

Spatio-temporal variation in river otter (*Lontra canadensis*) diet and latrine site activity¹

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Abstract: Fluctuations in the distribution and abundance of prey resources are an important influence on the foraging ecology of carnivores. Spatio-temporal variation in the diet of river otters (*Lontra canadensis*), however, is not well understood. In addition, we have limited knowledge about seasonal changes in otter activity at latrine sites and how these changes may relate to changes in otter diet. We used a combination of scat content and stable-isotope analyses to assess the contributions of different prey items to otter diet. We investigated the spatio-temporal variation in the availability of prey groups as it influenced the composition of otter diet and the number of scat deposited at latrine sites. A combination of fish spawning period, water-body type, and lake best described the presence of salmonidae, minnows, and insects in otter scats. The number of scats was best described by a two-week calendar time measurement and geographic location. Scat deposition was positively influenced by a time period when no fish were spawning (early July) and the kokanee (*Oncorhynchus nerka*) spawning period (early September). In general, the stable-isotope analysis agreed with the results of the scat content analysis: fish dominated the diet, with lesser contributions from other prey items. The stable-isotope analysis, however, suggested that sockeye salmon, larger species of fish (burbot, lake trout), and birds contributed more than was revealed by scat content analysis. Management strategies require accurate and unbiased information on wildlife distribution and abundance that is often measured from surveys of sign; this study provides some of the critical information needed to interpret surveys for river otters. We also suggest implications for other wildlife species.

Keywords: British Columbia, diet, latrine site, *Lontra canadensis*, river otter, stable isotope.

Résumé: Les fluctuations dans la distribution et l'abondance des proies ont une grande influence sur l'écologie de quête alimentaire des carnivores. Les variations spatio-temporelles du régime alimentaire des loutres de rivière (*Lontra canadensis*) ne sont cependant pas bien comprises. De plus, nous avons peu de connaissances sur les changements saisonniers de l'activité des loutres dans les lieux utilisés comme latrines et de la manière dont ces changements influencent le régime alimentaire des loutres. Nous avons combiné des analyses du contenu des fèces et des isotopes stables afin d'évaluer les contributions relatives des différentes proies au régime alimentaire des loutres. Nous avons examiné les variations spatio-temporelles de la disponibilité des types de proies puisqu'elles influençaient la composition du régime des loutres et le nombre de fèces déposées dans les latrines. La combinaison de variables prédisant le mieux la présence de salmonidés, de cyprinidés et d'insectes dans les fèces des loutres comprenait la période de frai des poissons, le type de plan d'eau et le lac étudié. Le moment de l'année (par période de deux semaines) et l'emplacement géographique prédisaient le mieux le nombre de fèces. Celui-ci était associé de façon positive à la période où aucun poisson n'était en frai (début juillet) et à la période de frai du saumon rouge (*Oncorhynchus nerka*) au début septembre. Dans l'ensemble, les résultats de l'analyse des isotopes stables concordaient avec ceux du contenu des fèces; les poissons dominaient le régime alimentaire alors que les autres types de proies étaient en plus faibles proportions. Cependant, l'analyse des isotopes stables suggérait que le saumon rouge, les plus gros poissons (lotte, touladi) et les oiseaux apportaient une plus grande contribution au régime des loutres que ce que révélait l'analyse du contenu des fèces. Les stratégies de gestion de la faune requièrent une information juste et non biaisée sur la distribution et l'abondance des espèces souvent obtenue à partir de signes de leur présence; la présente étude apporte donc des informations essentielles pour interpréter ces signes pour la loutre de rivière et ces résultats ont également des implications pour d'autres espèces.

Mots-clés: Colombie-Britannique, isotope stable, latrines, *Lontra canadensis*, loutre de rivière, régime alimentaire.

Nomenclature: Wilson & Reeder, 2005.

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Introduction

Knowledge of the spatial and temporal variation in the use of food resources is important for effectively managing wide-ranging carnivores (Molsher, Gifford & McIlroy, 2000; Eide, Jepsen & Prestrud, 2004). Seasonal variation in the use and availability of food resources can influence population dynamics (Fuller, 1989; Fuller & Sievert, 2001), habitat selection (Wang *et al.*, 2010), and foraging ecology (Gonzalez, 1997). However, for many carnivore species, there is limited information for predicting changes in diet across time and space. Such inference can provide insights into the mechanisms driving the distribution and activity patterns of individual populations and variation across populations of a single species. In the case of animal behaviour, the relationship between diet and spatio-temporal variation in activity helps us understand why wildlife species are using areas at different times of the year.

Surveys of animal sign are often employed as an inexpensive means for monitoring trends in wildlife populations. These surveys often provide information about population distribution or abundance, and are used as the basis for management decisions (*e.g.*, Kendall *et al.*, 1992; Patterson *et al.*, 2004). However, our ability to use animal sign to monitor the status of populations effectively is limited by the assumptions of many survey techniques. Monitoring activities that rely on sign must be able to differentiate between changes in activity that are related to seasonal fluctuations in food resources and/or different habitat types and changes that represent longer-term population trends. Concurrent information on diet and activity can provide direction for the timing of surveys to maximize detection of wildlife species and to interpret variations in the relative abundance of sign.

Although scat inventories are a long-standing method for assessing the diet of carnivores with predictable sampling locations, the analysis of stable isotopes within an animal's tissue is proving to be a widely applicable and perhaps more effective and efficient method for determining diet (Urton & Hobson, 2005; Mowat & Heard, 2006). Using this technique, one measures the ratios of naturally occurring carbon and nitrogen stable isotopes in blood, tissue, bone, or hair sampled from the focal species. The isotopic signatures of potential prey items are then related to the carbon and nitrogen signature of the predator to determine the contribution of each item to the total diet (Dalerum & Angerbjorn, 2005). Isotopic analysis of hair has been used to investigate seasonal shifts in the diets of wolves (*Canis lupus*; Darimont & Reimchen, 2002; Milakovic & Parker, 2011), brown bear (*Ursus arctos*; Ben-David, Titus & Beier, 2004), and arctic fox (*Alopex lagopus*; Roth, 2002). The metabolically inactive portion of the hair will retain isotopic signatures characteristic of the diet during the period of hair growth. In addition, many animals experience an annual moult that allows for predictable seasonal growth periods in hair—ideal for investigating spatio-temporal variation in diet. However, temporal trends in diet cannot be investigated after hair stops growing (Dalerum & Angerbjorn, 2005).

