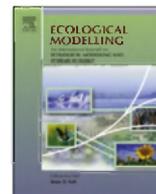




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How humans shape wolf behavior in Banff and Kootenay National Parks, Canada

Marco Musiani^a, Sk. Morshed Anwar^b, Gregory J. McDermid^c, Mark Hebblewhite^d,
Danielle J. Marceau^{b,*}^a Faculty of Environmental Design, University of Calgary, Calgary, AB, T2N 1N4 Canada^b Department of Geomatics Engineering, University of Calgary, 2500 University Drive NW, Calgary, AB, T2N 1N4 Canada^c Department of Geography, University of Calgary, Calgary, AB, T2N 1N4 Canada^d Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, ZIP code 59812, USA

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ABSTRACT

This paper describes the conceptualization and implementation of an agent-based model to investigate how varying levels of human presence could affect elements of wolf behavior, including highway crossings; use of areas in proximity to roads and trails; size of home ranges; activities, such as hunting, patrolling, resting, and feeding pups; and survival of individuals in Banff and Kootenay National Parks, Canada. The model consists of a wolf module as the primary component with five packs represented as cognitive agents, and grizzly bear, elk, and human modules that represent dynamic components of the environment. A set of environmental data layers was used to develop a friction model that serves as a base map representing the landscape over which wolves moved. A decision model was built to simulate the sequence of wolf activities. The model was implemented in a Java Programming Language using RePast, an agent-based modeling library. Six months of wolf activities were simulated from April 16 to October 15 (i.e., a season coherent with regard to known wolf behaviors), and calibrated with GPS data from wolf radiocollars ($n = 15$) deployed from 2002 to 2004. Results showed that the simulated trajectories of wolf movements were correlated with the observed trajectories (Spearman's $\rho = 0.566$, $P < 0.001$); other critical behaviors, such as *time spent at the den* and *not traveling* were also correlated. The simulations revealed that wolf movements and behaviors were noticeably affected by the intensity of human presence. The packs' home ranges shrank and wolves crossed highways less frequently with increased human presence. In an extreme example, a wolf pack whose home range is traversed by a high-traffic-volume highway was extirpated due to inability to hunt successfully under a scenario wherein human presence levels were increased 10-fold. The modeling prototype developed in this study may serve as a tool to test hypotheses about human effects on wolves and on other mammals, and guide decision-makers in designing management strategies that minimize impacts on wolves and on other species functionally related to wolves in the ecosystem.

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1. Introduction

Managers of protected areas must meet the challenging mandate of balancing demand for public opportunities to use and enjoy the landscape with the obligation to protect ecological integrity. As a result, there is an on-going need to develop research tools to explore human–environment relationships and predict the impact of human activities on wildlife species. This is the case for Banff and Kootenay National Parks, which provide habitat to a number of charismatic wildlife species including wolves (*Canis lupus*), grizzly (*Ursus arctos*) and black (*Ursus americanus*) bears, elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule

deer (*Odocoileus hemionus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). However, Banff and Kootenay National Parks also receive more than four million human visitors every year who partake in a variety of recreational activities including skiing, camping, and hiking. Considering these figures and the increasing conflicts between wildlife and humans in this rich landscape, Parks Canada (2007) recently stated the need to understand the degree of human impact on wildlife movement and habitat in this region.

Large carnivores are known to be susceptible to human impacts due to their low density, high trophic level, and low reproductive rate (Nielson et al., 2004), and to the loss and fragmentation of their habitats, human-induced mortality, and loss of prey base (Carroll et al., 2001; Larsen and Ripple, 2006). Wolves, in particular, can be greatly affected by the cumulative effects of human activities (Fritts et al., 2003), as has been demonstrated by the history of humans and

* Corresponding author. Tel.: +1 403 220 5314; fax: +1 403 284 1980.
E-mail address: dmarceau@ucalgary.ca (D.J. Marceau).

wolves in North America. In large areas of the Canadian Rockies, as in many other parts of North America, wolf populations were systematically reduced by predator control efforts from approximately 1850 to 1930 (Musiani and Paquet, 2004). Wolves were eventually extirpated from Banff and Kootenay National Parks in the late 1940s; however, they later recolonized the mountain Parks where upon the population grew and extended south to Montana, Idaho, and Washington in the USA (Paquet et al., 1996).

Nowadays, wolves are still impacted by human activities. Previous studies have demonstrated that wolves avoid man-made landscape features (e.g., roads) where human use is high, and in general wolf movements are influenced by human use (Whittington et al., 2004; Mech, 1995). However, wolves also use features like trails and roads where human activity is lower (Paquet et al., 1996; Callaghan, 2002). Wolves show a strong affinity to low-elevation valley bottoms in the Banff and Kootenay National Parks region due to the effects of physiography, weather, prey abundance, and prey distribution (Paquet et al., 1996). These valleys are also used by humans for convenient transportation, higher probability of observing wildlife, and scenic beauty and thus the potential for human influence on wolf behavior and survival is high.

A number of approaches have been used to study the important issue of human impacts on wolves using multiple regression models (Mladenoff et al., 1997; Purves and Doering, 1999; Larsen and Ripple, 2006; Boyd-Heger, 1997), discriminant function analysis (Corsi et al., 1999), hidden Markov models (Franke et al., 2006), spatial behavioral models (Haight et al., 1998), stochastic differential equations (Boyce, 1995) and a friction or modified “least-cost path” model (Paquet et al., 1996). These established techniques to model human–wolf interactions use a *snapshot* approach to analysis that is limited by coarse temporal (seasonal variation) and spatial (landscape level) resolutions, or are designed at the population level. Thus, they cannot predict the behavior of social units such as wolf packs. This is critical, since wolf packs have inherent behavioral variability (Mech, 1970) and may react differently to human-induced changes depending both on the timing of the interaction (Boitani, 1982) and its location (Mladenoff et al., 1995). For example, there is considerable variability in distances covered by wolf packs due to the differences in activities performed on a particular time frame (e.g., a day) such as hunting, patrolling of territory, and moving towards the den (Mech, 1970; Van Ballenberghe et al., 1975; Fritts et al., 1981; Jędrzejewski et al., 2001). Such variation of pack behavior is not taken into account in aggregated models or former models of human impacts.

From a methodological point of view, in addition to the need to model individuals belonging to populations, there is a parallel need to understand and model species within ecological communities comprised of other interacting species. Strong direct impacts of human presence on single species have been studied, and such impacts are frequently monitored for conservation purposes, although human impacts are often habitat-mediated (Ehrlich and Ehrlich, 1981). However, any species' response, and/or resilience to responses, also depends upon interactions with other species in the ecosystem (MacArthur, 1955).

In this study, a spatially and temporally explicit, individual-based modeling approach (Grimm and Railsback, 2005), hereafter called an agent-based model (ABM) (Bousquet and Le Page, 2004; Marceau, 2008) was used to investigate wolf–human interactions in Banff and Kootenay National Parks, in western Canada. ABMs are particularly suitable for formulating the processes of a system by taking into account the temporal and spatial dynamics at the individual level. They have been applied to study predation and competition dynamics (Bousquet et al., 1994), disease spread (Barrett et al., 2005), and population dynamics (Parry et al., 2004) and to investigate the effects of changing landscape structure, human activities or management practices on animal species

(Ahearn et al., 2001; Dumont and Hill, 2001; Cramer and Portier, 2001; Topping et al., 2003; An et al., 2005; Bennett and Tang, 2006; Anwar et al., 2007; Bennett et al., 2009).

This paper describes in detail an ABM that has been designed and implemented as a research and exploration tool to dynamically simulate the behavior of wolf packs in the Canadian Rockies. Our ABM considers human impacts on wolf packs and the interaction of wolves with grizzly bears (used as an example of a potentially competing predator), with elk (i.e., the most important prey species), and with other habitat factors of known importance to the species. The model was used specifically to investigate the impact of increasing levels of human presence on wolf movement patterns in Banff and Kootenay National Parks. It should be seen as a prototype that focuses on answering questions regarding how humans affect wolf habitat selection around roads and trails, create disturbances to crucial wolf activities that could lead to shrinkage of home ranges, and impact individual wolf mortality and survival. This model may serve as a useful tool to test hypotheses about human–wolf interactions, investigate future scenarios, and guide decision-makers in designing conservation management strategies.

