

Spatial and behavioral scales of habitat selection and activity by river otters at latrine sites

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Animals interact with their environment at multiple spatial, temporal, and behavioral scales. Few studies of selection for latrine sites by river otters (*Lontra canadensis*) have considered spatial scale, and no studies have integrated scales of behavior. We used an information theoretic model comparison approach to identify elements of otter habitat that influence the presence, consistency, and intensity of latrine-site activity at 2 spatial scales. We identified and monitored 73 latrine sites in central British Columbia, Canada, during the open-water season in 2007 and 2008. We inventoried latrines and randomly selected sites along the adjacent shoreline, and used those data in the form of a binary resource selection function to model fine-scale selection of latrine sites. At the scale of the landscape, we used a resource selection function and data from geographic information systems to model coarse-scale selection of latrine sites. Drawing on those same data, we used binary and count models to quantify factors that contributed to the consistency (high versus low use) and intensity (number of scats) of otter activity at latrine sites. Fine-scale habitat characteristics were better at predicting the presence of latrine sites when compared to coarse-scale geographic information system data. In general, the presence, consistency, and intensity of latrine activity at the fine scale were influenced by visual obscurity, larger trees, and characteristics of conifer trees. The presence of latrine sites at the coarse scale could not be accurately described by any of the models. The consistency and intensity of activity of otters at latrine sites at the coarse scale, however, was best predicted by habitat characteristics beneficial to fish. These results provide insight into the spatial and behavioral scales of latrine-site activity by river otters that can be incorporated into management, monitoring, and conservation strategies.

Key words: British Columbia, habitat selection, latrine site, *Lontra canadensis*, river otter, scale

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DOI: 10.1644/10-MAMM-A-362.1

The inclusion of scale in ecological studies is critical to the interpretation of resource selection (Johnson 1980; Wiens 1989). Variables at the coarse scale may be missed or fine-scale patterns may be averaged depending on the nature of the measurement (Dunning et al. 1992). In addition, by using scale to delimit behavior we can begin to infer mechanisms that drive resource selection (Johnson et al. 2002). A growing number of studies have investigated behavioral and spatial scale using detailed movement data and global positioning system technology (Frair et al. 2005; Fritz et al. 2003; Johnson et al. 2002). Variation in the amount of sign (i.e., scats or tracks) at sites used by animals also has the potential to reveal spatial and behavioral scales of habitat selection. For example, North American river otters (*Lontra canadensis*) visit latrines

and leave behind scat that is both identifiable and measurable through space and time.

Latrine sites are terrestrial locations where otters consistently deposit feces, scent-mark, and roll in vegetation and debris. Ben-David et al. (2005) investigated a coastal population of river otters and found that latrine sites served different purposes depending on the sex and social status of individuals. Social otters most likely scent-marked for intragroup communication, nonsocial otters to signal mutual avoidance, and females for defense of territories. Rostain et al.



(2004), using captive otters, suggested that feces are deposited at latrine sites to communicate social status. In Eurasian otters (*Lutra lutra*), latrine sites may signal the active use of food resources (Kruuk 1992). Regardless of their function, latrines are important to otter ecology and provide an opportunity to relate latrine characteristics to patterns of otter activity. The selection and degree of latrine-site use by otters is likely a trade-off between selective pressures influencing otter behavior at multiple spatial scales.

Researchers have used latrine sites to determine occupancy, distribution, and habitat selection of otters (Dubuc et al. 1990; Newman and Griffin 1994; Swimley et al. 1998). Tributaries, points of land, coniferous trees, rock formations, and fallen logs commonly characterize latrine sites (Dubuc et al. 1990; Newman and Griffin 1994; Swimley et al. 1998). Beaver activity also has been reported as an important factor describing habitat use by otters (Dubuc et al. 1990; Melquist and Hornocker 1983; Swimley et al. 1998). These studies assume latrine sites are an accurate predictor of river otter habitat use and distribution. There is very little information, however, relating the location and habitat features of latrine sites to variation in their use. The exceptions are the use of deposition rates at latrine sites to document differences in latrine use between lake and stream habitats during the spring and summer (Crait and Ben-David 2006), and to investigate coarse-scale differences in the use of beaver ponds or wetland types (Leblanc et al. 2007; Newman and Griffin 1994). Variation in latrine-site use among seasons also has been documented for Eurasian otters in Finland (Sulkava 2007).

Failure to investigate spatial and behavioral patterns in visitation rates can have implications for monitoring protocols and limits our understanding of otter ecology. For example, latrine sites found during short-term surveys often serve as indicators of habitats used by otters (Dubuc et al. 1990; Newman and Griffin 1994; Swimley et al. 1998). Spatial and behavioral differences in the use of latrine sites throughout the year by otters, however, could dramatically affect interpretations of habitat selection. Typically, the only criterion for documenting a latrine-site location is the presence of a minimum number of scats. For example, when documenting habitat selection of river otters in Pennsylvania, Swimley et al. (1998) required that a latrine site have ≥ 2 scats. Using this criterion, a latrine site that has only 2 scats and was visited only once during the season is treated the same as a latrine site used throughout the entire season with dozens of scat deposits. Such variation in use is likely the product of important ecological determinants of otter distribution and perhaps abundance; however, there is very little information relating habitat characteristics at latrine sites to the consistency and intensity of activity by otters. Information relating latrine habitat characteristics to the degree of otter activity at different spatial scales would be beneficial to natural resource professionals prioritizing management decisions that emphasize the habitat requirements of otters.

Studies of latrine sites in the past have typically focused on either fine- or coarse-scale habitat characteristics or have

combined characteristics across scale (Bowyer et al. 1995; Dubuc et al. 1990; Swimley et al. 1998). Selection by otters for latrine sites, however, may be driven by very different environmental factors depending on the scale of the observation. Frequently, habitat selection by wildlife species is strongly correlated with the presence and distribution of food resources. At the coarse scale (landscape), we hypothesize that otters will select latrine sites based on habitat characteristics that affect prey distributions. At the fine scale (shoreline patch), we hypothesize that otters will select areas with characteristics that provide vertical and horizontal security or environmental cover. There are 2 reasons why cover may be important for otters. First, otters may be vulnerable to predation by avian or terrestrial predators when transitioning from the water onto land. Although only anecdotal information exists, gray wolves (*Canis lupus*), black bears (*Ursus americanus*), brown bears (*Ursus arctos*), and bald eagles (*Haliaeetus leucocephalus*) are potential predators of otters that occur in the study area (Melquist et al. 2003). Second, the cover may protect scent from environmental influences, such as rain and sun, prolonging the impact of scent-marking behavior.

In this study, we investigated selection by river otters for latrine sites at multiple spatial and behavioral scales. We used an information theoretic model comparison approach to identify elements of otter habitat that influenced the presence, consistency, and intensity of latrine-site activity. We identified and inventoried latrine sites, and adjacent control locations, on 2 lake systems in British Columbia, Canada. Latrine sites were surveyed every 2 weeks for 2 years during the ice-free season to monitor visitation rates. We used the data describing the latrine and matched random control sites to develop fine-scale binary resource selection functions. At the scale of the landscape, we used resource selection functions and data from geographic information systems to model coarse-scale selection of latrine sites. Drawing on the visitation data, we used binary and count models to quantify factors that contributed to the consistency (high versus low use) and intensity (number of scats at latrine sites) of otter activity at latrine sites. The objectives of this study were to identify factors influencing latrine-site selection by river otters at 2 ecologically relevant spatial scales; and to identify factors influencing the behavior of otters at latrine sites.