Spatio-temporal variation in the diet of North American river otters (*Lontra canadensis*) is not well understood. Few studies have described changes in otter diet within or across seasons (Melquist & Hornocker, 1983; Reid *et al.*, 1994a), and the majority of studies have averaged diet over a broad time period with little account for seasonal differences (*e.g.*, Gilbert & Nancekivell, 1982). The majority of diet studies for otter have been premised on analysis of prey remains in scats. These studies suggest that the diet of river otters throughout their range consists predominately of fish (Greer, 1955; Larsen, 1984; Reid *et al.*, 1994b; Roberts *et al.*, 2008). Crayfish and frogs, however, can comprise a substantial portion of the diet of southern populations of otter (Wilson, 1954; Towell, 1974). In coastal environments, both crabs and mollusks can contribute to otter diet, but these occur in lower frequencies than fish (Larsen, 1984; Stenson, Badgero & Fisher, 1984). Insects, clams, snails, snakes, turtles, waterfowl, shore birds, beaver (*Castor canadensis*), and muskrat (*Ondatra zibethicus*) have all been documented as secondary prey items for both coastal and interior populations (Towell, 1974; Larsen, 1984; Stenson, Badgero & Fisher, 1984; Reid *et al.*, 1994b). Although fish are the predominant prey item for most populations of otter, the importance of individual fish species and the occurrence of secondary prey items can vary during the year (Melquist & Hornocker, 1983; Reid *et al.*, 1994b; Crait & Ben-David, 2006; Roberts *et al.*, 2008).

Although scat inventories can index the relative importance of different food categories, this technique has several known biases (Larsen, 1984; Crimmins, Roberts & Hamilton, 2009). First, the method relies on hard parts found in the scats that can be identified to species or family. Differences in the number, size, and digestibility of hard parts across individual prey species have the potential to bias diet estimates. Second, a high frequency of occurrence of hard parts in scats does not directly relate to the biomass consumed by otters. For example, Reid *et al.* (1994b) reported that the high frequency of insect remains in scats during the summer season may not be a meaningful indicator of the total biomass consumed. Finally, scats provide information only on an animal's recent meals, and large numbers of scat through time may be needed to draw accurate and unbiased conclusions about seasonal or annual patterns in prey consumption. Despite these biases, Erlinge (1968) concluded through captive feeding trials that frequency of occurrence data gave a reasonably accurate measure of the relative importance of prey species. Additional methods for measuring diet, however, would be useful as a complementary technique for revealing these biases and producing the most accurate representation of otter diet.

Stable-isotope analysis of diet has not been conducted on river otters living in freshwater systems, but given its use for many other carnivore species it has great potential for investigating otter diet. North American river otter have 2 cycles of hair shedding and replacement during the year. From May through August, otters shed and replace underfur, and from August to November they shed and replace guard hair (Ben-David, Williams & Ormseth, 2000). This pattern of hair loss and growth appears to be common among carnivores inhabiting northern environments,

and when combined with stable-isotope analysis it enables the identification of bi-seasonal patterns in diet (Harper & Jenkins, 1982; Maurel *et al.*, 1986).

Past studies of otter diet have reported descriptive statistics and graphs of prey remains throughout the year (Greer, 1955; Larsen, 1984; Reid *et al.*, 1994b). Although seasonal patterns of diet can be useful in understanding animal behaviour, spatio-temporal variation in diet can provide deeper insights into patterns of habitat selection and more generally why otter distribute themselves across annual ranges. Also, such information is critical for indexing scat deposition rates to population dynamics (Mowry *et al.*, 2011). However, few studies have modeled otter diet through space and time or assessed the predictability of those patterns using scat inventories. In addition, there is little information relating changes in the food consumed by otters to fluctuations in scat deposition rates. Most studies of latrine occupancy, distribution, and habitat selection have focused on the simple presence of scat to document a latrine location and have not taken into account spatio-temporal variation in the number of scat at latrine sites (Dubuc, Krohn & Owen, 1990; Newman & Griffin, 1994; Swimley *et al.*, 1998; Depue & Ben-David, 2010). 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 & Ben-David, 2006), to investigate coarse-scale differences in the use of beaver ponds or wetland types (Newman & Griffin, 1994; LeBlanc *et al.*, 2007), and, in combination with camera surveys, to document seasonal visitation and scent-marking behaviour (Olson, Serfass & Rhodes, 2008).

We used an information-theoretic model comparison approach to investigate variation in the diet of river otter and deposition rates at latrine sites in central British Columbia during the ice-free season. We used a combination of prey remains in scat and stable-isotopic signatures in otter hair to assess the contributions of different prey items to otter diet. We measured deposition rates at known latrines and used those data as a measure of otter behaviour. Both sets of data were related to explanatory variables that indexed the spatio-temporal variation in the availability of prey items. Our specific objectives were 1) to document the diet of otter in an interior freshwater system of British Columbia using a combination of assessment techniques; and 2) to investigate the relationship among otter diet, spatio-temporal variation in resources, and scat deposition rates. We hypothesized that 1) otter diet would vary throughout the ice-free season, while displaying predictable patterns in both space and time related to differences in life histories and fluctuations of prey resources, and 2) distribution and use of latrine sites would display predictable patterns related to the variation in food types consumed by otters.

Methods

STUDY AREA

The research was conducted in and adjacent to the co-managed (UNBC and Tl'azt'en Nation) John Prince Research Forest (JPRF). The JPRF is a 17 000-ha portion

of forested crown land 45 km northwest of Fort St. James, British Columbia (54°40'14"N, 124°25'13"W). The area is characterized by rolling topography with low mountains (elevation range between 700 m and 1267 m) and a high density of lakes, rivers, and streams. The JPRF is located between Pinchi and Tezzeron lakes and includes many smaller lakes and streams. Pinchi and Tezzeron lakes drain into the Stuart and Nechako rivers, but are not directly connected.