2. Methodology

In this section, a description of the study area and the datasets used to calibrate the agent-based model is provided. It is followed by a presentation of the conceptual model and its implementation.

2.1. Study area

The 6641 km² study area includes portions of Banff National Park in Alberta and Kootenay National Park in British Columbia, about 130 km west of the City of Calgary (Fig. 1). Topography is rugged, ranging from 1000 to 3500 m in elevation. The climate is strongly seasonal, and characterized by long, cold winters, and short, warm summers with most precipitation occurring in spring. Low-elevation valley-bottoms contain the highest-quality habitat for wolves and elk, and are characterized by lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) forests interspersed with riparian white spruce (*Picea glauca*)–willow (*Salix* spp.), aspen (*Populus tremuloides*) parkland, and grassland systems. Elk are the primary prey of wolves, although alternate prey species include white-tailed deer, mule deer, moose, bighorn sheep, and mountain goats. Other large mammals include grizzly and black bears, which are omnivorous and feed on vegetation and on the same prey items used by wolves.

The Banff and Lake Louise town sites are two very popular destinations located within the study area that draw tourists coming from Canada and internationally year-round. The study area is bisected by three major highways, namely the Trans-Canada Highway 1, Highway 1A, and Highway 93, and includes several other transportation corridors. The Trans-Canada Highway 1 has high volumes of traffic year-round. Additional details of the study area can be found in Paquet et al. (1996) and Callaghan (2002).

2.2. Environmental data

Several spatial datasets, including elevation, aspect, slope, land cover, and trail and road networks were used to characterize the study area's physical and biotic environments. A 30 m² spatial resolution digital elevation model (DEM) and the trail and road network datasets were provided by Banff and Kootenay National Parks. Aspect and slope were derived from the DEM using the Spatial Analyst extension of ArcMap 9.2 (ESRI, 2009). A 30 m² spatial resolution vegetation land-cover map including 16 classes generated from Landsat Thematic Mapper remote sensing images was

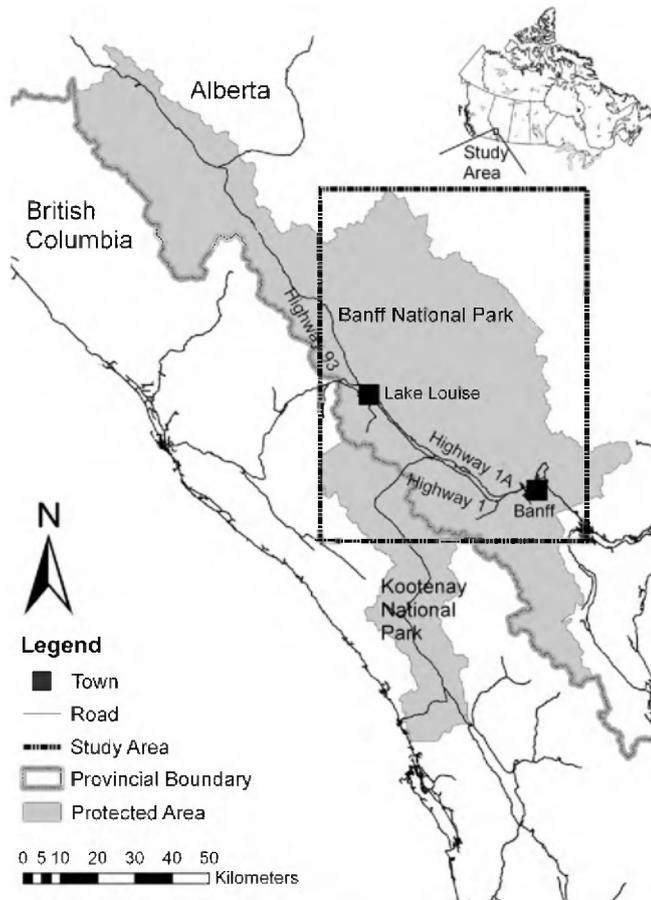


Fig. 1. Location of the study area within Banff and Kootenay National Parks within the Central Rocky Mountains of Canada.

provided by the Foothills Research Institute Grizzly Bear Research Program (McDermid et al., 2009).

Two resource selection function (RSF; Boyce and McDonald, 1999; Manly et al., 2002) models for elk and grizzly bears, respectively, were also used in this project to characterize the probable locations of elk and grizzly bears on the landscape. RSFs were used to model each species' preferred habitats (i.e., the relative probability of selecting a habitat) in the study area in a Geographic Information System (GIS). A *used-available* logistic regression RSF sampling design was employed where *used* locations were defined by locations provided by Global Positioning System (GPS) radio collars that were placed on individual elk and grizzly bears in the study area. Details on these datasets of GPS locations can be found in Hebblewhite et al. (2008) for elk and in Garshelis et al. (2005) for grizzly bears. Habitat characteristics of wildlife GPS locations were compared to characteristics at 10,000 randomly located points, which were produced with the Hawth's Tools Extension (Beyer, 2004) in ArcGIS 9.2 (ESRI, 2009) and represented *available* locations in the study area (Nielson et al., 2004).

Habitat characteristics used in elk and grizzly RSF models included canopy closure, the ratio of deciduous to coniferous trees, land-cover type, the annual maximum normalized difference vegetation index (NDVI), annual NDVI range, distance to roads, distance to facilities, distance to campgrounds, distance to trails, aspect (five classes: flat, north, south, east, west), elevation, and slope. A Spearman's rank correlation (Zar, 1984) was calculated for all variables considered in each of the models (elk and grizzly bear). If the correlation coefficients for any two variables were greater than 0.7, these variables were considered highly correlated and removed

from further analyses (Manly et al., 2002). For each species (elk and bear), a logistic regression analysis was conducted on a set of candidate models that included different combinations of the above-described habitat variables. Akaike's Information Criteria (AIC), an information-theoretic approach, was used to select the logistic regression model that best predicted species occurrence (Burnham and Anderson, 2002; Anderson and Burnham, 2002; Johnson and Omland, 2004; Stephens et al., 2005).

The elk and grizzly bear RSF models were validated. For both species, linear regression R^2 values calculated between each withheld subset of data and the model predictions, using 4/5 of data, were significant ($n=5$ iterations, $P<0.001$), and close to 1 (average value of 0.993 for elk and 0.899 for grizzlies) indicating that the models were valid according to Johnson et al.'s (2006) criteria. Valid elk and grizzly bear RSFs were used to generate maps of the relative probability of habitat selection of elk and grizzly bears across the study area during the summer (i.e., the study period) using Raster Calculator in ArcGIS 9.2 (ESRI, 2009).

2.3. Human presence data

Human presence was determined by using two datasets. The first one was gathered by Pacas (1996) who categorized roads and trails within the study area into one of six human-use classes based on relative use (Table 1). Pacas' classes 1 and 2 represent the Trans-Canada Highway 1 and all other roads, respectively, while classes 3–6 represent high-use to low-use trails. Secondly, data on individuals, groups or cars originally collected by Parks Canada and Alberta Economic Development and Tourism Authority using traffic and trail counters at different entry points into Banff and Kootenay National Parks were compiled to assess levels of and changes in traffic by hour. By combining both datasets, human use on all trails and roads in the study area and its hourly changes was characterized (Table 1).

2.4. Den locations and home ranges of wolf packs

GPS collar data acquired during the winter and summer seasons between 2002 and 2004 from 15 wolves belonging to five packs were used to identify wolf den locations and home ranges. The locations were collected at 15-min, half an hour, 1-h, or 2-h intervals, depending upon some known limitations of the satellites' signal, on variation in vegetation and topography, and on the ability to compute and record locations by the GPS collar units (Hebblewhite et al., 2007). An analysis of the quality and frequency of these GPS locations revealed that the signals recorded at 2-h intervals were consistent and unbiased (according to the definition of Hebblewhite et al., 2007) and were therefore retained for further analyses.

Home ranges were delineated by calculating a 95% kernel density estimator with a smoothing factor of 7000 m (Seaman and Powell, 1996) of the wolf telemetry data using Hawth's Tools (Beyer, 2004) in ArcGIS 9.2. Dens were detected visually by identifying the maximum concentration of observed wolf locations within the 95% kernel polygon. The location of dens was later confirmed by field observations. The home ranges of wolf packs 1 and 5 are traversed by highways (Fig. 2). Pack 1 contains a small segment of Highway 93 and Highway 1 in the southwest part of the home range, whereas Pack 5's home range is literally split by Highway 1, 1A, and 93.