MATERIALS AND METHODS

Study area.—The research was conducted in and adjacent to the John Prince Research Forest (<http://researchforest.unbc.ca/jprf/jprf.htm>) on or near Tezzeron and Pinchi lakes (Fig. 1). The John Prince Research Forest is a 13,000-ha portion of forested crown land 45 km northwest of Fort St. James, British Columbia, Canada (54°40'14"N, 124°25'13"W). The area is characterized by rolling topography with low mountains (elevation 700–1,267 m) and a high density of lakes, rivers, and streams. Tezzeron Lake's shoreline stretches for 82 km (area = 8,079 ha), whereas the perimeter of Pinchi Lake is

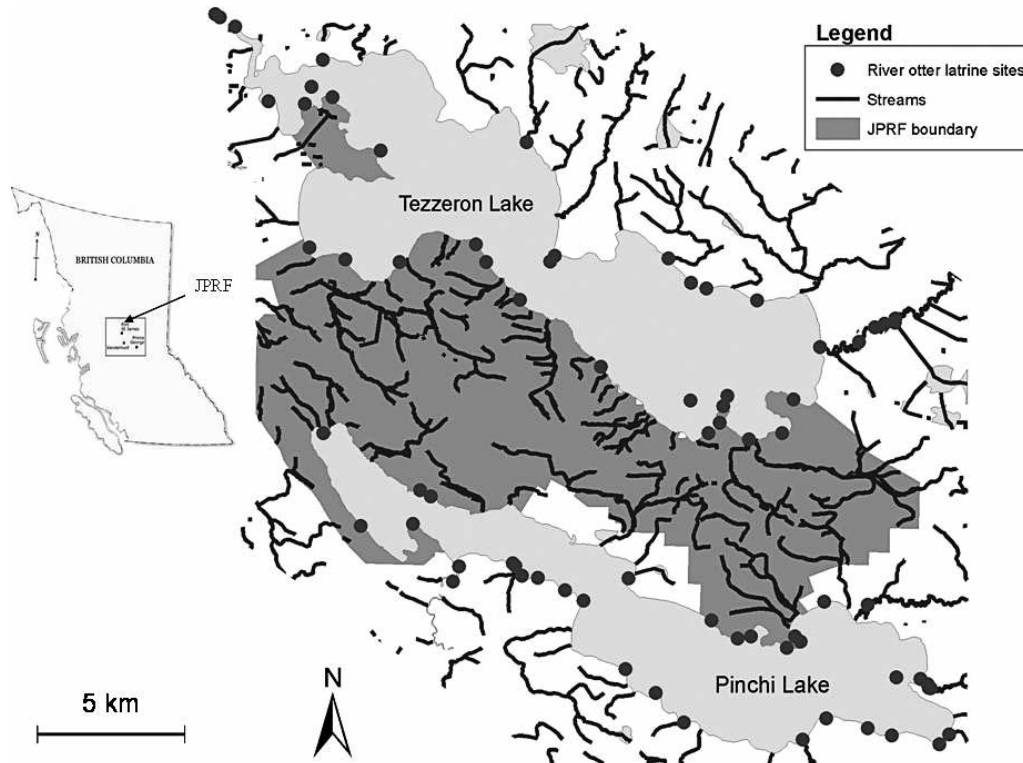


FIG. 1.—Map of river otter (*Lontra canadensis*) study site and John Prince Research Forest (JPRF) located 45 km northwest of Fort St. James, British Columbia, Canada ($54^{\circ}40'14''N$, $124^{\circ}25'13''W$), including locations of latrine sites, 2007–2008.

67 km (area = 5,586 ha). The mean depths of Tezzeron and Pinchi lakes are 11.2 and 23.9 m, respectively. Shoreline topography varies considerably along both lakes, but the area surrounding Pinchi Lake is generally more mountainous with steeper slopes. Tezzeron Lake has very little development, whereas Pinchi Lake has a mercury mine (nonoperational) and some residences. There is a long history of timber management and activity within the forests surrounding these lake systems.

Sucker (Castomidae), trout (Salmonidae), minnow (Cyprinidae), and sculpin (Cottidae) fish families are abundant in both lake systems. Although distribution and abundance are unclear, burbot (*Lota lota*) also are present in both lakes. Sockeye salmon (*Oncorhynchus nerka*) spawn in 2 major drainages during the autumn and kokanee (*Oncorhynchus nerka*) spawn in creeks and rivers during the late summer and early autumn. A multitude of water fowl species nest on or near the 2 lake systems with common mergansers (*Mergus merganser americanus*) and red-necked grebes (*Podiceps grisegena*) being especially common. Freshwater clams (*Anodonta*) are locally abundant in shallow areas throughout both lakes. Beaver (*Castor canadensis*) and muskrat (*Ondatra zibethicus*) are common throughout the watershed.

Data collection.—We identified latrine-site locations through a series of shoreline surveys on Pinchi and Tezzeron lakes as well as tributary streams that were fish-bearing and navigable by canoe or kayak (1 km from lake–stream confluence). We conducted shoreline surveys by canoe, kayak, and on foot. Two complete surveys of all shorelines

were conducted in 2007. The 1st survey occurred from 5 to 27 June and the 2nd from 20 July to 5 August. From 15 August to 15 September 2008, we randomly selected and intensively surveyed two hundred 200-m segments of shoreline split evenly between the Tezzeron and Pinchi lake systems. This intensive survey was a test of detection accuracy and allowed us to determine if the majority of the active latrine sites were being monitored.

We chose to conduct surveys during 3 distinct time periods, late spring, summer, and early autumn, to account for differing prey availability and biological constraints. In late spring, suckers and trout species move into stream systems to spawn and the movements of female otters are restricted by maternal care of offspring. In summer, prey diversity is at its highest and adult female movements are less restricted as pups become more mobile and leave the natal den. In autumn, kokanee and sockeye salmon move into streams, pup mobility is at its highest, and female movements are least restricted. After latrine sites were identified, we surveyed each site every 2 weeks to collect scats and record the number of scats deposited. Otter scats were marked with craft glitter during surveys to differentiate old and new scat deposits. In 2007, latrine-site monitoring began in July and ended in late October. In 2008, latrine-site monitoring began in mid-May and ended in mid-October. Collection protocols were in accordance with guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

Fine-scale selection and activity.—A latrine site was included in the habitat-selection analysis only if it contained

≥ 3 scats combined across all visits, and was visited ≥ 3 times during the duration of the study. We used a 1:1 sampling design to generate a paired random site as a control for each latrine site. We used a random number table to locate the random site between 21 and 100 m along the adjacent shoreline from the reference latrine site. Plots at latrine and nonlatrine sites consisted of a 5.64-m-diameter half circle. Plots at latrine sites were centered on the most frequently used entrance trail from the water. All plot centers were located 1 m inland from the origin of terrestrial vegetation and perpendicular to the shoreline. Habitat measurements included visual obscurity, percent cover, conifer cover, bank height, slope, substrate, and tree characteristics. Data collection protocols were guided by British Columbia's *Vegetation Resources Inventory Guidelines* (Resources Inventory Committee 2006). Visual obscurity was measured using a cover pole at 5 m inland from the shoreline. Percent cover for all vegetation layers was measured to the nearest 5% using an ocular estimate. Tree diameter at breast height (DBH), distance, and drip-line extent measurements were taken for all trees at the site and averaged. Tree distances were measured from the tree trunk to the edge of the terrestrial vegetation line. Tree drip-line was measured from the tree trunk to the outer edge of the longest branches in the direction of the water. Tree DBH was measured for all trees > 7.5 cm. Percent slope was measured within the latrine site using a clinometer (Suunto PM-5 Suunto, Vantaa, Finland). Tree DBH, distance, and drip-line extent measurements were grouped into categories based on the distribution of measurements, plot size, and potential ecological significance of cover attributes (DBH = 0–29, 30–49, ≥ 50 cm; tree distance = 0–1.9, 2–3.9, ≥ 4 m; drip-line = 0–0.9, 1–1.9, 2–2.9, ≥ 3 m). Categorization of these variables was thought to provide a simpler generalization of model results to other study areas.