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*) are also present in both lakes. Sockeye salmon (*Oncorhynchus nerka*) spawn in both the Kuskwa and Pinchi Rivers during the fall. Kokanee (*Oncorhynchus nerka*) spawn in creeks and rivers during the late summer and early fall. A multitude of waterfowl species nest on or near the 2 lake systems, with common mergansers (*Mergus merganser americanus*) and red-necked grebes (*Podiceps grisegena*) especially common on the major lakes throughout the ice-free season. Freshwater clams (genus: *Anodonta*) are locally abundant in shallow areas throughout both lakes. Beaver and muskrat are common throughout the study area.

DATA COLLECTION

We conducted shoreline surveys by canoe, by kayak, and on foot to identify river otter latrines along all significant tributary streams (1 km from lake-stream confluence and navigable by canoe or kayak) on Pinchi and Tezzeron lakes. Two complete surveys of all shorelines were conducted in 2007. The first occurred from 5 to 27 June and the second from 20 July to 5 August. In 2008, we randomly selected and intensively surveyed 200, segments of 200 m of shoreline split evenly between the Tezzeron and Pinchi lake systems from 15 August to 15 September. The 2008 survey was conducted both to identify new latrine sites and to determine if we had found most or all of the active latrine sites in 2007. We surveyed latrine sites every 2 weeks to collect scats and record the frequency of use. In 2007, scat collection began in July and ended in late October. In 2008, scat collection began in mid-May and ended in mid-October. We randomly selected a sub-sample of scats at latrine sites for collection and diet analysis. We left approximately 25% of the scat at latrine sites to maintain active scent for revisits by otters. Scats not collected at latrine sites were marked with silver glitter. Continued high activity at latrine sites suggested our surveys had a minimal influence on otter visitation rates. Scats were stored in Ziploc bags, frozen after collection, and later washed through a 1- × 1-mm strainer and air-dried.

Scats were sub-sampled for prey identification using a stratified random sampling method to maintain relatively equal sample sizes among time periods and locations. After washing and drying, each scat was spread evenly over a grid containing 36 cells of 1 × 1 cm. We randomly selected 8 of the 36 cells for prey identification. The contents of each cell were recorded: bone, scale, hair, feather, clam shell, and/or insect exoskeleton. We recorded the presence/absence of each prey type. Scales were used as the primary identifier

of fish family groups, supported by intact jaw bones with teeth. Identification of fish remains was conducted using a reference collection that we generated for the study area as well as available literature (McAllister & Lindsey, 1961; Lagler, 1970; Nelson, 1973; Cannon, 1987). We used a 10–20× dissecting microscope to identify scales. A total of 5 fish family groups were identified in the scat content analysis: Salmonidae (salmon, whitefish), Cyprinidae (minnow), Cottidae (sculpins), Castomidae (suckers), and Gadidae (burbot). Additionally, we differentiated salmon (genera) from whitefish (species genus). Mammals and birds were primarily identified by the presence of hair and feathers, respectively. Insects were identified by exoskeletons, and mollusks by shell fragments. Composition of food types within scat was summarized as the percentage of the total number of scats analyzed that contained a particular prey type.

Prey tissue samples for stable-isotope analysis were collected during late summer of 2008 (British Columbia Ministry of Environment Fish Collection Permit No: PG08-45338). Potential prey items were identified from a review of past studies of otter diet (Toweill, 1974; Melquist & Hornocker, 1983; Larsen, 1984; Reid *et al.*, 1994b), from published accounts of fish and wildlife species in the study area (Dodds, unpubl. data; McPhail, 2007), and from initial observations of prey remains in otter scat. We attempted to collect consumable tissue (*i.e.*, muscle) from 3 different individuals within each prey group. Prey tissue samples were dried at approximately 60–70 °C for 48 h and ground to a fine powder using a WIG-L-BUG grinder (Crescent Dental Company, Chicago, Illinois, USA) (Ben-David, Flynn & Schell, 1997). Guard hairs were pulled from river otter during capture efforts associated with a radiotelemetry study on Tezzeron and Pinchi Lakes in October 2007 and May 2008. In addition, samples of guard hair were collected from otters commercially trapped in the vicinity of the study area (approximately 30 km radius) during November 2008. Hair was cleaned of surface oils in 2:1 chloroform:methanol solution, rinsed with distilled water, and air-dried (Hobson, McLellan & Woods, 2000). A subsample (1–1.2 mg) of the fine powder tissue sample or intact hairs were weighed into a tin capsule (5 × 9 mm) (Costech Analytical Technologies Inc., Valenica, California, USA), encapsulated, and placed into a 96-well plate. Samples were measured for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopes at the University of California Davis Stable Isotope Facility using a continuous flow isotope-ratio mass spectrometer. Values for insects (mayfly, stonefly, caddisfly) were taken from a study in the nearby Stuart River watershed (Johnston *et al.*, 1997); we used values for insects collected in areas with low sockeye salmon density.

STABLE-ISOTOPE ANALYSIS

For the stable-isotope analysis, we used the dietary mixing model Isosource (Version 1.3.1; Phillips & Gregg, 2003) to quantify the relative range of proportions of potential prey items within otter hair (Phillips & Gregg, 2003; Phillips, Newsome & Gregg, 2005). In this model, all combinations of each source contribution are examined and any combination that sums to the observed mixture of isotopic signatures is a feasible solution (Phillips & Gregg, 2003).

For this reason, a distribution of feasible solutions is reported rather than a single value. The model requires that isotopic signatures be corrected for enrichment from prey to consumer. Consumer diet-to-hair fractionation values are not established for river otters; however, we used a fractionation value of 1‰ for carbon and 2‰ for nitrogen based on captive feeding trials of mink and bear (Ben-David, 1996; Hilderbrand *et al.*, 1996). These values were used for 2 reasons: 1) they are enrichment values based on the most functionally related carnivore species; and 2) these values have been used with success on a study of river otters in a coastal environment (Ben-David *et al.*, 1998). We investigated the sensitivity of the analysis to variations in carbon and nitrogen fractionation values by examining prey source contributions when values were manipulated up to $\pm 15\%$. We set a tolerance of 0.1‰ and source increment value of 1‰ to incorporate measurement error and sample variability within the Isosource model (Urton & Hobson, 2005).