2.5. Conceptualization and implementation of the ABM model

The ABM model developed in this study consists of four inter-related sub-models for wolves, bears, elk, and humans (Fig. 3).

Table 1
Human-use levels at each hour of the day on six different classes of roads and trails in Banff and Kootenay National Parks, Canada.

Hour	Class 1 (Highway 1)	Class 2 (roads)	Class 3 (high-use trails)	Class 4 (medium use trails)	Classes 5 and 6 (low-use trails)
1	12	1	0	0	0
2	0	0	0	0	0
3	0	0	0	0	0
4	0	0	0	0	0
5	0	0	0	0	0
6	24	2	0	0	0
7	84	8	1	0	0
8	228	23	2	0	0
9	527	53	5	1	0
10	1054	105	11	1	0
11	1462	146	15	1	0
12	1581	158	16	2	0
13	1438	144	14	1	0
14	1390	139	14	1	0
15	1414	141	14	1	0
16	1402	140	14	1	0
17	1282	128	13	1	0
18	1066	107	11	1	0
19	779	78	8	1	0
20	539	54	5	1	0
21	383	38	4	0	0
22	204	20	2	0	0
23	96	10	1	0	0
24	36	4	0	0	0

The primary component is the wolf model, wherein wolves are simulated as cognitive agents that have a mental representation of their environment. Bears, elk, and humans are represented as objects without cognitive abilities, and contribute to the dynamic components of the environment in which wolves move and perform activities. Each sub-model is described in the following sections.

2.5.1. *Wolf sub-model*

The wolf sub-model is comprised of two components: (i) the landscape over which wolves move, and (ii) their movement behavior. The landscape is represented as a friction map, which is composed of several static environmental layers, while the wolf's movement behavior is simulated as a correlated and biased random walk based on a decision model. The wolf model is composed

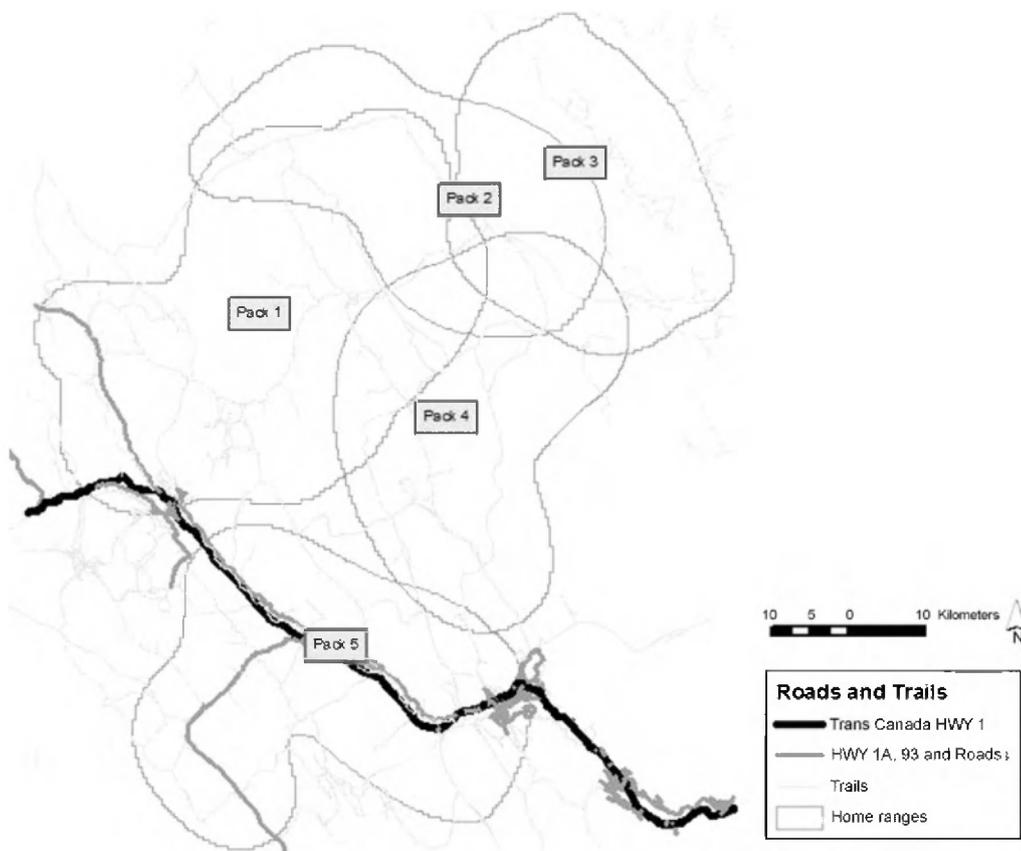


Fig. 2. Estimated home ranges of five wolf packs in Banff and Kootenay National Parks, Canada. Road and trail networks are also illustrated. Home ranges were delineated by calculating a 95% kernel density estimator of wolf telemetry locations.

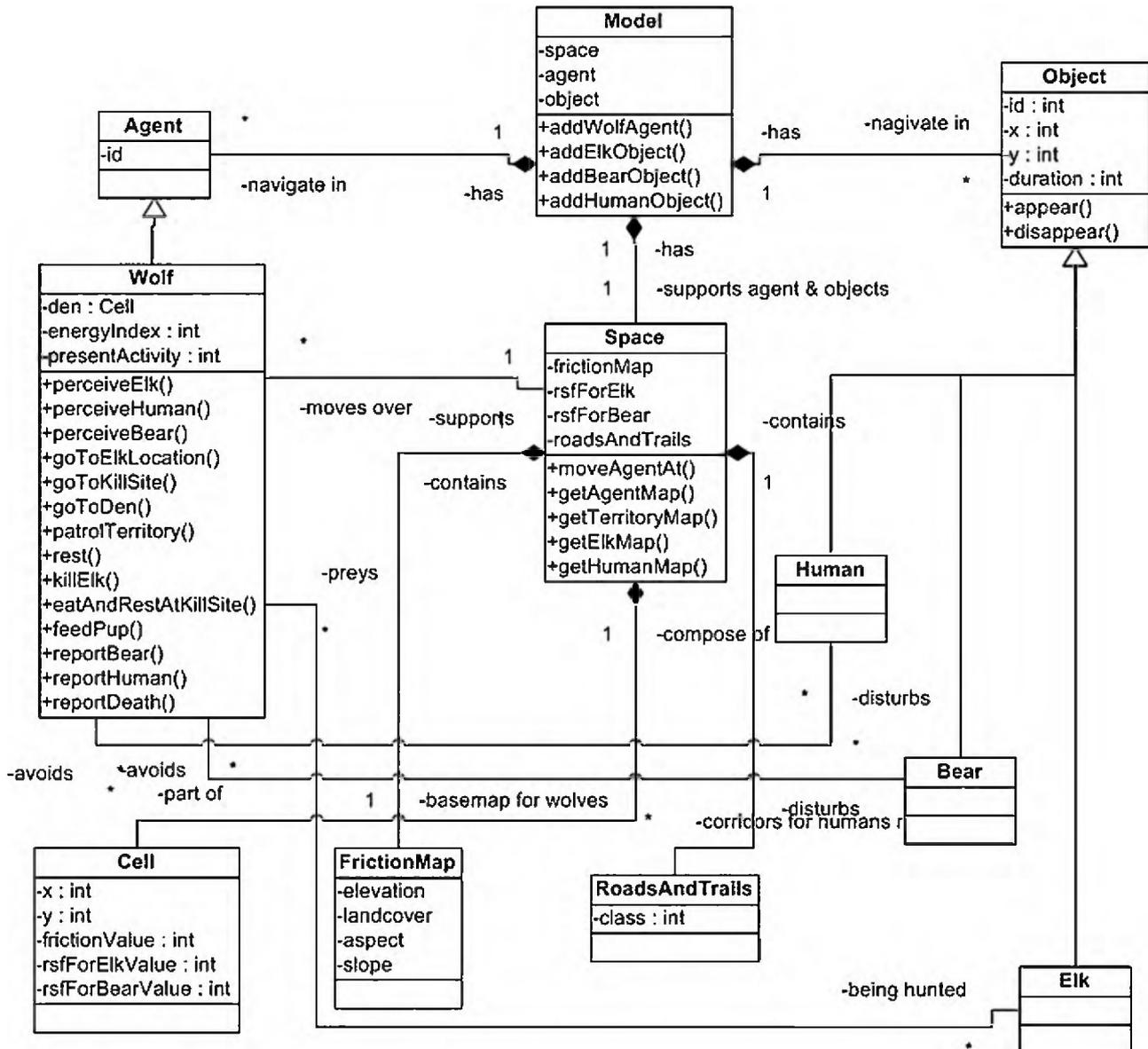


Fig. 3. The conceptual agent-based model of wolves in Banff and Kootenay National Parks, Canada.

of five individual wolves. Each wolf represents a pack, based on the assumption that wolves belonging to the same pack have similar behavioral patterns, an established notion in behavioral studies on wolves (Young and Goldman, 1944; Mech, 1970). Wolves are represented as agents in that they have cognitive capabilities and are associated with a specific den and a home range. They have a mental representation of their environment in which they move to perform various activities.