Coarse-scale selection and activity.—For coarse-scale selection of latrine sites, random points ($n = 200$) and associated spatial data were generated using ArcMap in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California). Variables for coarse-scale selection represented aquatic habitat relative to fish ecology, characteristics of terrestrial vegetation, and shoreline topography. Coarse-scale variables measuring aquatic habitat relative to fish ecology included distance to beaver lodge, distance to reed patch edge, distance to navigable fish-bearing stream mouth, and water depth (100 m from shoreline). Areas with beaver ponds are often rich sources of biomass because of the productive invertebrate and fish habitat created by beaver structures (Gard 1961; McDowell and Naiman 1986). Reed patches create structure that may be important rearing, foraging, and escape cover for many fish species. Stream mouths are often productive areas, especially during times when a fish species moves from deeper lake water into shallower streams to spawn. Otters cannot productively forage in water that is very deep and water depth may affect the vulnerability of different prey species (Melquist et al. 2003). Water depth was measured directly from 1975 bathymetry maps created by the British

Columbia Ministry of the Environment Victoria, British Columbia, Canada. Vegetation measurements were taken from provincial Vegetation Resources Inventory data (Resources Inventory Committee 2008) and included dominant tree species, percent dominant tree species, average tree height, and canopy closure. We included these vegetation characteristics because they may influence the availability of horizontal or vertical cover and, thus, the locations of latrine sites at the landscape level. We included convexity as a measure of shoreline topography (Albeke et al. 2010). We used a window size of 100 m and a step size of 10 m when calculating the standardized boundary convexity index. The variation in the shape of the shoreline, including peninsulas and bays, may influence the accessibility of terrestrial habitat for river otters or movement through the aquatic environment.

Habitat models.—We developed 3 types of predictive models to investigate spatial and behavioral scales of resource selection of latrines and activity by otters. The 1st model, latrine-site selection, allowed us to investigate habitat characteristics that influenced the presence of latrine sites. The other 2 models representing the consistency and intensity of use investigated the importance of habitat characteristics on the visitation behavior of otters. Consistency of use was measured as the number of times that a latrine site was observed as active. We considered a site active if an otter had deposited scats, regardless of the level of disturbance or number of feces at the latrine site. Intensity was measured by counting the number of scats deposited at latrine sites during each survey. Consistency measured how often a latrine was active, whereas intensity measured the amount of activity when it was active. All 3 model types were conducted at 2 spatial scales, the landscape and shoreline patch.

Selection of latrine sites.—We used a binary resource selection function to investigate habitat characteristics that influenced the selection of latrine sites by otters (Johnson et al. 2006). We used a presence–absence design and conditional fixed-effects regression to develop a set of models to investigate selection at the scale of the shoreline patch. In contrast to conventional logistic regression, the conditional fixed-effects model takes into account matched groups (Hosmer and Lemeshow 2000). At the scale of the landscape, we used a resource selection function and data from geographic information systems to model coarse-scale selection of latrine sites. For this analysis, the entire shoreline was surveyed and considered available, thus, we used a conventional logistic regression, not a matched design.

Latrine consistency.—The influence of habitat characteristics on the consistency, or the number of visits by otters to a latrine site, was modeled using conventional logistic regression. Latrine sites were split into low- and high-use categories based on the number of surveys in which a latrine site was observed as active. A latrine site was considered to be high-use if it was active $> 65\%$ of the times it was surveyed. This delineation was based on the distribution and median value of the data so that 50% of latrine sites were categorized as high-use. Observations of monitored latrine sites indicated that a

TABLE 1.—Variables used in the development of binary and zero-inflated negative binomial count models for the selection of latrine sites and activity by river otters, based on fine-scale habitat data collected on Tezzeron and Pinchi lakes in central British Columbia, Canada, from 2007 to 2008. DBH = diameter at breast height.

Parameter	Description	Variable type
herb	% herb (<15 cm)	Continuous
shrub1	% shrub (2–10m)	Continuous
shrub2	% shrub (0–2m)	Continuous
tree	% tree (10+ m)	Continuous
sh1tree	% shrub1 and tree combined	Continuous
distance	Average distance of trees to vegetation line (m)	Categorical
dbh	DBH maximum of all trees (cm)	Categorical
obscuritytot	% visual obscurity total (0–1.5 m)	Continuous
obscurity115	% visual obscurity (1–1.5 m)	Continuous
slope	% slope within latrine site	Continuous
bankheight	Bank height (cm)	Continuous
substrate	Substrate between water and vegetation line	Categorical
spruce	No. spruce trees	Continuous
subfir	No. subalpine fir trees	Continuous
birch	No. birch trees	Continuous
willow	No. willow trees	Continuous
conifer	No. conifer trees	Continuous
dripline	Average conifer drip-line distance (m)	Categorical
condistance	Average conifer distance to water (m)	Categorical
condbh	Maximum conifer DBH (cm)	Categorical

value > 65% was a conservative delineation for defining a high-use latrine.

Latrine intensity.—We used the number of scats counted at a latrine site during a survey event as an index of the intensity of use by otters. We used these count data and a zero-inflated negative binomial model to investigate the influence of habitat characteristics on the intensity of activity at each latrine site. A zero-inflated negative binomial model accounts for both overdispersion and the presence of excess zeros in the data set. We used a likelihood ratio test to confirm that the negative binomial distribution was preferable to the Poisson. We then used a Vuong test to determine if a zero-inflated model was required (Vuong 1989). All data analyses were performed using Stata (version 9.2; Statacorp, College Station, Texas).

Habitat model development.—Eighteen different variables were used to develop models for the fine-scale selection of latrine sites (Table 1). Variables were a combination of vegetation characteristics and shoreline topography. We used 9 variables in the development of models to explain coarse-scale selection of latrine sites (Table 2). None of the parameters for the fine-scale analysis were expected to have nonlinear distributions, so quadratic equations were not required. Many of the distance values in the coarse-scale selection model, however, would be expected to display a nonlinear distribution. Parameters such as distance to beaver lodges, reed patches, and stream mouths were tested with and without a quadratic term. We used deviation coding, in which the effect of each variable is compared with the overall mean effect of the independent variable, to represent the categorical variables (Menard 2001).

We developed a total of 9 models as hypotheses to explain the presence or absence of latrine sites (Table 3), and 6

TABLE 2.—Variables used in the development of binary and zero-inflated negative binomial count models for the selection of latrine sites and activity by river otters, based on coarse-scale habitat data collected on Tezzeron and Pinchi lakes in central British Columbia, Canada, from 2007 to 2008.