The most important factor in controlling uncertainty in estimates of source proportions is the existence of large isotopic differences among sources (Phillips & Gregg, 2001). Due to the large number of potential sources, we used a combination of *a priori* and *posteriori* methods to combine sources for mixing analysis (Phillips, Newsome & Gregg, 2005). We first combined sources *a priori* into logically related groups based on the biology (*e.g.*, trophic level, marine *versus* freshwater, terrestrial *versus* aquatic) of prey sources and on the relative similarity of isotopic signatures. When the Isosource model produced indeterminate results (broad range of solutions), we examined the ranges and aggregated the sources where needed. Sources were grouped only if the majority of their estimated contributions (>75%) overlapped and ecological significance (*i.e.*, functionally related prey) was maintained. The combination of methods resulted in narrower and constrained results for interpretation.

DIET AND SCAT MODEL DEVELOPMENT

For each prey group identified in otter diet, we used logistic regression to identify factors that explained variation in occurrence within sampled scats (Menard, 2001). The presence (1) or absence (0) of a particular prey group was the dependent variable in the model. We constructed a zero-inflated negative binomial (ZINB) count model to investigate the relationship between the number of scats deposited at a latrine site and variables that represented the spatio-temporal variation in the availability of prey groups (Nielsen *et al.*, 2005). A negative binomial regression allows for the overdispersion of counts that is often characteristic of ecological data (Long & Freese, 2006). We tested this assumption with a likelihood ratio test. A zero-inflated model incorporates excess zero counts through a mixture of 2 separate processes: a data-generating process of zeros and another of either a Poisson or negative binomial distribution (Long & Freese, 2006). We used a Vuong test to determine if a zero-inflated model was appropriate (Vuong, 1989). All data analyses were performed using Stata (version 9.2, Statacorp, College Station, Texas, USA).

We used 5 spatio-temporal variables to explain both the presence of diet items in individual scat samples

(logistic regression) and the frequency of scats (zero-inflated negative binomial) at latrine sites. Variables representing the spatial distribution of latrine sites included geographic zone (classified by the adjacency [<1 km] and location of sites along the shoreline) and water-body type (stream, open lake, reedy bay). We hypothesized that the distribution and abundance of the range of prey species varied spatially throughout the 2 lake systems. Thus, geographic zones were used to represent 5 distinct areas across each lake. Drawing on our understanding of fish ecology, we hypothesized that there would be spatial heterogeneity in the diet of otters because of variation in the life history requirements of major fish species. Different prey species and cohorts inhabit different water-body types throughout the year depending on their habitat requirements. For example, rainbow trout are found in both stream and lake habitats, while lake trout are found almost exclusively in deep water lakes (McPhail, 2007). The movement of kokanee from lake into stream habitats to spawn during the fall is another example of a variable spatial distribution related to habitat (McPhail, 2007). Temporal variables included season (measured as sequential two-week periods throughout the study's duration) and fish spawning period (time of spawning for fish species found in the study lakes). The season variable captured the variability in the distribution and abundance of all potential prey species throughout the year.

For the fish spawning variable, we hypothesized that fish would be most vulnerable to otter predation when they aggregate in shallow water to spawn and, thus, should constitute a larger portion of otter diet during those periods. The timing of spawning for major fish groups was estimated from published data and local knowledge of fish in the study area (McPhail, 2007). This resulted in 4 time periods: late June–early August (fishspawn 1 = no spawn), early June (fishspawn 2 = rainbow trout, sucker, lake chub, northern pikeminnow, sculpin), late September–October (fishspawn 3 = sockeye salmon, lake trout, whitefish), and late August–early September (fishspawn 4 = kokanee). As a fifth variable, we modeled the effect of the larger geographic areas, Tezzeron and Pinchi lakes, as a possible explanatory factor for variation in otter diet and scat deposition rates. Variations in the topography, water depths, and habitat characteristics of the 2 lakes may affect the relative distributions and abundance of different prey sources.

We used biologically plausible combinations of the 5 temporal and spatial variables to develop each explanatory model. We combined the spatial and temporal variables of geozone and season into the same model because they were measurements of space and time not directly correlated with fish prey sources. Water-body type and spawning period were included together because they were spatio-temporal measurements based on descriptions of fish prey sources. We used 8 models as hypotheses to explain the presence of each food group and the number of scats at latrine sites. Year was not included in any of the models due to differences in the start and end date of data collection between years. We used deviation coding (desmat.ado; Hendrickx, 2001) to represent all categorical variables and variance inflation factors (VIF) to assess multicollinearity.

An individual VIF value > 10 or a mean VIF value > 1 suggested that a model had high levels of multicollinearity (Chatterjee, Hadi & Price, 2000).

DIET AND SCAT MODEL SELECTION

We used Akaike's Information Criterion (AIC_c) for small sample sizes to identify the most parsimonious explanatory models of otter diet and scat numbers (Burnham & Anderson, 2004). AIC_c values are a relative metric that must be compared in the context of a set of *a priori* models. We used both ΔAIC_c and Akaike weights ($AIC_c w$) 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 & Anderson, 2002). When models had ΔAIC_c values that were nearly equivalent, we selected the most parsimonious model (*i.e.*, fewest parameters). Given the large set of models that we tested, we only report the ranks of models with an $AIC_c w \geq 0.001$. An $AIC_c w$ 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 model parameters. Given the large set of models that we tested and for ease of interpretation, we present coefficients from only the most parsimonious model.

PREDICTIVE ABILITY OF DIET AND SCAT MODELS

Data for all count models were randomly divided into training (85%) and testing (15%) groups (Fielding & Bell, 1997). We used the receiver operating characteristics (ROC) and resulting area under the curve (AUC) to assess the predictive ability of the "best" model from the binary analyses. The AUC measures the relative proportions of correctly and incorrectly classified predictions (Pearce & Ferrier, 2000). AUC values 0.5 to 0.7 were considered to have poor model accuracy, from 0.7 to 0.9 good model accuracy, and > 0.9 high model accuracy (Swets, 1988). We used the predicted counts as well as the predicted probabilities of counts to evaluate the performance of the most parsimonious count models (prcounts.ado; Long & 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 model's predictive ability across the range of values we observed.

Results

SCAT CONTENT ANALYSIS

We counted 4470 scats at latrine sites during the duration of the study. A sub-sample of 901 scats were cleaned and analyzed. The diet of otter was comprised mostly of fish, with sucker species being the most dominant (Figures 1 and 2). Throughout the ice-free season, the

percentage of sucker species remained relatively constant and high, sculpin species remained constant and low, and the remaining species were intermediary, with fluctuations in their frequency of occurrence throughout the season (Figure 1). The only large decrease in sucker occurrence was in late August and corresponded with a peak in the frequency of salmonid species. Although the occurrence of non-fish prey items fluctuated throughout the season, their frequency was consistently low (Figure 2).