Paquet et al. (1996) found that wolves in the study area selected flat valley-bottoms, south and southwest facing slopes, and deciduous vegetation at elevations below 1850 m. These findings were used to weigh the influence of these environmental factors on wolf movements (Table 2) and, with this objective, a friction map (i.e., the landscape over which wolves move) was produced using spatial datasets of land cover, elevation, slope, and aspect. However, as a first step needed to obtain the map, the original land-cover layer was re-classified into a reduced number of classes (Table 3) to match those used by Paquet et al. (1996). Weightings were equivalent to preference assessments that took into consideration the options available to wolves to choose any habitat classes; they

do not correspond to selection coefficients that in ecology typically compare used vs. available habitats. The chosen spatial resolution of the friction map was 100 m², to take into account the fact that the minimum distance at which wolves perceive bears and humans is 200 m (see below). Thus at each time step, wolves move 100 m, i.e., from one 100 m² cell to a neighbouring 100 m² cell. The temporal resolution (time step) of the model is 1 min, a very fine scale level of structuring that is appropriate for the variability in speed and resting periods exhibited by wolves in nature (Musiani et al., 1998; Mech, 1970).

Table 2
Weighting of habitat variables used to build a friction map of wolf movement in Banff and Kootenay National Parks, Canada.

Habitat variables	Eigenvector weights
Elevation	53.1
Aspect	17.9
Land cover	13.7
Slope	15.3
Total	100.0

Table 3

Reclassification of the land-cover map to match the classes used by Paquet et al. (1996) in their friction model of wolf movements.

New class	Old class	Preference
1	Coniferous (Douglas-fir, pine, spruce)	84.2
2	Aspen (mixed forest and treed wetland)	2.8
3	Meadows (shrubs)	7.2
4	Grassland (herbs)	1.2
5	Barren land, snow/ice	0.8
6	Water	3.8
No data	Cloud, shadow	

Whittington et al. (2004) compared three types of simulated walks with actual wolves' movements. The authors concluded that the best fit was obtained with a 'biased correlated random walk' in which the next cell is selected with minimal random turning angles from the direction of the last cell, as well as minimal random turning angles towards a preferred destination. The directional vector can be chosen randomly or preferentially. In this study, we assumed that wolves choose where to go purposefully (e.g., a wolf seeks some known elk density patches) and that their activity was not completely random (Bartumeus et al., 2005). However, to accurately simulate animal movements on the landscape, several other factors must be taken into account at the same time, including preferred direction, a weight factor indicating attraction strength towards the directional vector, and a habitat quality index, which represents the cumulative suitability of all habitat variables (Topping et al., 2003).

We therefore applied the theoretical approach of Topping et al. (2003) and methods first developed for wolves by Whittington et al. (2004), wherein wolves pick a random cell within eight neighbouring cells using information regarding the directions of their previous movement and that towards a destination, and the habitat quality of these cells (often referred to as its inverse: friction value). Fig. 4 displays how in this study a wolf agent selects the next cell based on its past location and direction of movement, a directional vector indicating preference towards a destination (dashed arrow), and a weight factor indicating habitat suitability (grey shade). In the figure's sample case, habitat suitability is higher in darker grey cells. This method is similar to the ABM of Florida panther movement developed by Cramer and Portier (2001).

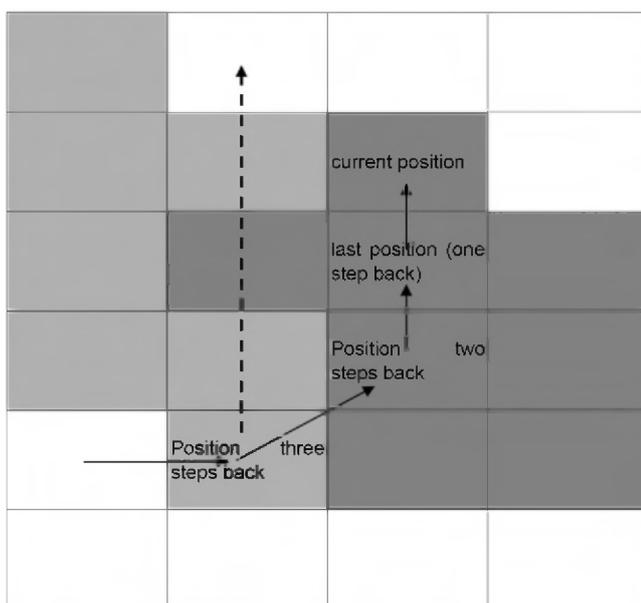


Fig. 4. Illustration of the correlated and biased random walk model to simulate how wolves move on the landscape.

The wolf's movements are determined by the spatial distribution of resources (such as prey, for example) and of threats to safety (such as the presence of humans or bears), and by the internal motivation and activity wolves are engaged in. The activities simulated in our model (Fig. 5) are hunting, patrolling territory, feeding pups, and resting. The model encompasses the period from April 16 to October 15, which is homogenous for key ecological factors involving wolves and other organisms affecting wolves. During this period, in the study area wolves are central place foragers around a den and/or rendezvous sites for the pack; the level of human use is orders-of-magnitude greater than that of the winter season; grizzly bears are present, whereas in the winter they are in hibernation; and finally, migratory and non-migratory elk are distributed depending on plant phenology characteristic of the summer (Hebblewhite et al., 2008).

Behavioral rules for wolves were derived from the scientific literature, from experts' opinions, and from our field observations (Fig. 5). Each wolf agent (representing a pack) was assigned an energy index value that ranged from 0 to 100. At every minute, which corresponds to the temporal resolution (time step) of the model, the energy index value decreases based on this equation ($energy_{t+1} = energy_t - 0.3$). The value 0.3 is given by: $100/14$ days/24 h to simulate the fact that the mortality of a wolf might happen after 14 days without food, a period consistent with the literature (Mech, 1970). When a wolf agent finishes eating, it reaches satiation and its energy value is 100; when the energy index reaches 0, the wolf dies. Wolves embark from their dens towards an intended destination picked randomly within the pack's home range, and then wolves attempt to move towards that direction using the path with the least friction. They are attracted to trails for ease of navigation, but do not use them if the encounter rate with humans increases. Wolf preference for trails at low human-use levels is known from the literature and documented also in the study area (Whittington et al., 2005; Paquet et al., 1996; Callaghan, 2002). When wolves reach the targeted destination, they aim at another location as a new destination.

As wolves patrol their territory, they are allowed to deviate towards a food source (example, elk). Practically, when their energy index is below 80% and they perceive the presence of elk within a 3 km range, wolves move towards the elk location. The threshold of 80% for the energy index was selected based on a sensitivity analysis of the model, which demonstrated that wolves could not start searching for food at lower energy levels or they would risk starvation due to a lack of time to hunt successfully. When pursuing elk, there is a 30% probability of a kill, which is consistent with empirical data on hunting success (Mech, 1970; Peterson and Page, 1988; Post et al., 1999).

If a wolf is successful at killing an elk, it will start consuming the carcass and keep eating for 6.5 h. This duration is consistent with the spatio-temporal clusters of wolf locations that are attributable to elk kills in western Canada and in the study area in particular, for the summer denning period (Hebblewhite et al., 2005a; Webb et al., 2008), which is the focus of our modeling effort. Once a wolf has finished eating, it returns by the shortest least friction route possible to the den to feed the pups. After a successful hunting bout, a wolf will make return trips to the kill to collect more food; such food is often regurgitated for the pups at the den site (Harrington and Mech, 1982). In the summer denning period, these return trips for ferrying food back to the pups may also be separated by about 6–7 h of eating, feeding pups, and resting both at dens and killing sites (Hebblewhite et al., 2005a). If a wolf does not encounter any elk while patrolling its territory, it returns to its den after 4 days to attend to pups.