Parameter	Description	Variable type
tree height	Tree height	Continuous
dspecies	Dominant tree species	Categorical
canopycover	Canopy cover	Continuous
dspecies%	% dominant tree species	Continuous
dbeaverlodge	Distance to nearest beaver lodge	Continuous
dbeaverlodge ²	Distance to nearest beaver lodge squared (quadratic)	Continuous
dreedpatch	Distance to nearest reed patch edge	Continuous
dreedpatch ²	Distance to nearest reed patch edge squared (quadratic)	Continuous
dstreammouth	Distance to nearest fish-bearing stream mouth	Continuous
dstreammouth ²	Distance to nearest fish-bearing stream mouth squared (quadratic)	Continuous
waterdepth	Water depth measured 100 m perpendicular to shoreline	Continuous
convex	Standardized boundary convexity index (BCI)	Continuous

models to explain the consistency and intensity of use of individual latrine sites at the scale of the shoreline patch (Table 3). Models were combinations of vertical or horizontal cover, all tree characteristics, conifer characteristics, or shoreline topography, or a combination of these factors, that may be important to otters because of their vulnerability to predators or scent-marking behaviors. Habitat variables such as visual obscurity, percent cover, or conifer trees may provide cover that reduces exposure to terrestrial predators or protects scent-marking areas from environmental influences. Topographical features such as bank height and slope may increase access to areas that remain available for scent-marking throughout the ice-free season (i.e., during spring flooding).

For the coarse-scale selection of latrine sites, we developed a set of 8 biologically plausible models for the binary and count analyses (Table 3). Global, terrestrial vegetation, aquatic habitat, and shoreline topography models were developed as well as 4 models that provided different combinations of variables for terrestrial vegetation, aquatic habitat, and shoreline topography. Terrestrial vegetation may be important for cover, aquatic habitat may influence the prey distributions and abundance of prey sources, and shoreline topography may influence river otter communication, movement, and scent-marking behavior.

For all analyses, we used variance inflation factors to assess each variable for excessive multicollinearity. We removed variables from a model if they had a variance inflation factor value greater than 10 or a mean variance inflation factor value greater than 1 (Chatterjee et al. 2000). In this study, none of the model variables had excessive multicollinearity.

Habitat model selection.—We used Akaike's information criterion for small sample sizes (AIC_c) to identify the most-parsimonious explanatory models of latrine selection and activity by otters (Burnham and Anderson 2004). The AIC_c values are a relative metric that must be compared in the

TABLE 3.—A priori candidate models for the selection of latrine sites and activity (presence, consistency, and intensity) by river otters, based on fine- and coarse-scale data collected on Tezzeron and Pinchi lakes in central British Columbia, Canada, from 2007 to 2008. The numbers of parameters or categories within each variable are represented by *K*. Model covariates are as described in Tables 1 and 2.

Model name	Model covariates	<i>K</i>
Fine-scale selection of latrine sites		
Global	dbh+distance+shrub2+herb+sh1tree+conifer+bankheight+obscurity115	11
Vertical cover	conifer+sh1tree	3
Conifer cover/tree characteristics	dbh+distance+conifer	6
Tree characteristics	distance+dbh	5
Cover and tree distance	distance+shrub2+herb+conifer	6
Tree species	spruce+subfir+birch+willow	5
Horizontal cover	obscurity115+shrub2+herb	4
Shore topography	substrate+slope+bankheight	7
Cover/tree characteristics	dbh+shrub2+conifer+sh1tree+obscurity115	7
Fine-scale consistency and intensity		
Vertical cover	shrub1+tree	3
Tree characteristics	dbh+distance	5
Topography	slope+bankheight	3
Tree characteristics/cover	dbh+distance+conifer+obscurity115+shrub2+sh1tree	9
Conifer characteristics	condbh+spruce+dripline+condistance	9
Conifer characteristics/horizontal	spruce+dripline+shrub2+obscurity115	7
Coarse-scale selection, consistency, and intensity		
Shoreline vegetation	treeheight+dspecies+canopycover+dspecies%	8
Aquatic habitat	dbeaverlodge+dbeaverlodge ² +dreedpatch+dreedpatch ² + dstreammouth ² +dstreammouth+waterdepth	8
Global	treeheight+dspecies+canopycover+dspecies%+dbeaverlodge ² +dbeaverlodge+ dreedpatch ² +dreedpatch+dstreammouth ² +dstreammouth+waterdepth+convex	16
Shoreline vegetation/spawning habitat	dspecies+canopycover+waterdepth+dstreammouth+ dstreammouth ²	9
Shoreline vegetation/fish+beaver habitat	dspecies+canopycover+dbeaverlodge ² +dbeaverlodge+dreedpatch ² +dreedpatch	10
Aquatic habitat/shoreline topography	dbeaverlodge+dbeaverlodge ² +dreedpatch+dreedpatch ² +dstreammouth ² +dstreammouth+ waterdepth+convex	9
Shoreline vegetation/shoreline topography	treeheight+dspecies+canopycover+dspecies%+convex	9
Shoreline topography	convex	2

context of a set of a priori models. We used both ΔAIC_c and Akaike weights (w_i) to rank and compare models. The model with the lowest AIC_c score is considered the “best” or the most-parsimonious model given the data and the set of models compared. A model with a $\Delta AIC_c < 2$, however, was considered to be equivalent to the model with the minimum score (Burnham and Anderson 2002). When models had ΔAIC_c values that were nearly equivalent, we selected the most-parsimonious model (i.e., fewest number of parameters). A w_i is a value from 0 to 1 that represents the approximate probability that a model is the best among a set of candidate models. We used beta-coefficients and *z*-statistics ($P < 0.05$) to assess the importance of individual parameters contained within the most-parsimonious explanatory models.

Predictive ability of habitat models.—Data for all count models were randomly divided into training (85%) and testing (15%) groups using a random number generator and a uniform distribution. The count models were developed using the data training group and then validated using the data testing group (Fielding and Bell 1997). We located too few latrine sites to conduct an independent evaluation of the predictive accuracy of binary models. We used the receiver operating characteristics and resulting area under the curve (AUC) to assess the predictive ability of the “best” model from the binary analyses (Pearce and Ferrier 2000). Models with AUC values

from 0.5 to 0.7 were considered to have poor model accuracy, from 0.7 to 0.9 good model accuracy, and >0.9 were considered to have high model accuracy (Swets 1988). We used Pearson’s standardized residuals to identify outliers (Menard 2001).

We used the predicted counts as well as the predicted probabilities of counts to evaluate the predictive performance of the most-parsimonious count models (Long and Freese 2006). We evaluated the performance of the model by visual inspection of graphs plotting the observed probability of a count using the model testing data and the predicted probability of a count generated from model training data. The residual difference between observed and predicted counts allowed us to further examine the models predictive ability across the range of values we observed.

RESULTS

We located a total of 73 latrine sites across 155 km of shoreline. Sixty-seven and 6 unique latrine sites were found in 2007 and 2008, respectively. Only 2 new latrine sites were found in areas already surveyed in 2007. The other 4 latrine sites were found in areas of Tezzeron Creek not surveyed in 2007. The 2008 survey was conducted to validate survey intensity and effort during 2007. The results demonstrate that

TABLE 4.—Summary of Akaike’s information criterion for small sample sizes (AIC_c) model selection statistics for candidate models (binary and zero-inflated negative binomial [ZINB] count) predicting latrine selection and activity (occurrence, consistency, and intensity), based on fine-scale habitat data collected on Tezzeron and Pinchi lakes in central British Columbia, Canada, from 2007 to 2008. w_i = Akaike weight.