STABLE ISOTOPES

We used hair samples from 22 individual otters to conduct the stable-isotope analysis. We adopted a process with 2 models to overcome the low resolution associated with increased complexity (*i.e.*, too many sources) in the Isosource model. For the first model, all fish were combined into a single prey source with the exception of sockeye salmon (Figure 3, Fish 1). Sockeye salmon are a marine-derived food source and differ greatly in their ecology and isotopic signatures from other freshwater species (Ben-David, Flynn & Schell, 1997). The fish species included in the aggregate group were rainbow trout, lake trout, kokanee, sucker species, northern pikeminnow, whitefish, burbot, and sculpin species (Fish 1). The remaining

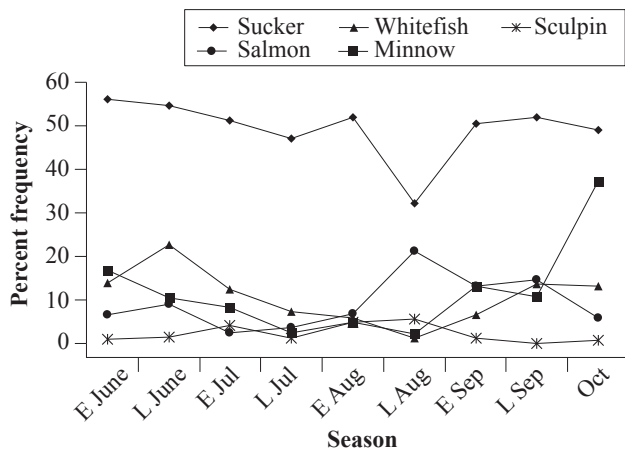


FIGURE 1. Percent frequency of occurrence of fish prey groups in river otter scats on and near Tezzeron and Pinchi lakes, central British Columbia, from late May to October, 2007–2008 (E = early, L = Late).

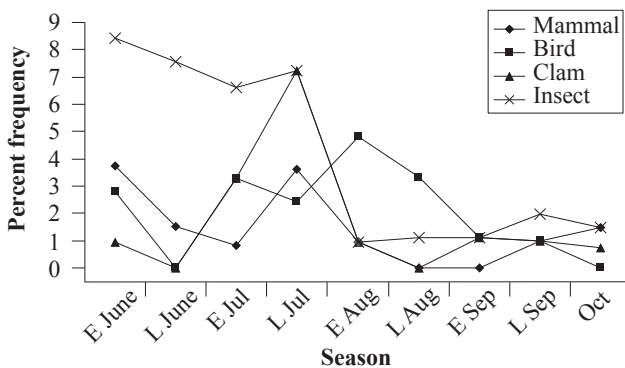


FIGURE 2. Percent frequency of occurrence of non-fish prey groups in river otter scats on and near Tezzeron and Pinchi lakes, central British Columbia, from late May to October, 2007–2008 (E = early, L = Late).

4 prey sources belonged to different taxonomic groups and had dissimilar isotopic values (mammal, bird, clam, and insect) (Figure 3).

The first stable-isotope model produced results with a narrow range of solutions that were easily interpretable. The aggregate fish group (Fish 1) was the dominate prey contributing to otter diet during the hair growth period, followed by sockeye salmon (Model 1, Table I). Bird species were also a contributing source to otter diet, but had a wider range of potential solutions. The stable-isotope data suggested that all other prey sources made very small contributions. Given that all non-fish prey sources overlapped zero, they were removed for the second stable-isotope model to examine the relative contributions of different fish groups. For the second model, we divided the fish into separate groups based on their ecology and relative isotopic similarity: 1) kokanee (unique ecology and isotopic signatures), 2) sockeye salmon (marine-derived and unique isotopic signatures), 3) burbot and lake trout (large deep-water carnivorous fish), and 4) rainbow trout, sucker species, northern pikeminnow, whitefish, and sculpin species (very similar isotopic signatures) (Fish 2, Figure 3). Once again, the aggregate fish group (Fish 2) was the dominate food source (Model 2, Table I). Both the sockeye salmon and the burbot/lake trout prey source contributed equally to the mixing model. Kokanee made a small contribution to the solution. In general, the overall pattern of results was insensitive to small changes in fractionation values (Table I).

DIET MODELS

We developed a set of logistic regression models relating the presence-absence of minnows, salmonidae, suckers, sculpins, whitefish, and insects in scat to the set of spatio-temporal variables describing the ecology of the major prey types of otter. Low frequencies of body parts of mammal, bird, clam, and burbot in scat prevented analysis of these diet items. Only 3 of the prey groups resulted in models with good to excellent predictive ability. A model consisting of spawning period, water-body type, and lake best explained the presence of salmonid, minnow, and insect

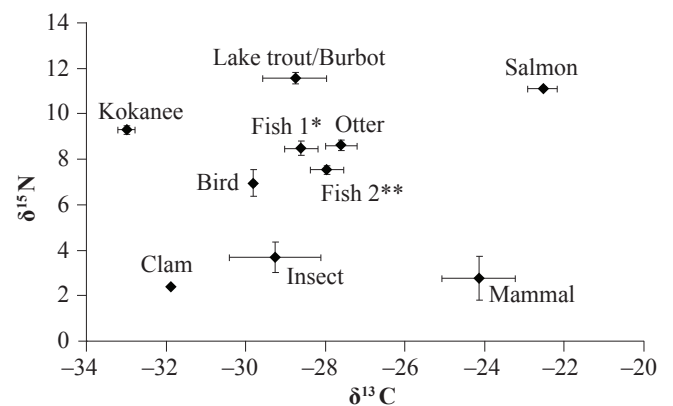


FIGURE 3. Mean (\pm SE) stable-isotopic signatures for potential prey items of river otters on Tezzeron and Pinchi lakes, central British Columbia. *Fish 1: Rainbow trout, lake trout, kokanee, sucker species, northern pikeminnow, whitefish, burbot, and sculpin species. **Fish 2: Rainbow trout, sucker species, northern pikeminnow, whitefish, and sculpin species.

groups (Table II). Models for the sculpin and whitefish family had poor predictive performance ($AUC < 0.6$).