While a wolf is patrolling its territory, if it perceives the presence of any human or bear within a 200 m range, it stops its activity and remains at the same location for the duration of the bear or

Table 4

Percentage of time actual (observed) and simulated wolf packs spent at the den and not traveling at normal estimated levels of human presence (H1X) on roads and trails, and 5 times (H5X) and 10 times (H10X) normal estimated levels of human presence in Banff and Kootenay National Parks, Canada.

	Time at den						Time not traveling					
	Observed (%)	H1X (%)	H5X (%)	H10X (%)	Mean (%)	SD (%)	Observed (%)	H1X (%)	H5X (%)	H10X (%)	Mean (%)	SD (%)
Pack 1	12.41	2.62	2.11	2.11	4.81	5.07	78.30	34.53	33.79	32.92	44.88	22.29
Pack 2	0.56	2.62	2.57	2.80	2.14	1.06	91.63	37.42	37.24	38.06	51.09	27.03
Pack 3	1.99	3.35	2.94	3.54	2.95	0.69	89.72	35.31	35.86	36.96	49.46	26.85
Pack 4	4.01	2.20	1.93	2.25	2.60	0.95	90.59	32.28	34.07	33.10	47.51	28.73
Pack 5	4.73	1.33	0.78	0.51	1.84	1.96	88.70	35.49	77.87	94.86	74.23	26.76
Mean	4.74	2.42	2.07	2.24			87.79	35.00	43.76	47.18		
SD	4.59	0.74	0.82	1.12			5.41	1.86	19.12	26.75		

2.6. Simulation framework

Seven sets of parameters were used in the model of wolf behavior: number of bears (12, 21, and 30), number of elk herds (12, 24, and 36), and human presence (H1X, H5X and H10X). To account for environmental stochasticity and for variability in the model outputs, runs with each set of parameters were replicated 15 times. The simulation results correspond to the average of the values obtained in these 15 replicates, with error bars representing the standard error.

The model has a reporting mechanism describing the instances of various events at each time step of 1 min. Important outputs of the model include the trajectories of wolves, which are represented

as a series of point locations (*x, y* coordinates and time stamp). This allowed comparison with the *observed* dataset for GPS-collared wolves, which is also comprised of point locations. For this purpose, point locations for simulated wolves were sub-sampled at 2-h intervals similar to the temporal resolution for GPS-collared wolves. The model also reports other critical parameters, such as when a wolf agent crosses a highway or trail, encounters a human or a bear during either navigation or feeding on prey, chases an elk or kills it, rests, leaves the den, or dies. The model was implemented in JAVA programming language using NetBean IDE with RePast 3.1 library (North et al., 2006). The RePast library was used primarily to visualize the outputs and control the simulation engine.

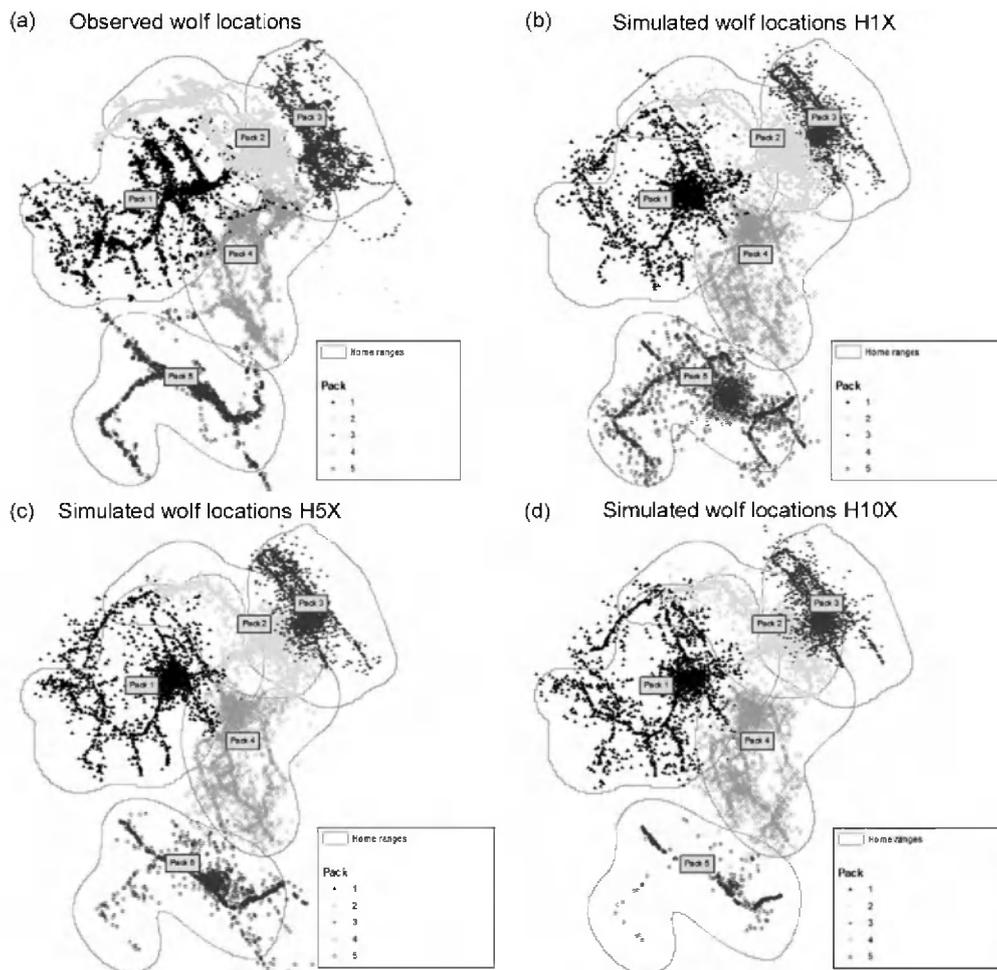


Fig. 6. Wolf locations within the study area obtained from: (a) wolf GPS radiocollar points acquired from 2002 to 2004, (b) simulated wolf locations with estimated actual human presence (H1X), (c) simulated wolf locations with human presence 5 times estimated actual human presence (H5X), and (d) simulated wolf locations with human presence 10 times estimated actual human presence (H10X).