Model name	Rank	AIC _c	ΔAIC _c	w_i
Latrine selection binary model				
Cover/tree characteristics	1	57.5	0.0	0.738
Global	2	61.0	3.5	0.127
Vertical cover	3	61.1	3.6	0.122
Cover and tree distance	4	66.0	8.5	0.011
Conifer cover/tree characteristic	5	69.8	12.3	0.002
Tree species	6	72.6	15.1	<0.001
Horizontal cover	7	73.7	16.2	<0.001
Tree characteristics	8	79.5	22.0	<0.001
Topography	9	89.0	31.5	<0.001
Consistency binary model				
Conifer characteristics/horizontal cover	1	95.5	0.0	0.887
Topography	2	101.8	6.3	0.039
Vertical cover	3	101.8	6.3	0.037
Conifer characteristics	4	102.2	6.7	0.032
Tree characteristics/cover	5	106.8	11.3	0.003
Tree characteristics	6	107.7	12.2	0.002
Intensity ZINB count model				
Tree characteristics/cover	1	4,352.6	0.0	0.923
Conifer characteristics/horizontal cover	2	4,357.9	5.3	0.065
Conifer characteristics	3	4,361.2	8.6	0.012
Vertical cover	4	4,394.8	42.2	<0.001
Topography	5	4,399.8	47.2	<0.001
Tree characteristics	6	4,402.0	49.4	<0.001

we were monitoring the majority of latrine sites found along shorelines in the study area. We measured latrine habitat characteristics at 70 (96%) of 73 of our detected latrine sites. The 3 sites not included in this analysis were not measured due to time constraints.

Selection of latrine sites.—The tree characteristic/cover model best explained the presence of latrine sites at the scale of the shoreline patch (Table 4). The 2nd- and 3rd-ranked model had some support but had ΔAIC_c scores that were 3.5 and 3.6 points, respectively, greater than the 1st-ranked model, and were not considered equivalent. Vertical cover > 2 m and the number of conifer trees were 2 variables that were common to the 3 top models. The receiver operating characteristic score showed that the top-ranked model had good predictive accuracy (AUC = 0.821). A maximum tree DBH > 50 cm had a positive statistically significant influence on the presence of latrine sites, whereas a tree DBH < 29 cm had a negative influence. Visual obscurity (1–1.5 m) had a significant positive influence on the presence of latrine sites (Table 5).

The shoreline vegetation/spawning habitat and shoreline topography models best explained the presence of latrine sites at the coarse scale. The w_i indicated that 2 top-ranked models had an equal chance (41%) of being the best among the candidate models. The models, however, had poor predictive accuracy (AUC = 0.658 and 0.533, respectively).

TABLE 5.—Estimated coefficients for Akaike’s information criterion for small sample sizes (AIC_c) selected models (binary) predicting the selection of latrine sites and consistency of activity by river otters, based on fine-scale habitat data collected on Tezzeron and Pinchi lakes, central British Columbia, Canada, from 2007 to 2008. Parameters are as described in Table 1. 95% CI = 95% confidence interval.

Parameter	Coefficient	SE	95% CI	P
Latrine selection (cover/tree characteristics model)				
dbh (0–29 cm)	−1.128	0.546	−2.198–−0.058	0.039
dbh (30–49 cm)	−0.353	0.442	−1.219–0.513	0.424
dbh (50+ cm)	1.481	0.630	0.246–2.716	0.019
shrub2	−0.029	0.018	−0.064–0.006	0.112
conifer	0.219	0.144	−0.063–0.501	0.129
sh1tree	0.023	0.012	−0.001–0.047	0.053
obscurity (1–1.5 m)	0.028	0.012	0.004–0.052	0.021
Consistency (conifer characteristics/horizontal cover)				
spruce	0.430	0.185	0.067–0.793	0.020
dripline (0–0.9 m)	0.793	0.608	−0.399–1.985	0.192
dripline (1–1.9 m)	−0.897	0.576	−2.026–0.232	0.120
dripline (2–2.9 m)	−1.053	0.566	−2.162–0.056	0.063
dripline (3+ m)	1.157	0.578	0.024–2.290	0.045
shrub2	−0.017	0.016	−0.048–0.014	0.300
obscurity (1–1.5 m)	0.018	0.009	0.000–0.036	0.049
constant	−1.015	0.930	−2.838–0.808	0.275

Latrine consistency.—The conifer characteristics/horizontal cover model best explained the consistency of otter activity at latrine sites at the fine scale (Table 3). The w_i indicated that the top-ranked model had an 89% chance of being the best among the candidate models; this model also had good predictive accuracy (AUC = 0.765). The number of spruce trees, visual obscurity (1–1.5 m), and extent of conifer dripline had a positive influence on the consistency of latrine-site activity (Table 5). At the coarse scale, the aquatic habitat model best explained the consistency of activity at latrine sites (Table 6). The w_i indicated it had a 57% chance of being the best model, which was 3.8 times higher than the 2nd-ranked model. In addition, the 2nd-ranked model was the same as the top-ranked model with 1 additional variable. The additional variable convex did not compensate for the resulting loss in parsimony (Burnham and Anderson 2002). The aquatic habitat model had good predictive accuracy (AUC = 0.774). The distance to beaver lodge had a statistically significant negative influence on the consistency of use of latrines by otters, whereas the distance to reed patch had a positive influence (Table 7).

Latrine intensity.—For the analysis of intensity of use of latrines at the fine scale, a negative binomial regression model performed better than a Poisson regression model ($G^2_{1,8} = 2,007.28, P < 0.001$), and because of the large number of zeros in the data set a zero-inflated negative binomial model provided a better fit than a negative binomial regression model (Vuong = 2.91, $P < 0.002$). We found a similar result for the coarse-scale analysis; a negative binomial regression model performed better than a Poisson regression model ($G^2_{1,11} = 1,830.29, P < 0.001$), and a zero-inflated negative binomial

TABLE 6.—Summary of Akaike's information criterion for small sample sizes (AIC_c) model selection statistics for candidate models predicting latrine activity (consistency and intensity) by river otters, based on coarse-scale habitat data collected on Tezzeron and Pinchi lakes in central British Columbia, Canada, from 2007 to 2008. w_i = Akaike weight; ZINB = zero-inflated negative binomial.

Model name	Rank	AIC_c	ΔAIC_c	w_i
Consistency binary model				
Aquatic habitat	1	95.5	0.0	0.567
Aquatic habitat/shoreline topography	2	98.1	2.6	0.152
Shoreline vegetation/spawning habitat	3	98.6	3.1	0.122
Shoreline topography	4	99.5	4.0	0.077
Shoreline vegetation/fish and beaver habitat	5	99.6	4.1	0.073
Shoreline vegetation characteristics	6	104.3	8.8	0.007
Shoreline vegetation/shoreline topography	7	106.6	11.1	0.002
Global	8	108.7	13.2	0.001
Intensity ZINB count model				
Global	1	4,142.3	0.0	0.999
Shoreline vegetation/fish and beaver habitat	2	4,164.5	22.2	<0.001
Shoreline vegetation/spawning habitat	3	4,173.5	31.2	<0.001
Aquatic habitat/shoreline topography	4	4,178.9	36.6	<0.001
Aquatic habitat	5	4,179.2	36.9	<0.001
Shoreline vegetation characteristics	6	4,188.5	46.2	<0.001
Shoreline vegetation/topography	7	4,188.6	46.3	<0.001
Shoreline topography	8	4,227.4	85.1	<0.001

model provided a better fit than an negative binomial regression model ($Vuong = 4.26$, $P < 0.001$).

The tree characteristics/cover model best explained the intensity of latrine-site activity by river otters at the fine scale (Table 4). Average tree distance (2–3.9 m), visual obscurity (1–1.5 m), and shrub cover (0–2 m) had a negative influence on the number of scats at latrine sites (Table 8). At the coarse scale, the global model best explained the intensity of latrine-site activity by river otters (Table 6). The w_i indicated that the top-ranked model had a near 100% chance of being the best among the candidate models. Latrines with a large amount of otter activity were associated with stream mouths, as shown by a negative and significant coefficient for this distance variable (Table 9).