For the salmonid group, the Akaike weight indicated that the top-ranked model had a 99% chance of being the best model. The model had good predictive ability for both the model training ($AUC = 0.738$) and the model testing ($AUC = 0.808$) data groups. The presence of salmonidae in otter scats was positively influenced by stream water-body types, a late August–early September spawning period, and Pinchi Lake (Table III). Statistically significant negative coefficients included lake water-body type, late June–early August spawning period, and Tezzeron Lake.

Three models explaining the presence of minnow in otter scats had nearly equivalent AIC_c scores (Table II). The highest-ranked model (waterbody+fishspawn+lake) also had the fewest parameters ($K = 7$) and, thus, was the most parsimonious and the best of the set. Other spatio-temporal variables (geozone and season) from the second- and third-ranked models may also have influenced the presence of minnow in otter scat. The waterbody+fishspawn+lake model had good predictive ability for both the model training and the model testing data sets, with scores of 0.732 and 0.850, respectively. Coefficients indicated that the late June–early August spawning period and Pinchi Lake had a negative influence on the presence of minnow, while the late September–October spawning period and Tezzeron Lake had a positive influence (Table III).

The top-ranked model for the insect prey group was convincingly the best of the set and included spawning period, water-body type, and lake ($AIC_{c,w} = 0.98$; Table II). This model had good predictive ability for both the model training ($AUC = 0.790$) and the model testing ($AUC = 0.741$) data sets. Lake water-body type and Pinchi Lake had a negative influence on the presence of insect remains in the otter scats that we analyzed (Table III). Alternatively, stream water-body type, early June and late June–early August time periods, and Tezzeron Lake had a positive influence on the presence of insects in otter scats.

SCAT DEPOSITION MODELS

The number of otter scats at a latrine site was best explained by a model that contained covariates for season and geographic zone ($AIC_{c,w} = 0.607$; Table II).

Two areas on Tezzeron Lake, Big Bay (coef. = 0.409, 95% confidence interval = 0.111–0.707, $P = 0.021$) and North Side (coef. = 0.768, 95% confidence interval = 0.194–1.342, $P = 0.002$), had a positive influence on the number of otter scats, while 2 areas on Pinchi Lake, Southeast (coef. = -0.385 , 95% confidence interval = -0.606 to -0.164 , $P = 0.001$) and West Bay (coef. = 0.583, 95% confidence interval = -0.916 to -0.250 , $P = 0.002$), had a negative influence. The number of scats was positively associated with the early July (coef. = 0.367, 95% confidence interval = 0.120–0.614, $P = 0.004$) and early September (coef. = 0.163, 95% confidence interval = 0.098–0.424, $P = 0.044$) time periods.

TABLE II. Summary of AIC_c model selection statistics for candidate binary models used to predict prey occurrence and counts of river otter scats on Tezzeron and Pinchi lakes in central British Columbia from 2007 to 2008. Results provided only for prey group models with AIC_c weights ≥ 0.001 .

Models*	Rank	AIC_c	ΔAIC_c	$AIC_{c,w}$
Salmonid binary model				
Waterbody + fishspawn + lake	1	408.6	0.0	0.998
Geozone + season	2	422.9	14.3	0.001
Waterbody + fishspawn	3	422.9	14.3	0.001
Minnow binary model				
Waterbody + fishspawn + lake	1	545.4	0.0	0.455
Geozone + season	2	546.7	1.3	0.242
Season	3	546.9	1.5	0.218
Geozone + season + lake	4	548.8	3.4	0.085
Insect binary model				
Waterbody + fishspawn + lake	1	243.1	0.0	0.980
Waterbody + fishspawn	2	251.9	8.8	0.012
Geozone + season + lake	3	253.8	10.6	0.005
Geozone + season	4	254.7	11.5	0.003
Fishspawn	5	258.0	14.8	0.001
Scat count model				
Geozone + season	1	4373.7	0.0	0.607
Geozone + season + lake	2	4374.7	1.0	0.374
Geozone	3	4382.2	8.5	0.009
Waterbody + fishspawn + lake	4	4382.3	8.6	0.008
Waterbody + fishspawn	5	4385.5	11.8	0.002

* Season = seasonal increments in two-week periods; Geozone = geographic zone (separated by latrine site clusters and distance); Waterbody = water-body type (stream, open lake, reedy bay); Fishspawn = occurrence of fish spawning period; Lake = latrine occurred on Tezzeron or Pinchi Lake.

TABLE I. Estimated range (%) of prey sources in river otter diet on Tezzeron and Pinchi lakes, central British Columbia, from 2007 to 2008. Estimates generated by analysis of stable isotopes using a dietary mixing model (Isosource), including a sensitivity analysis with a 15% change in fractionation values for carbon (ΔC) and nitrogen (ΔN).

Model 1: All prey items	Salmon	Fish 1*	Clam	Bird	Mammal	Insect
Range	14.0–22.0	50.0–80.0	0.0–5.0	0.0–27.0	0.0–4.0	0.0–6.0
Range ΔC	11.0–28.0	31.0–86.0	0.0–8.0	0.0–41.0	0.0–4.0	0.0–8.0
Range ΔN	0.0–28.0	14.0–80.0	0.0–13.0	2.0–57.0	0.0–7.0	0.0–12.0
Range $\Delta C + \Delta N$	9.0–32.0	4.0–76.0	0.0–15.0	0.0–63.0	0.0–8.0	0.0–14.0
Model 2: Fish prey items	Salmon	Fish 2**	Burbot/Lake trout	Kokanee		
Range	10.0–17.0	66.0–82.0	7.0–17.0	1.0–10.0		
Range ΔC	10.0–20.0	65.0–70.0	4.0–16.0	3.0–12.0		
Range ΔN	10.0–17.0	66.0–76.0	5.0–17.0	0.0–10.0		
Range $\Delta C + \Delta N$	6.0–25.0	52.0–80.0	2.0–18.0	0.0–20.0		

* Fish 1: Rainbow trout, lake trout, kokanee, sucker species, northern pikeminnow, whitefish, burbot, and sculpin species.