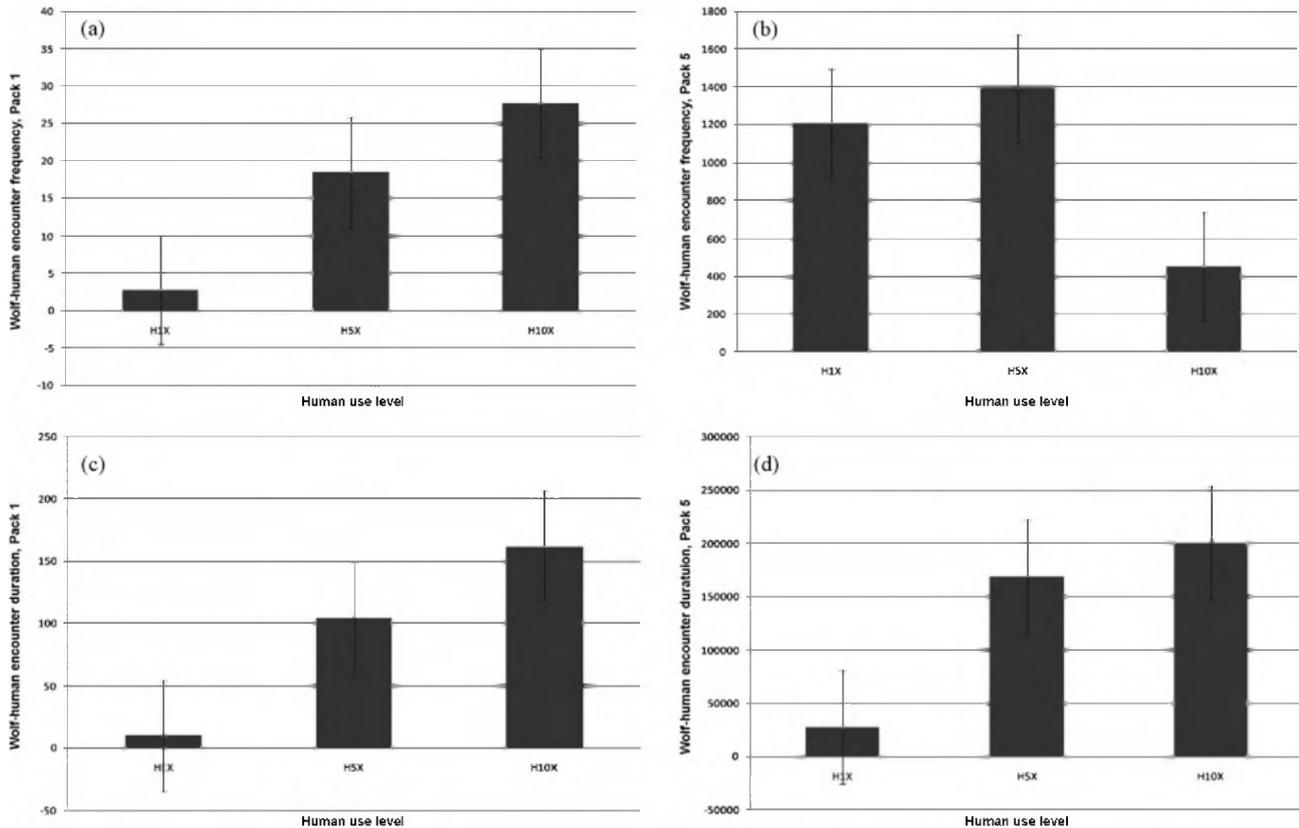


Fig. 7. Frequency of wolf–human encounters on roads at varying levels of human presence for: (a) Pack 1 and (b) Pack 5; simulated duration of wolf–human interaction on roads at varying levels of human use for: (c) Pack 1 and (d) Pack 5. The results represent an average of 15 replicates; error bars represent the standard deviation.

2.7. Model validation

The validation of the model was performed by comparing the simulated trajectories of wolf packs within five known home ranges with the observed trajectories of real wolves. Following *Tew and Macdonald (1994)*, nonparametric utilization distribution analyses were applied to measure the overlap between the simulated and observed wolf locations at 2-h time intervals. Using ArcMap 9.2, the area encompassing all wolf home ranges was divided into a grid of 426 cells measuring 4 km × 4 km (*Mech, 1970*) and covering five home ranges in such a way that each home range was covered by at least fifty grid cells. This cell size satisfies the conditions suggested by *Doncaster (1990)* that the size of the cells must be large enough that some cells contain several fixes, but not so large as to obscure the overall configuration of the range. The visit frequency of simulated and observed wolf locations was calculated for each cell. Spearman correlation (two-tailed) was used for testing the association between these two measures over all grid cells, representing correlations in range use. A high correlation implies not only a high overlap, but also similar spatial utilization. A permutation test implemented in SPSS version 10.0 was applied to test whether the observed value of Spearman's rho was significantly different from zero.

We also compared the percentage of time spent at and around dens (200 m buffers) for observed wolves and for wolves simulated at the three levels of human presence (H1X, H5X and H10X). The 200 m value was consistent with wolves' perception of the environment, as explained previously. It is likely that wolves consider themselves in proximity of a den at such distance, similar to how they perceive proximity to a disturbance activity by a human or a bear. With similar approaches, we compared the percentages of time spent not traveling (speed < 1 km/h) for the five packs at the

observed and the three simulated levels of human presence. We used this 1 km/h threshold as wolves are described in the literature as 'traveling' at speeds of higher than 1.5 km/h (*Musiani et al., 1998; Mech, 1970, 1994*). Differences were evaluated using a Friedman test, which provides Chi-square and associated *P*-values. We also reported mean and standard deviation values of percentages for *time at den* and *time not traveling*.

3. Results and discussion

3.1. Distribution of observed wolf locations and locations simulated with increasing human use

Fig. 6 shows the distribution of observed wolf locations taken regularly at 2-h intervals (Panel a) and the distribution of simulated wolf locations also at 2-h intervals with estimated typical human presence (H1X), projected 5 times human presence (H5X), and projected 10 times human presence (H10X) (Panels b, c, and d, respectively). A visual comparison of simulated locations draws attention to similar distributions as those observed with real wolves, with some notable exceptions. A closer examination of observed and simulated wolf locations with estimated human presence H1X (Panels a and b, respectively) reveals that the observed locations for Pack 5 were clustered around a valley-bottom that contains highways and trails used by humans. The observed locations for Pack 1 were also clustered around a valley-bottom that contains in this case a network of trails (see Fig. 2). This result indicates that our model underestimates wolves' selection for valley-bottoms at moderate human presence levels, likely due to ease of movement and to the presence of important resources for wolves in these locations, a phenomenon that has been documented in the study area (*Paquet et al., 1996; Callaghan,*

2002). However, with simulated increased human presence, the similarities between simulated and observed locations increased, especially for Packs 1 and 5, which have home ranges that encompass areas with relatively higher human use (Panels c and d). Our model therefore indicates that when human use is high or very high (H5X and H10X), wolf locations may be clustered at valley-bottoms, where most basic resources for the species are concentrated. In fact, valley-bottoms are characterized by concentration of prey, water and security cover for wolves, especially in the study area (Percy, 2003; Shepherd and Whittington, 2006). Under these circumstances wolves might travel less to other less critical areas of their home ranges, likely because moving more increases the chance of encountering people (see below).

In addition to a visual comparison, an analysis of spatial utilization within home ranges suggests correspondence between observed and simulated wolf locations over grid cells covering each of the five wolf pack home ranges. Within cells, locations for real wolves and for simulated wolves experiencing estimated typical human presence (H1X) are highly correlated (Spearman's rho 0.566, $P < 0.001$), which suggests correspondence in range use and high overlap (i.e., similar utilization). The correlation values further increase between observed wolves and simulated wolves experiencing levels of human presence 5 times (H5X) and 10 times (H10X) higher (Spearman's rho 0.589, $P < 0.001$ and Spearman's rho 0.612, $P < 0.001$, respectively). However, analyses conducted

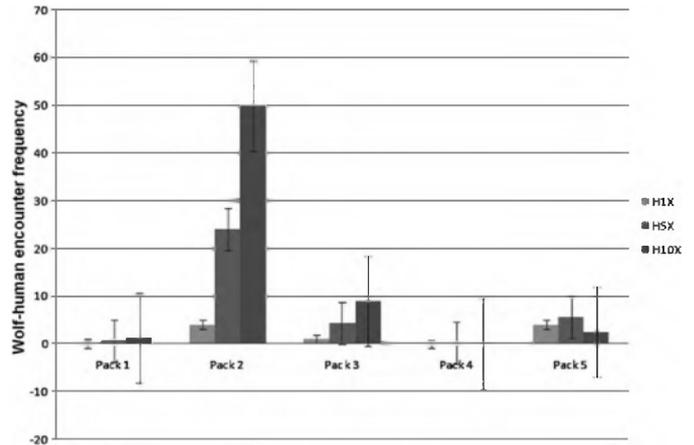


Fig. 8. Simulated frequency of wolf-human encounters on trails at varying levels of human use for each wolf pack (Packs 1, 2, 3, 4 and 5). The results represent an average of 15 replicates; error bars represent the standard deviation.

separately for each home range and pack demonstrated that such increases with higher human presence are not a pattern common to all packs. Correlation values increase between observed wolves and simulated wolves of Pack 2 with human presence increas-