At the fine scale, the count model describing the intensity of use of latrine sites resulted in a good fit between the observed and the predicted probability of the number of scats (Fig. 2). Furthermore, the Wilcoxon rank-sum test did not find a statistically significant difference between the predicted and observed counts ($z = 1.126$, $P = 0.26$). The mean of the residual analysis was close to zero ($\bar{X} < 0.001$), with residuals converging toward zero as the number of scats increased. The count model describing latrine intensity at the coarse scale had a good fit to the data, as suggested by a large positive correlation between the observed and predicted probabilities of scat counts and the Wilcoxon rank-sum test ($z = -1.396$, $P = 0.163$; Fig. 2). For the residual analysis, the mean difference in the probability of a scat count was close to zero. The model slightly overpredicted the number of zero counts and to a lesser degree underpredicted the number of single and double scat counts with residuals converging toward zero as the number of scats increased.

TABLE 7.—Estimated coefficients for the Akaike's information criterion for small sample sizes (AIC_c) selected model (binary) predicting the consistency of activity by river otters at latrine sites, based on coarse-scale habitat data collected on Tezzeron and Pinchi lakes, central British Columbia, Canada, from 2007 to 2008. Parameters are as described in Table 2. 95% $CI = 95\%$ confidence interval.

Aquatic habitat model parameter	Coefficient	SE	95% CI	P
dbeaverlodge	2.357	1.057	0.285–4.429	0.023
dbeaverlodge ²	–0.001	<0.001	–0.001–0.001	0.054
dreedpatch	–1.812	0.802	–3.384–0.240	0.045
dreedpatch ²	<0.001	<0.001	<–0.001–<0.001	0.087
dstreammouth	–0.684	0.603	–1.866–0.498	0.109
dstreammouth ²	<0.001	<0.001	<–0.001–<0.001	0.176
waterdepth	0.053	0.040	–0.025–0.131	0.062
constant	0.432	1.044	–1.614–2.478	0.901

DISCUSSION

Past research has shown that the environmental factors dictating animal distribution can vary in importance across scale (Ciarniello et al. 2007; Forchhammer et al. 2005; Johnson et al. 2002); our results provide an additional example of scale-specific selection of resources. Environmental variables had little influence on the distribution of latrine sites at the coarse scale and activity of otters was most closely associated with features describing the aquatic habitat of fish. In contrast, a number of models explained selection of latrines at the fine scale; both selection and otter activity were influenced by horizontal cover and tree characteristics along the shoreline. A geographic information system–type analysis of coarse-scale selection would have missed habitat characteristics important to otters within shoreline patches.

A multiscale approach provided a more-detailed and complete description and understanding of the selection and use of latrine sites. Multiple spatial and behavioral scales allow us to answer the questions of both *what* and *why* otters select for and use latrines. Such inference can provide insights into the possible mechanisms driving the distribution and activity patterns of otters. Only with knowledge of scale-specific processes, can we begin to initiate appropriate and efficient conservation and management strategies for otter populations.

An information theoretic model comparison approach was well suited for both the presence–absence and count data collected in this study. Ideally, we would have tested the presence and consistency models on an independent data set, but we lacked the sample size to divide the data into training and testing groups. This was not a result of sampling bias or an insufficient search effort because we located nearly every latrine site ($n = 73$) across approximately 155 km of shoreline. We did a complete survey of a large geographic area twice in 2007. Furthermore, results of an intensive survey of 200 random sections of shoreline in 2008 suggested that we were monitoring the majority of latrine sites in the study area during both years. This also was supported by the high percentage

TABLE 8.—Estimated coefficients for the Akaike's information criterion for small sample sizes (AIC_c) selected model (zero-inflated negative binomial count) predicting the intensity of activity by river otters at latrine sites, based on fine-scale habitat data collected on Tezzeron and Pinchi lakes, central British Columbia, Canada, from 2007 to 2008. Parameters are as described in Table 1. 95% CI = 95% confidence interval.

Parameter	Coefficient	SE	95% CI	P
Tree characteristics/cover model				
dbh (0–29 cm)	0.079	0.123	–0.161–0.320	0.517
dbh (30–49 cm)	–0.030	0.089	–0.205–0.145	0.739
dbh (50+ cm)	–0.050	0.093	–0.232–0.133	0.594
distance (0–1.9 m)	0.137	0.111	–0.803–0.354	0.217
distance (2–3.9 m)	–0.218	0.115	–0.443–0.008	0.048
distance (4+ m)	0.081	0.160	–0.232–0.394	0.613
conifer	0.037	0.028	–0.017–0.091	0.181
obscurity (1–1.5 m)	–0.005	0.002	–0.010–0.001	0.037
shrub2	–0.014	0.005	–0.023–0.005	0.002
sh1tree	–0.003	0.003	–0.009–0.004	0.403
constant	2.468	0.350	1.782–3.315	<0.001
Inflate portion				
dbh (0–29 cm)	10.282	1.419	–7.500–13.065	<0.001
dbh (30–49 cm)	–1.137	0.298	–1.721–0.553	<0.001
dbh (50+ cm)	–9.145	1.243	–11.582–6.709	<0.001
distance (0–1.9 m)	10.830	1.020	–8.832–12.828	<0.001
distance (2–3.9 m)	9.947	0.948	8.089–11.805	<0.001
distance (4+ m)	–20.777	1.928	–24.556–16.997	<0.001
conifer	2.488	0.408	1.689–3.287	<0.001
obscurity (1–1.5 m)	–0.300	0.041	–0.0381–0.0220	<0.001
shrub2	–0.112	0.017	–0.145–0.0780	<0.001
sh1tree	–0.308	0.046	–0.398–0.219	<0.001
constant	3.636	1.043	1.592–5.680	<0.001

(96%) of latrine sites that were identified in 2007 and were also active in 2008. Sample size would have increased only after expanding the study area.

We found that habitat characteristics at the fine scale were better at predicting the presence of latrines when compared to coarse-scale environmental features measured at the same sites. Examination of the data also suggested that the consistency and intensity of use of latrine sites can be predicted by both fine-scale and coarse-scale habitat characteristics. In general, latrine-site activity by otters at the coarse scale was best described by aquatic habitat, and by vegetation cover at the fine scale. These results support the hypothesis that otter activity is influenced by habitat characteristics that support their prey at the scale of the landscape, and by habitat characteristics that provide cover at the scale of the shoreline patch. Cover may be important for otters for security from terrestrial predators, to protect scent or scat from the elements and prolong its use for communication, or a combination of both of these functions.

Interpretations of habitat selection may be confounded by the influence of otter activity on vegetation characteristics at latrine sites. Otter scat and disturbance can influence the nitrogen content of vegetation at latrine sites (Ben-David et al. 1998, 2005; Crait and Ben-David 2007; Roe et al. 2010). Although Roe et al. (2010) provide evidence of increased

TABLE 9.—Estimated coefficients for the Akaike's information criterion for small sample sizes (AIC_c) selected model (zero-inflated negative binomial count) predicting the intensity of activity of latrine sites by river otters, based on coarse-scale habitat data collected on Tezzeron and Pinchi lakes, central British Columbia, Canada, from 2007 to 2008. Parameters are as described in Table 2. 95% CI = 95% confidence interval.