** Fish 2: Rainbow trout, sucker species, northern pikeminnow, whitefish, and sculpin species.

TABLE III. Estimated coefficients for AIC_c selected models (binary) describing the presence of prey items in river otter (*Lontra canadensis*) diet on Tezzeron and Pinchi lakes, central British Columbia, from 2007–2008.

Parameter	Coef.	SE	95% CI	P
Salmonid (Salmonidae)				
Waterbody 1 (lake)	-0.812	0.233	-1.268 to -0.355	<0.001
Waterbody 2 (reedy bay)	-0.069	0.252	-0.563 to 0.425	0.785
Waterbody 3 (stream)	0.881	0.187	0.514 to 1.248	<0.001
Fishspawn 1 (L June–E Aug)	-0.932	0.247	-1.416 to -0.448	
Fishspawn 2 (E June)	0.100	0.328	-0.543 to 0.743	0.760
Fishspawn 3 (L Sep–Oct)	0.062	0.236	-0.401 to 0.525	0.792
Fishspawn 4 (L Aug–E Sep)	0.770	0.217	0.345 to 1.195	<0.001
Lake 1 (Tezzeron)	-0.555	0.141	-0.831 to -0.279	<0.001
Lake 2 (Pinchi)	0.555	0.141	0.279 to 0.831	<0.001
Constant	-2.488	0.171	-2.823 to -2.152	<0.001
Minnnow (Cyprinidae)				
Waterbody 1 (lake)	-0.298	0.163	-0.617 to 0.0215	0.067
Waterbody 2 (reedy bay)	0.235	0.166	-0.090 to 0.560	0.157
Waterbody 3 (stream)	0.064	0.155	-0.240 to 0.368	0.682
Fishspawn 1 (L June–E Aug)	-0.645	0.202	-1.041 to -0.249	0.001
Fishspawn 2 (E June)	0.293	0.247	-0.190 to 10.777	0.235
Fishspawn 3 (L Sep–Oct)	0.736	0.172	0.399 to 1.073	<0.001
Fishspawn 4 (L Aug–E Sep)	-0.383	0.237	-0.848 to 0.082	0.106
Lake 1 (Tezzeron)	0.541	0.135	0.277 to 0.805	<0.001
Lake 2 (Pinchi)	-0.541	0.135	-0.806 to -0.277	<0.001
Constant	-2.078	0.145	-2.361 to -1.793	<0.001
Insect				
Waterbody 1 (lake)	-0.675	0.321	-1.304 to -0.046	0.035
Waterbody 2 (reedy bay)	-0.043	0.311	-0.653 to 0.567	0.889
Waterbody 3 (stream)	0.718	0.256	0.216 to 1.220	0.005
Fishspawn 1 (L June–E Aug)	0.654	0.310	0.046 to 1.262	0.035
Fishspawn 2 (E June)	1.278	0.377	0.539 to 2.017	0.001
Fishspawn 3 (L Sep–Oct)	-0.912	0.487	-1.867 to 0.0425	0.061
Fishspawn 4 (L Aug–E Sep)	-1.020	0.568	-2.133 to 0.093	0.073
Lake 1 (Tezzeron)	0.493	0.215	0.072 to 0.914	0.022
Lake 2 (Pinchi)	-0.493	0.215	-0.914 to -0.072	0.022
Constant	-3.700	0.302	-4.292 to -3.100	<0.001

Observed probabilities of scat counts at latrine sites corresponded well with predicted probabilities generated from the withheld data, suggesting that the most parsimonious model had good predictive performance. Supporting this conclusion, a Wilcoxon rank-sum test did not find a significant difference between predicted scat counts and observed counts ($Z = -0.824$, $P = 0.41$). Also, an analysis of residuals suggested very small differences between observed and predicted probabilities of scat counts.

Discussion

This study investigated patterns in otter diet in central British Columbia using a combination of dietary assessment techniques. Knowledge of factors influencing diet is essential for understanding the foraging ecology of river otter. This understanding can help explain the mechanisms behind changes in scat deposition rates at latrine sites. Furthermore, responses to food resources will ultimately influence the distribution and density of otter populations. Management strategies require accurate and unbiased information on wildlife distribution and abundance that is often measured from surveys of sign; this study provides some of the critical information needed to achieve this objective for river otters, with implications for other wildlife species.

Results of the diet analysis of scat were similar to those reported in other studies in northern freshwater systems

(Melquist & Hornocker, 1983; Reid *et al.*, 1994b) with some notable exceptions. Although fish dominated the diet, our study found an even smaller frequency of occurrence of secondary prey items than was reported by other researchers. No single non-fish prey group exceeded 9% frequency of occurrence during any season. For insects, the large difference may be explained by the techniques used to identify hard parts in scats in our study. We used a systematic approach that incorporated a random quadrant selection process for prey identification. This method is more sensitive to the total volume of a prey item in a scat sample and, thus, does not count as many trace insect remains (*i.e.*, lower probability of being found in a randomly selected quadrant). Another difference between this study and past work is the prevalence of sucker fish in the diet of otters from Tezzeron and Pinchi Lakes. Although suckers were also dominant in a study in Alberta, Canada, (Reid *et al.*, 1994b), their peak occurrence in otter scats was similar to the average frequency of occurrence (approximately 50%) throughout the duration of our research.

In general, the stable-isotope analysis agreed with the results from the visual examination of hard body parts in scat. Both approaches suggested that fish were the dominant diet item for river otter. The stable-isotope analysis, however, revealed that marine-derived salmon food sources may be more prevalent in otter diet than was estimated in scat content analysis. There are several explanations for

the differences between the 2 analyses. Marine-derived salmon species did spawn in streams that were directly connected to the lakes in the study area. If otters were making short- or long-distance movements out of the study area to gain access to aggregations of sockeye salmon, the scats containing those remains may have been undetected. Alternatively, otters may have concentrated on the most digestible or accessible parts of the salmon carcass when salmon were abundant and not consumed the hard parts necessary for identification in scats (Quinn *et al.*, 2009).

When comparing results from the 2 analytical techniques, the largest difference involved the percentage contribution of the bird group to otter diet. Although the wide range in possible values from the stable-isotope analysis (0–27%) suggested some uncertainty, the presence of birds in otter diet during the summer months was supported by other studies in northern freshwater systems (Gilbert & Nancekivell, 1982; Melquist & Hornocker, 1983; Reid *et al.*, 1994b). There are several possible explanations for the differences in results between the stable-isotope and scat content analyses. The presence of birds in otter scats may have occurred at the lower end of the range generated by the Isosource model. Alternatively, otters may have eaten muscle tissue of birds but not large quantities of feathers, affecting the detection of bird remains in the scat we sampled.