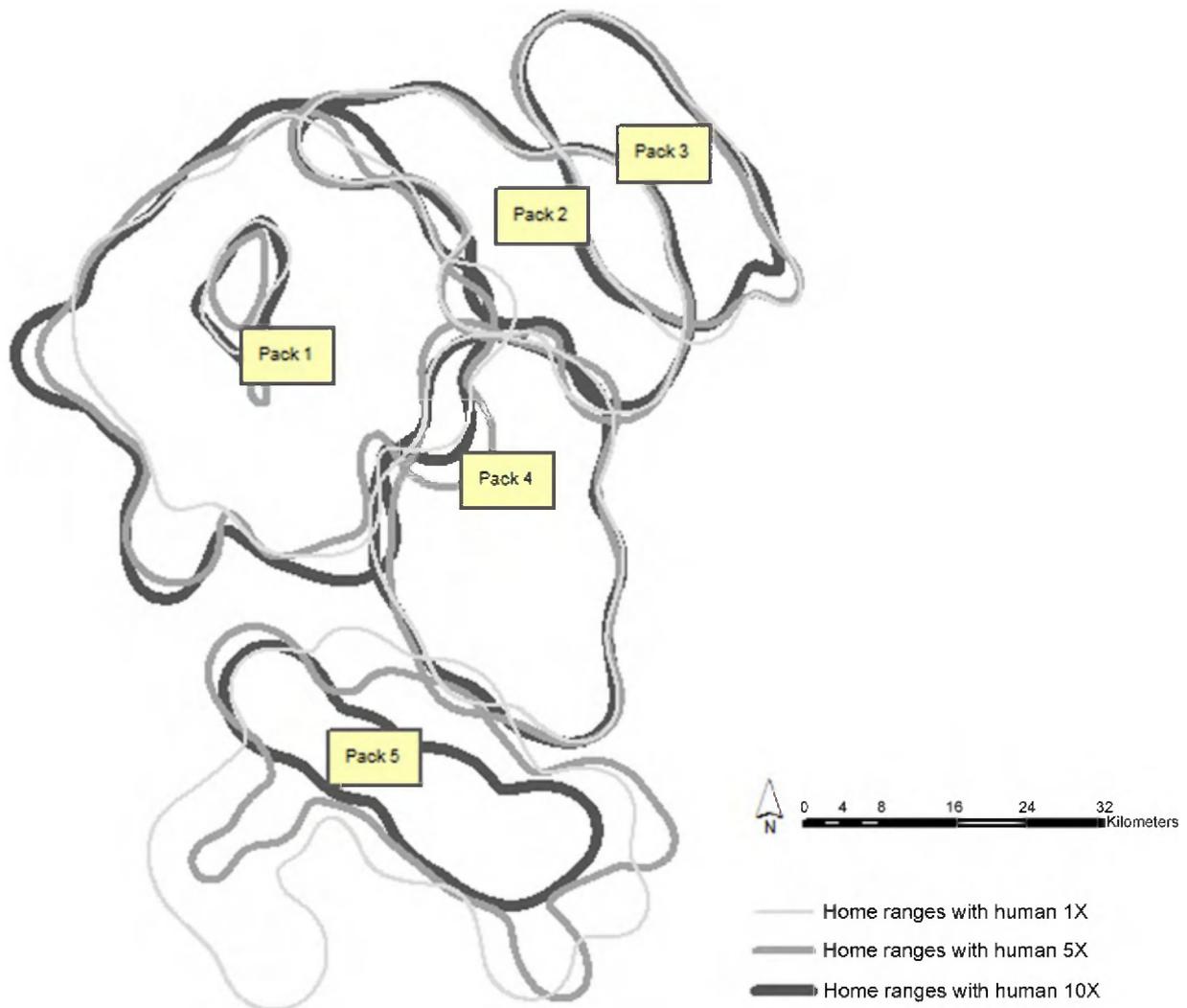


Fig. 9. Shrinkage of wolf home ranges associated to different levels of human presence.

ing 5 times (H5X) and 10 times (H10X) (with Spearman's rho peaking at 0.726, $P < 0.001$). Similarly, correlation values increase with human presence for Pack 5, with Spearman's rho peaking at 0.651 ($P < 0.001$). However, correlation values did not increase with increasing human presence for Packs 1, 3 and 4.

Finally, Table 4 shows the validation results for time spent at dens and for time spent not traveling by wolves. Percentage of time spent at and around dens (200 m buffers) for observed wolves and for wolves simulated at three levels of human use did not vary across packs ($n = 5$, Chi-square = 2.63, $P = 0.452$), or across the observed and the three simulated levels of human use ($n = 4$, Chi-square = 5.72, $P = 0.221$). Therefore, there is fit between our model and the observed behaviors. Validation results were more variable for the analysis of time spent not traveling. The five packs spent different percentages of time not traveling (speed < 1 km/h) at the

observed and the three simulated levels human use ($n = 5$, Chi-square = 8.28, $P = 0.041$), largely due to the observed packs resting more than the simulated packs. Differences were also detectable with regard to traveling behavior across the observed and the three simulated levels of human use ($n = 4$, Chi-square = 11.00, $P = 0.027$), largely due to Pack 5 spending less time traveling than the other packs. These validation results are consistent with those explained above for the spatial distribution of locations. There are discrepancies between our simulations and the observed patterns. As a general pattern, wolves seem to move less in reality than in our model, perhaps due to their reaction to high levels of human use. Consistent with this interpretation, the pack experiencing the highest level of human use (Pack 5) moves less than the other packs and, as explained above, has movement patterns consistent with those simulated with the highest human-use values.

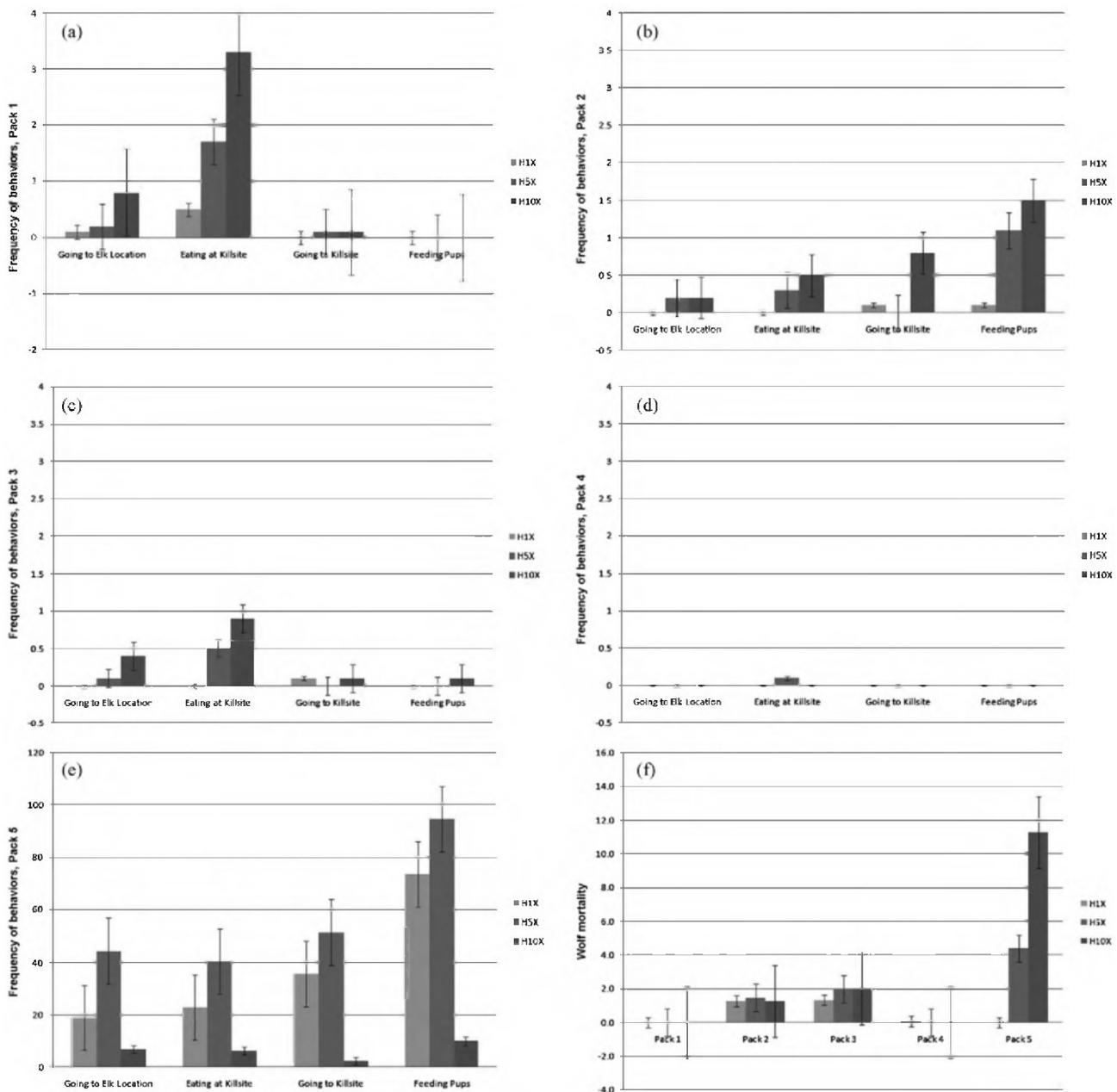


Fig. 10. Frequencies of human disturbance of various wolf activities that are important for survival, including finding prey ('going to elk location'), eating at kill sites, going to kill sites, and feeding pups (Panels a, b, c, d and e for Packs 1, 2, 3, 4 and 5, respectively) and effects on wolf mortality (Panel f) of varying human-use levels. The results represent an average of 15 replicates; error bars represent the standard deviation.