Parameter	Coefficient	SE	95% CI	P
Global model				
treeheight	0.022	0.012	–0.003–0.047	0.087
dspecies (aspen, birch)	–0.123	0.206	–0.526–0.280	0.549
dspecies (Douglas fir)	–0.018	0.271	–0.551–0.515	0.918
dspecies (no trees)	0.447	0.887	–1.293–2.186	0.615
dspecies (lodgepole pine)	0.174	0.470	–0.747–1.094	0.712
dspecies (white spruce)	–0.075	0.209	–0.486–0.335	0.718
canopycover	0.003	0.004	–0.005–0.012	0.437
dspecies%	–0.001	0.005	–0.011–0.001	0.862
dbeaverlodge	0.011	0.283	–0.543–0.566	0.968
dbeaverlodge ²	–0.010	0.067	–0.140–0.121	0.886
dreedpatch	–0.499	0.267	–1.021–0.024	0.061
dreedpatch ²	0.096	0.062	–0.025–0.217	0.121
dstreammouth	–0.334	0.153	–0.633–0.0347	0.029
dstreammouth ²	0.043	0.020	0.004–0.082	0.029
waterdepth	–0.004	0.007	–0.019–0.011	0.564
constant	2.014	0.671	0.698–3.33	0.003
Inflate portion				
treeheight	–0.013	0.061	–0.132–0.106	0.832
dspecies (aspen, birch)	–9.518	3.923	–17.207–1.829	0.015
dspecies (Douglas fir)	–12.397	5.655	–23.482–1.313	0.028
dspecies (no trees)	1.176	2.018	–2.778–5.130	0.139
dspecies (lodgepole pine)	–2.603	3.154	–8.786–3.579	0.409
dspecies (white spruce)	–0.573	0.693	–1.932–0.786	0.408
canopycover	0.210	0.035	–0.047–0.089	0.545
dspecies%	–0.019	0.034	–0.086–0.047	0.570
dbeaverlodge	–2.394	1.741	–5.806–1.019	0.169
dbeaverlodge ²	0.506	0.349	–0.177–1.190	0.147
dreedpatch	0.715	0.762	–0.780–2.210	0.349
dreedpatch ²	0.029	0.126	–0.275–0.218	0.820
dstreammouth	0.597	0.489	–0.361–1.556	0.222
dstreammouth ²	–0.128	0.051	–0.228–0.028	0.012
waterdepth	–0.068	0.121	–0.305–0.169	0.572
convex	2.568	4.331	–5.920–0.169	0.572
constant	–0.232	2.936	–5.987–5.524	0.937

nitrogen uptake by shrubs and trees at latrine sites and some effects from otter fertilization and disturbance on tree and shrub production, there is limited information suggesting that river otters are the ultimate determinant of riparian communities near latrine sites. In addition, most studies have focused on the transport of marine-derived nutrients into terrestrial systems, whereas our study occurred in a freshwater system. In general, the nitrogen content of organisms in freshwater systems is lower than in marine systems (France 1994; MacAvoy et al. 2000). In a study of the effects of river otter activity on terrestrial plants in a freshwater system, there were no difference in plant diversity and percent cover between latrine and nonlatrine sites (Crait and Ben-David 2007). Although otter activity may have some limited influence on riparian vegetation in our study area, habitat characteristics at latrine sites are most likely the product of selective pressures on river otters for cover and food resources.

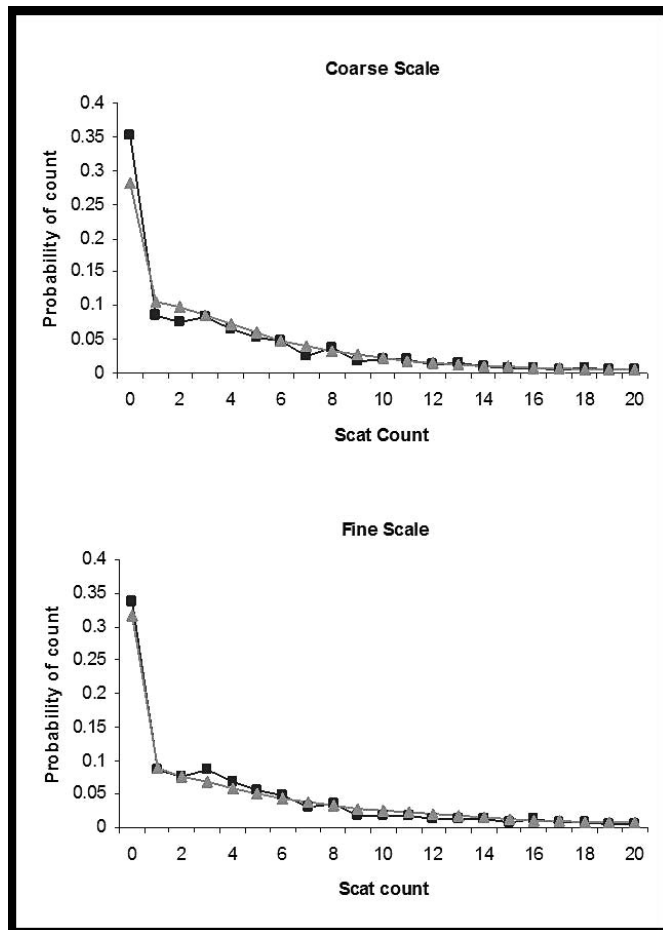


FIG. 2.—Predicted (gray triangle) versus observed (black square) probability of scat counts for river otters on Tezzeron and Pinchi lakes, British Columbia, Canada, from May to October (2007–2008). Predictions were generated with the best zero-inflated negative binomial model and an independent data set for both coarse-scale and fine-scale models.

At the fine scale, we conducted detailed measurements of latrines that exceeded simpler descriptions of habitat features such as the presence or absence of conifer trees. Using these data, we found that fine-scale variation (e.g., drip-line extent, DBH, and number of trees) predicted the presence of latrines and the activity of otters. Selection of latrine sites by otters was positively influenced by large-diameter trees and horizontal visual obscurity. Consistently used latrine sites were associated with conifer trees that had a large drip-line extent, a higher number of spruce trees, and increased horizontal cover. Although not significant, the presence and consistency of use of latrine sites was negatively influenced by shrub cover (0–2 m). These results indicate that horizontal cover for otters is important; however, cover is a function of large-diameter conifer trees with low-hanging branches and not shrubs. Consistent and frequent use of these habitat types suggests they play an especially important role in the ecology of otter populations. Other studies documented the presence of large conifer trees at latrine sites (Newman and Griffin 1994; Swimley et al. 1998), but failed to provide a detailed description of those vegetation communities.

For the intensity of activity at latrine sites, shrub cover also had a negative influence on scat numbers; however, unlike the other models, visual obscurity had a significant negative influence on scat numbers. These results suggest that horizontal cover from trees is not as prevalent at latrine sites with a high intensity of use. This difference is most likely explained by the pulsed, frequent visitation rates in areas near the mouths of streams where cover is often not as abundant. This hypothesis is supported by the coarse-scale behavioral models where latrine sites near stream mouths were associated with greater numbers of scats.

When tested, the 2 top-ranked models describing the presence of otter latrines at the landscape scale had poor predictive accuracy. Otter latrines were well distributed throughout the study area (Fig. 1) and the results suggest otters do not select latrine sites based on the coarse-scale variables used in this study, namely food resources, cover, and shoreline topography. Otters may require an even distribution of latrine sites on the landscape for sociality, or may simply travel frequently and far enough along the shoreline to maintain latrine sites at many locations.

