp. 230–233. Compiled by G.P. Contreras and K.E. Evans, U.S.D.A. Forest Service General Technical Report INT-207.

Elgmork, K. 1978. Human impact on a brown bear population (*Ursus arctos L.*). Biol. Conserv. 13: 81–103.

Forman, R.T.T. and Godron, M. 1986. Landscape ecology. John Wiley and Sons, New York.

Hillis, M. 1986. Enhancing grizzly bear habitat through timber harvesting. *In* Proceedings – Grizzly Bear Habitat Symposium. pp. 176–179. Compiled by G.P. Contreras and K.E. Evans, U.S.D.A. Forest Service General Technical Report INT-207.

Huston, M., DeAngelis, D. and Post, W. 1988. New computer models unify ecological theory. BioScience 38: 682–691.

Johnson, A.R., Wiens, J.A., Milne, B.T. and Crist, T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology 7: 63–75.

Knight, R.R. 1980. Biological considerations in the delineation of critical habitat. *In* Bears – their biology and management. pp. 1–4. Edited by C.J. Martinka and K.L. McArthur. The Bear Biology Association, Kalispell, Montana.

Knight, R.R., Blanchard, B.M. and Eberhardt, L.L. 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. Wildl. Soc. Bull. 16: 121–125.

Knight, R.R., Blanchard, B.M. and Mattson, D.J. 1987. Yellowstone grizzly bear investigation: report of the Interagency Study Team, 1986. U.S. Department of the Interior, National Park Service. Washington, D.C.

MacCracken, J.G., Goble, D. and O'Laughlin, J. 1986. Grizzly bear recovery in Idaho. Idaho Forest, Wildlife and Range Policy Analysis Group, Report No. 12. University of Idaho, Moscow.

Mangel, M. and Clark, C.W. 1988. Dynamic modeling in behavioral ecology. Princeton University Press. Princeton, New Jersey.

Mattson, D.J., Blanchard, B.M. and Knight, R.R. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. Can. J. Zool. 69: 1619–1629.

Mattson, D.J. and Reid, M.M. 1991. Conservation of the Yellowstone grizzly bear. Conserv. Biol. 5: 364–372.

Mattson, D.J. and Knight, R.R. 1986. Evaluation of grizzly bear habitat using habitat type and cover type classifications. *In* Proceedings – Grizzly Bear Habitat Symposium. pp. 135–143. Compiled by G.P. Contreras and K.E. Evans, U.S.D.A. Forest Service General Technical Report INT-207.

McLellan, B.N. and Shackleton, D.M. 1989a. Grizzly bears and resource-extraction industries: habitat displacement in response to seismic exploration, timber harvesting and road maintenance. J. Appl. Ecol. 26: 371–380.

McLellan, B.N. and Shackleton, D.M. 1989b. Immediate reactions of grizzly bears to human activities. Wildl. Soc. Bull. 17: 269–274.

McLellan, B.N. and Shackleton, D.M. 1988. Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. J. Appl. Ecol. 25: 451–460.

McLellan, B.N. 1986. Use-availability analysis and timber selection by grizzly bears. *In* Proceedings – Grizzly Bear Habitat Symposium. pp. 163–166. Compiled by G.P. Contreras and K.E. Evans, U.S.D.A. Forest Service General Technical Report INT-207.

Miller, S.D. and Ballard, W.B. 1982. Homing of transplanted Alaskan brown bears. J. Wildl. Manage. 46: 869–876.

Picton, H.D. 1986. A possible link between Yellowstone and Glacier grizzly bear populations. Int. Conf. Bear Res. and Manage. 6: 7–10.

Servheen, C. 1983. Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. J. Wildl. Manage. 47: 1026–1035.

Servheen, C. and P. Sandstrom. 1993. Ecosystem management and linkage zones for grizzly bears and other large carnivores in the Northern Rocky Mountains in Montana and Idaho. U.S. Department of the Interior, Fish and Wildlife Service, Endangered Species Technical Bulletin XVIII (3): 10–13.

Servheen, C., Kasworm, W.F. and Thier, T.J. 1995. Transplanting grizzly bears *Ursus arctos horribilis* as a management tool – resulting from the Cabinet Mountains, Montana, USA. Biol. Conserv. 71: 261–268.

Stamps, **J.A.,** Buechner, M. and Krishnan, V.V. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. Am. Nat. 129: 533–552.

Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72: 1253–1266.

U.S. Department **of** Agriculture, Forest Service. 1990. Trail Creek final environment impact statement. U.S. Department of Agriculture, Northern Region, Wisdom, Montana.

U.S. Department of Agriculture, Forest Service. 1991. Trail Creek supplemental information report. U.S. Department of Agriculture, Northern Region, Wisdom, Montana.

U.S. Department of the Interior, Fish and Wildlife Service. 1975. 40 Fed. Reg. 31736.

U.S. Department of the Interior, Fish and Wildlife Service. 1982. Grizzly bear recovery plan. U.S. Department of the Interior. Washington, D.C.

Young, D.L. 1986. Cumulative effects analysis of grizzly bear habitat on the Lewis and Clark National Forest. *In* Proceedings – Grizzly Bear Habitat Symposium. pp. 217–221. Compiled by G.P. Contreras and K.E. Evans, U.S.D.A. Forest Service General Technical Report INT-207.

Zager, P.E. 1980. The influence of logging and wildlife on grizzly bear habitat in Northwestern Montana. M.S. Thesis, Univ. of Montana, Missoula.