3.2. Frequency and duration of encounters with humans on roads and trails

The home ranges of wolf Packs 1 and 5 are traversed by highways. Pack 1's home range includes a small segment of Highway 93 and Highway 1, whereas Pack 5's home range is literally split by Highway 1. Potentially, this pack might be severely affected by humans, as there is considerable traffic on Highway 1 throughout the year. Fig. 7(a and b) shows the frequency of encounters with humans on roads for Pack 1 and Pack 5, respectively. With human presence increasing from current, to five and to ten times current levels of human presence (H1X, H5X, H10X), Pack 1's encounters with humans on roads increased; whereas, for Pack 5, encounters decreased at very high levels of human presence (H10X). The result for Pack 5 seemed counterintuitive. However, in-depth investigation revealed that in case of sustained and continued human presence, the wolf perceives and registers a single, but continued encounter/disturbance event. Such an event is the result of the interaction between one wolf agent (i.e., a pack) and several human objects appearing on consecutive occasions within the same 200 m buffer zone of the wolf locations. Fig. 7 (Panels c and d) illustrates this notion by highlighting how the duration of wolf–human encounters (and therefore the disruption of wolf behavior) for both Packs 1 and 5 increased with increasing human presence. Therefore, for Pack 5 the frequency of encounters decreased, but its duration increased (Fig. 7b and d, respectively). Another feature worth highlighting is that the duration of human-caused disruptions of Pack 5's behaviors initially increased sharply, and then moderately, which might relate to an attenuation effect consistent with the mortality rate findings that are explained below.

Increased human presence affected wolf movements not only on roads, but also on trails, with distinct patterns for each wolf pack (Fig. 8). Compared to Packs 1, 3, 4 and 5, Pack 2 had higher encounter rate with people, likely because of its small home range (1224 km²), which encompasses a concentrated network of trails. At the other extreme, Packs 1 and 4 were the least affected, since they have larger home ranges (2085 and 1359 km², respectively) and more options available to move to areas with lower trail density.

3.3. Human influence on size of wolf home ranges

If there are high levels of human presence on the landscape, wolves might be forced into areas that are not optimal in terms of prey density, and this might have a significant effect on survival. In addition, under high human-use conditions wolves may not be able to hunt successfully, because humans might interfere with hunting wolves or with their consumption of prey. Fig. 9 illustrates these scenarios wherein the home range of wolf Pack 5 shrank visibly as human presence increased. Such human-caused effects on home range size might also result in decreased ability to use habitats frequented by wolf prey, with patterns analyzed in detail below.

3.4. Disruption of crucial activities and effects on survival

Fig. 10 illustrates the frequencies of human disturbance of various wolf activities that are important for survival, including finding prey (*going to elk location*), eating at kill sites, going to kill sites, and feeding pups (Panels a, b, c, d and e for Packs 1, 2, 3, 4 and 5, respectively). When the level of human presence increased to 10 times, the impact on all wolf activities increased for Packs 2 (Fig. 10b) and 5 (Fig. 10e), while only some activities were disturbed for the other packs (Fig. 10a, c, and d). Wolf Pack 4 experienced little disturbance (Panel d), likely because its home range is in 'backcountry' areas, less frequented by visitors. Wolf Pack 5 seemed to experience fewer impacts when human presence was 10 times greater, com-

pared to 5 times (Fig. 10e). A closer analysis illustrates that traffic on two important transportation routes present in the home range may cause increased duration of disturbance, which is perceived by Pack 5 as continuous disturbance, as explained previously. As a result, Pack 5 has limited time for hunting and for other critical activities; circumstances that lead to increased mortality of this pack (Fig. 10f).

4. Conclusions

Recreation and transportation may have an array of immediate and long-term influences on animal behavior even within national parks (Boyle and Samson, 1985; Forman and Alexander, 1998; Trombulak and Frissell, 2000). Activities such as hiking and biking on trails, and vehicle activity on roads may affect a wide range of species such as for example in large mammals: moose (Yost and Wright, 2001), deer (Freddy et al., 1986), bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) (George and Crooks, 2006), bighorn sheep (Keller and Bender, 2007), bison (*Bison bison*) and pronghorn (*Antilocapra americana*) (Taylor and Knight, 2003), and black bears (*Ursus americanus*) (Kasworm and Manley, 1990). However, the impact of human-caused behavioral changes in animals and on their survival is often unknown.

ABM can assist in discovering knowledge gaps and can provide theoretical insights by formalizing the components of a system (for example, an ecosystem including wolves and other species) and exploring their interactions. This can be particularly useful for investigating the impact of behavioral changes by humans and the identification of adequate management practices to reduce this impact. Such an approach is clearly illustrated by Bennett et al. (2009) who implemented a behavioral-explicit ABM to explore wildlife species responses to patterns of anthropogenic disturbances to be used as a management tool in order to minimize the detrimental impact on wildlife populations.

In attempts to fulfill a similar goal, the strength of our model lies in its ability to capture the outcome of interactions between wolves and humans at a fine temporal scale (with human-use data gathered at every hour) and spatial resolution (in 100 m units), and at the individual level. The performed simulations reveal that wolf movements and behaviors are considerably affected by increasing intensity of human presence. Wolves have less time to search for prey, to hunt, to access and consume a prey item, and to attend to their pups, which might result in mortality. The most affected wolf pack (Pack 5) is the one whose den is closest to an important transportation route (the Trans-Canada Highway 1) and to another highway. Overall, the model probably under-represents human impact because wolf activities are resumed once encounters with humans are over, which might not be the case in reality. In fact, a number of studies have shown that human-caused disruption of animal behaviors might not be reversible, and forces animals to permanently shift to other activities (Boyle and Samson, 1985; Forman and Alexander, 1998; Trombulak and Frissell, 2000). Even with this under-representation of human impact, severe impacts on wolf behavior and also on survival were observed.

Despite the focus given to predators and wolves specifically (e.g., Soulé et al., 2003), in most ecosystems humans arguably constitute the most important keystone species, i.e., a species with effects on the ecosystem are greater than its numerical representation or biomass (Paine, 1995). The notion that humans are a keystone species is not new (McDonnell et al., 1993) and the effects of humans on ecosystems at various trophic levels are well documented (Vitousek and Mooney, 1997). However, as indicated by Castilla (1999), there is an urgent need to incorporate humans into ecological studies and to understand their functional relationships with other organisms. Our study indicates that in addition to playing a keystone role, humans may outnumber wild predators in most

ecosystems, including protected areas, therefore potentially producing even greater effects. Our results on the potential effects of human presence on wolf survival, through interaction with other biotic and physical variables, confirm empirical findings obtained in the study area by Hebblewhite et al. (2005b), Percy (2003) and Whittington et al. (2005).

Despite some limitations, the modeling prototype developed in this study for wolves may serve as a useful tool to test hypotheses about human–wolf interactions, such as for determining the level of territory fragmentation or the threshold of human use in the study area beyond which wolf survival could be significantly affected. It may guide decision-makers in designing adequate management strategies that are compatible with conservation of mammals in National Parks and other areas with significant human presence. Such management strategies that could be investigated include limiting the access to certain trails during periods particularly critical to wildlife populations, improving the number and location of highway crossing corridors to facilitate the movement and activities of animals, and reducing the level of fragmentation of areas particularly suitable to wildlife species.

Two areas of further development are considered to refine the actual modeling prototype. Firstly, a set of more sophisticated rules could be incorporated to better mimic prey behavior based on knowledge gathered from behavioral ecology studies. Prey behaviors could also be dependent upon predator presence and activity, following principles of predator–prey theory. Secondly, the human module could be enriched by a representation of movements and activities along the roads and trails based on decision rules of cognitive human agents rather than a static representation of their presence/absence.

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