A more-detailed examination of latrine sites with consistent or high-use visitation by otters produced models that were predictive at the coarse scale. The distance to beaver lodge had a negative influence on activity patterns. This result was at first surprising given previous studies that describe the importance of beaver activity to otters (Melquist and Hornocker 1983; Reid et al. 1994). Reid et al. (1994), however, found that selection for areas near beaver lodges was at its highest during the winter months. During the winter, lodges are thought to provide cover and access to feeding areas below the ice. In summer, lodges along lakes and streams may not serve as important a role. The relationship between otter distribution and beaver activity in summer may be attributed to the ponds they create rather than the lodges they construct (LeBlanc et al. 2007). The majority of the beaver lodges located in this study were in close proximity to major streams and lakes. Beaver lodges associated with flooded forests, just offshore behind latrine sites, may have not been detected even though they were located a relatively short distance from a latrine site. Lastly, LeBlanc et al. (2007) found that otter activity was most closely associated with beaver ponds that had current resident beavers. No attempt was made to delineate between inactive and active beaver lodges. Exclusion of inactive beaver lodges from the data set may have changed the results.

The consistency of activity at latrine sites at the coarse scale was associated with reed patches. These areas may provide important foraging habitat and cover for river otters while hunting fish. In addition, several studies describe otters hunting waterfowl by attacking from underneath while birds float on the water (Harris 1968; Meyerriecks 1963). Waterfowl are frequently found in this habitat and the cover provided by reeds may help otters go undetected while hunting. The intensity of activity at latrine sites at the coarse scale was associated with stream mouths. Intensity of activity at these features may be attributed to variable, but high

densities of fish during the spawning seasons (e.g., kokanee and sockeye salmon). Consistent with the fluctuations in the availability of this food source, distance to stream mouth was not a significant variable for the consistency model. Activity of otters at the coarse scale likely correlates with the spatial distribution of prey. In addition to fisheries and waterfowl values, management of riparian areas should consider the requirements of river otters.

Other studies documented the importance of lakeshore topography for influencing the distribution of latrine sites at a coarse spatial scale (Newman and Griffin 1994; Swimley et al. 1998). For example, Albeke et al. (2010) used the convexity or concavity of shorelines to predict the presence of river otter latrine sites. Although the shoreline topography model was the best among those tested in our study, the model had poor predictive accuracy. Alternative measures of shoreline topography or other boundary convexity index measures at different scales may be more appropriate for freshwater systems in central British Columbia than what was reported by Albeke et al. (2010). Detailed investigations of shoreline topography metrics, however, were beyond the scope of our study and could be a focus for future research.

Considering differences in the ecology of otter populations across their North American range, the results of this study can be generalized in a number of ways. The fine- and coarse-scale characteristics of specific habitat features (i.e., conifer drip-line extent or reed patches) that influence otter selection or activity are most applicable to otter populations in central British Columbia. The results of this study, however, also may be relevant to otter populations inhabiting areas with similar predators, prey bases, and habitat types. The specific habitat characteristics may vary (i.e., cover may be provided by different vegetation types or terrain), but the importance of cover at the fine scale and the distribution of food resources at the coarse scale are likely a result of selective pressures common to many river otter populations. Lastly, this study provides an example of the importance and feasibility of combining spatial and behavioral scales into the design of studies that measure wildlife sign. Habitat-selection and population-monitoring studies that do not include scale in their study design may misinterpret important components of otter habitat or population indexes that influence management decisions. For example, important habitat features may be missed when making land-use decisions, or wildlife management actions may be misguided by misinterpretations of population trends from surveys of otter sign.

Scale is a fundamental component in the design and interpretation of ecological investigations. The same ecological processes might show different patterns if observed at a different scale (Wheatley and Johnson 2009; Wiens 1989). The influence of habitat characteristics on latrine-site occurrence and activity at one spatial scale may be very different at another scale. The majority of past studies of habitat selection by otters have failed to address this issue, aggregating data across scales or focusing on a single scale during study design and analysis (Bowyer et al. 1995;

Dubuc et al. 1990; Swimley et al. 1998). Fine-scale measurements of presence-absence data (e.g., presence of conifer trees) were used by Swimley et al. (1998) to measure habitat selection; however, variables at a coarser scale (e.g., minimum distance from coves, tributaries, or islands) also were included. Leblanc et al. (2007) were concerned with selection at the scale of the beaver pond, and Dubuc et al. (1990) focused on selection of habitat by otters at the watershed and forest-stand scales.

There have been no published studies that investigated latrine selection and activity at multiple spatial and behavioral scales. There are a few examples, however, of past research that has investigated elements of this scalar continuum. For example, Newman and Griffin (1994) adopted a multiscale approach, relating presence-absence data to habitat characteristics at the fine scale and wetland-type categories at the coarse scale. In addition, Newman and Griffin (1994) and Leblanc et al. (2007) investigated otter visitation rates in relation to coarse-scale wetland types. We measured latrine selection and otter behavior at 2 spatial scales: landscape and shoreline patch. We recognize that finer-scale variables are potentially a product of or related to coarse-scale variables. However, we were not attempting to develop the most-predictive model across all scales of selection, but to test the relative strength of selection at 2 ecologically relevant scales. Our results provide evidence that modeling activity patterns at latrine sites, in relation to different spatial and behavioral scales, is critical for understanding the mechanisms and processes driving selection and use of latrines by river otters.

One reason that past studies of latrine selection have focused on the presence and not the level of activity (measured by scat abundance) at latrine sites is that presence-absence data are much easier to collect (Dubuc et al. 1990; Swimley et al. 1998). Our study did not address river otter abundance; however, if deposition rates of scats are directly related to otter abundance, then the number of scats at latrine sites could provide important information on the relative abundance and distribution of otter populations. Nielsen et al. (2005) used 2 dissimilar species to investigate the relationship between occurrence and abundance. Our research provides some tentative support for their conclusions; environmental influences affecting abundance may be different than those limiting distribution. Coefficients and models differed when comparing the selection of latrines to measures of otter activity at those sites. This was especially evident when habitat selection and activity were measured at the coarse scale, suggesting that different processes may influence the selection and use of latrine sites by otters. These findings, however, are only tentative because we had indexes of otter activity only. There has been considerable debate on the utility of using scat surveys to monitor populations of Eurasian otters (Kruuk et al. 1986; Macdonald and Mason 1987). In North America, Gallant et al. (2007) cautioned against using latrine sites to predict the number of otters in an area. Their study, however, was conducted during winter when environmental factors

influencing otter behavior and sign are very different than during ice-free months. Future studies need to investigate the relationship between otter abundance and the number of scats at latrine sites during the ice-free season.

The scales of analysis addressed in our research should be applied to conservation and management actions that incorporate the habitat requirements of otters. The presence of otter latrine sites along shorelines may not be limited by coarse-scale factors such as forest-stand type or distance to aquatic features. Habitat characteristics such as conifer trees and cover influence latrine-site presence along smaller sections of shoreline, and the level of activity at latrine sites is affected by environmental features at both scales. The interaction among behavioral and spatial scales helps us understand the *why* behind latrine-site selection and use by otters. The more we understand about the *why*, the more we know about *what* to protect when managing or conserving otter populations and their habitat. If latrine-site consistency and intensity reflect increased activity by otter populations, then habitat characteristics, such as conifer trees and horizontal cover or stream mouths and reed patches, may require additional consideration when prioritizing management actions, protecting areas as a critical habitat, or limiting activities that disturb otters.

ACKNOWLEDGMENTS

We thank the Habitat Conservation Trust Fund, Teck Cominco, the John Prince Research Forest, and the University of Northern British Columbia for providing funding to support this project. We thank M. Gillingham and D. Heard for their guidance and support of this project. We thank S. Grainger, B. John, and A. Stark for their support and shared space. A special thanks to S. Champagne and N. Tom for their hard work, positive attitude, and sense of humor. We thank V. Crowley for her support and hard work on this project.

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Submitted 2 November 2010. Accepted 21 August 2011.

Associate Editor was Samantha M. Wisely.