Appropriate fractionation values are critical when developing stable-isotope mixing models (Tiezen *et al.*, 1983; Milakovic & Parker, 2011). We used the best available approximation for our study population, but we were aware of the potential weakness in using a fractionation value not specific to central interior river otters. The successful use of these values in the past (Ben-David *et al.*, 1998) and similar results from the scat content and stable-isotope analyses provide some support for the use of these fractionation values. Furthermore, a sensitivity analysis indicated that observed patterns of prey contributions were relatively robust to small changes in fractionation values. Complete validation of the mixing models we developed requires fractionation values specific to North American river otters.

It is unclear what stage of hair growth otters captured in the fall were experiencing. The length of hair was similar for otter in both spring and fall, however, suggesting most hairs were close to fully grown. Although the scat content analysis covered the majority of this time period, it did not cover November. In contrast, food sources integrated into hair during this month would have influenced the results of the stable-isotope analysis. A closer examination of the ecology of prey items suggests that the minor variation in diet between techniques may be attributed to the growth cycle of otter hair. For example, the presence of the sockeye salmon and burbot/lake trout source groups in otter diet may have been affected by changes in the location of the larger fish species that coincided with the time period for otter guard hair regeneration. Sockeye salmon and lake trout move into shallow areas to spawn during late September and October, making them more vulnerable to otter predation (McPhail, 2007). In addition, burbot will move into shallower areas at the mouth of sockeye salmon spawning streams in the fall (McPhail, 2007).

When attempting to explain variation in the occurrence of hard body parts in scats, low frequencies of occurrence for some diet items (mammal, burbot, mollusks, bird) prevented us from fitting robust logistic regression models. For other items, we had sufficient sample sizes, but the resulting models had poor predictive power (sucker, whitefish, sculpin). Although these prey items did not demonstrate predictable patterns relative to the covariates we tested, important information was gained from the scat and stable-isotope analyses. Most non-fish prey items were consumed in relatively low numbers. Suckers were consumed consistently and in large quantities throughout the ice-free season, while sculpins were consumed in low numbers in all seasons. All of these prey sources were important contributing factors to otter diet but were invariant relative to time of year and location of otter across the study area.

Models for the presence of salmonid, minnow, and insect groups had good predictive power. Kokanee spawn in large numbers in streams on Pinchi Lake in late August and probably accounted for the predictability of the salmonid group. The location and timing agreed with coefficients that showed a significant positive influence for stream habitats, a late summer/early fall spawning period, and Pinchi Lake. Kokanee were seasonally abundant and high energy food sources. A concurrent radio-telemetry study of otters in our study area as well as a radio-telemetry study in Idaho documented long-distance movements that coincided with kokanee spawning seasons (Melquist & Hornocker, 1983). These long-range movements suggest that seasonally abundant prey sources were important and had significant influences on the distribution and abundance of otters across the landscape. For minnows, differences in the contribution to otter diet between the 2 lakes highlight the need to develop predictive models that incorporate appropriately large geographic variation. The spawning period also had a positive influence on minnow occurrence in scat samples; however, this time period does not correspond with the spawning season of the minnow group and is not easily explained by minnow ecology. Reid *et al.* (1994b), however, found that the occurrence of minnows increased in the fall and dominated the diet during the winter months. For insects, the positive influence of the early June and late June–early August time periods was not surprising given that many insects emerged in large numbers during that time. Although insects may be overestimated in otter diet, large numbers of scats containing only insect remains suggest that this prey source was not purely incidental.

Investigations of carnivore diet can help us to interpret variation in carnivore behaviour and enable us to begin addressing the question of why activity varies across space and time. Also, the effects of prey distributions on carnivore activity and movements will strongly impact the results of surveys designed to measure and manage carnivore populations. We developed a count model to investigate the relationship between otter behaviour at latrine sites, as indexed using scat numbers, and variables that captured the spatio-temporal variation in the availability of prey groups. Although numbers of scats at latrine sites were influenced by different geographic locations across the lakes, this

variation could not be explained ecologically. The positive influence of the early July time period on scat numbers did not correspond with the spawning periods of any fish groups. Furthermore, the spawning period of fish, with the exception of kokanee, did not have a significant effect on the number of scats deposited at latrine sites. One explanation for the seasonal trend is that prey species diversity and abundance increases in the summer (Reid *et al.*, 1994b), leading to increased movement, social grouping, and use of latrine sites. During the summer months, otters often travel in family or bachelor groups while foraging (Reid *et al.*, 1994b; Gorman *et al.*, 2006). We observed similar behaviour during the summer months. The increase in otter activity at latrine sites during early September was most likely explained by concentrations of spawning kokanee. This explanation was consistent with an observed increase in the occurrence of the salmonid family in scats during that time period.

The paired application of scat and stable-isotope analysis provided an opportunity to compare results and offset biases associated with each approach. Corresponding results suggest that in this case the 2 techniques have similar utility for describing the diet of otter. From the perspective of sampling efficiency, the stable-isotope approach offers considerable time savings, contingent on a ready supply of hair or other tissue. The successful use of stable isotopes in this study and publication of baseline C–N values will be useful for the application of this approach to other populations of river otter. Although the results of this study are specific to the Tezzeron and Pinchi watersheds, they should have applicability to other areas of central British Columbia that have similar habitats and prey resources.

Prey distribution and availability has a strong influence on carnivore movements and abundance. Furthermore, surveys of wildlife sign are easily biased without knowledge of the mechanisms influencing the distribution and amount of sign. An understanding of spatio-temporal patterns of diet and latrine site activity is essential for interpreting the results of such studies (*e.g.*, Mowry *et al.*, 2011). We provide information specific to the diet of interior river otter populations found across central British Columbia that can assist with the proper design and interpretation of scat surveys. Predictive models of the presence–absence of diet items or frequency of scat at latrines offer a more general technique that can assist with understanding otter behaviour at latrine sites. In combination with field data, such models could be used by wildlife managers to monitor the effects of harvest or land development on otter populations.

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