The role of demographic and environmental variables on the presence of snow tracks by river otters *Lontra canadensis*

Shannon Crowley, Chris J. Johnson & Dexter Hodder

Unknown causes of heterogeneity in the presence or detection of wildlife tracks and other signs could bias interpretations of population indices derived from surveys. These surveys can be the basis of management decisions for populations of wildlife. However, we know very little about potential biases affecting the presence of tracks in the landscape. We used an Information Theoretic Model Comparison approach to investigate the role of environmental, demographic and behavioural influences on the presence of river otter *Lontra canadensis* snow tracks in central British Columbia, Canada, from January to March 2008. We repeatedly located five radio-collared otters and recorded the presence of tracks within an estimated 100-m radius of the otter's location. We used combinations of five variables to develop logistic regression models that predicted the presence or absence of snow tracks when the location of otters was known. The presence of snow tracks was best described by a model containing covariates for gender and movement distance per day. The probability of detecting snow tracks was higher for male compared to female otters and was positively related to the daily movement distance of the individual animal. Track-sign heterogeneity among individuals could bias surveys that assess and monitor river otter populations, and should be incorporated into the design and interpretation of track surveys.

Shannon Crowley, Natural Resources and Environmental Studies Graduate Program, University of Northern British Columbia, 3333 University Way, Prince George, British Columbia, Canada V2N 4Z9 - e-mail: crowley@unbc.ca
Chris J. Johnson, Ecosystem Science & Management Program, University of Northern British Columbia, 3333 University Way, Prince George, British Columbia, Canada V2N 4Z9 - e-mail: johnsoch@unbc.ca
Dexter Hodder, John Prince Research Forest, P.O. Box 2378, Fort St. James, British Columbia, Canada V0J 1P0 - e-mail: dexter@johnprinceresearchforest.com

Corresponding author: Shannon Crowley

Field surveys of tracks and other signs are used to assess and monitor the presence, distribution, abundance and habitat use of many wildlife species (Thompson et al. 1989, St-Georges et al. 1995, Squires et al. 2004, Patterson et al. 2004). Information from these surveys is often the basis for management decisions and actions, such as harvest quotas and conservation status. Snow-track surveys are especially common because of their low cost, lack of equipment needs and detection efficiency (Reid et al. 1987, Gompper et al. 2006). Snow-track surveys are particularly applicable to river otters *Lontra canadensis* because their tracks are identifiable from other wildlife, and otters are often found across easily surveyed habitats such as frozen lakes and rivers (Reid et al. 1987). However, our ability to monitor the status of river otters using snow tracks may be imprecise or biased because we do not understand factors influencing snow-track presence and detection.

Variations in environmental, demographic and behavioural parameters are potential sources of bias that may affect the accuracy of snow-track surveys. First, snowfall events may influence the number of tracks detected during surveys. The number of days since the last snowfall event may make tracks more detectable as tracks accumulate in the days following snowfall (Becker et al. 1998, Linnell et al. 2007).

Second, temperature has been shown to influence animal movements and may affect the detection of tracks and other signs (Kanda et al. 2005, Long et al. 2005, Zimmerling 2005). River otters have high metabolic rates, and temperature may affect their movement and behaviour (Melquist et al. 2003). We hypothesize that otters move less and remain under subnivean shelter to reduce the energetic costs of maintaining body temperatures during colder weather. Lastly, differences in movement and behavioural patterns among individuals of different age and gender may affect the amount and location of signs observed during surveys as well as capture rates (Reid et al. 1994, Gehrt & Fritzell 1996, Vashon et al. 2008). Studies that rely on data from marked animals have found that males are often captured more frequently than females (e.g. Gehrt & Fritzell 1996, Boulanger et al. 2004, Lofroth et al. 2008). Heterogeneity in capture probability is typically explained by more frequent and longer movements by males (i.e. males come into contact with traps more often) or variation in behavioural tendencies between the two genders (e.g. females are more cautious). These differences in behaviour may be reflected in where and when tracks are detected in the landscape.

Past researchers have suggested snow-track surveys as an inventory technique for understanding the distribution and abundance of river otters in both North America (Reid et al. 1987, Gallant et al. 2007, Gallant et al. 2008) and Europe (Eurasian otter *Lutra lutra*; Sulkava 2007). However, the potential sources and magnitude of bias on track detection are not well known. The objective of our study was to investigate the influence of environmental, demographic and behavioural factors on the detectability of river otters from track surveys during winter. We discuss the implications of our findings for population indices that rely on information from snow-track surveys.

Material and 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; Fig. 1). The JPRF is a 13,000-ha portion of forested crown land 45 km northwest of Fort St. James, British Columbia, Canada. The area is characterized by rolling topography with low mountains (elevation range between 700 m and 1,267 m a.s.l.) and a high density of lakes, rivers and streams. Found in the subboreal spruce biogeoclimatic zone, 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 to each other. Major drainages of Tezzeron and Pinchi Lakes are the Kuskwa and Pinchi Rivers, respectively.

Tezzeron Lake's shoreline stretches for 82 km (area = 8,079 ha), while the perimeter of Pinchi Lake is 67 km in length (area = 5,586 ha), and the mean depth of Tezzeron and Pinchi Lakes are 11.2 and 23.9 m, respectively. Shoreline topography varies considerably along both lakes, and the area surrounding Pinchi Lake is generally more mountainous with steeper slopes. There is a long history of timber management and activity within the forests surrounding these lake systems, and Pinchi Lake has a mercury mine (non-operational) and some residences.

The average mean daily temperature from January to March 2008 was -6.97°C (SD = 7.65). The average minimum and maximum daily temperatures were -12.85°C (SD = 8.13) and -1.12°C (SD = 8.15), respectively. The accumulated snowfall from January to March was 80 cm, and the accumulated snowfall over the entire winter was 192 cm. There were 15 and 10 days from January to March with snowfall events > 1 cm and < 1 cm, respectively. Only a single stretch of water remains open during the winter, despite of the ice cover being largely complete throughout the rest of our study area. Only one marked otter (an adult female) had access to open water in our study area where most otters on the other hand gained access to water through near-shore burrows and small subnivean access holes.

Data collection

As part of a concurrent study on the habitat selection and movement patterns of river otters, we used padded #3 softcatch leg-hold traps to capture otters at consistent and high-use areas along the lakeshores of Pinchi and Tezzeron Lakes in central British Columbia during late autumn 2007. We used custom-built cages made of 1-m sections of 40-cm diameter PVC pipes to transport otters to the location of a veterinarian. Otters were immobilised with an intramuscular injection of 4-6 mg/kg Telazol using a syringe mounted on a jab stick. Sedated animals were implanted with an intraperitoneal Advanced Telemetry Systems M1250B radio-transmitter (30 × 112 × 30 mm weighing approximately 100 g; ranging from 0.9-1.4% of the animal's body
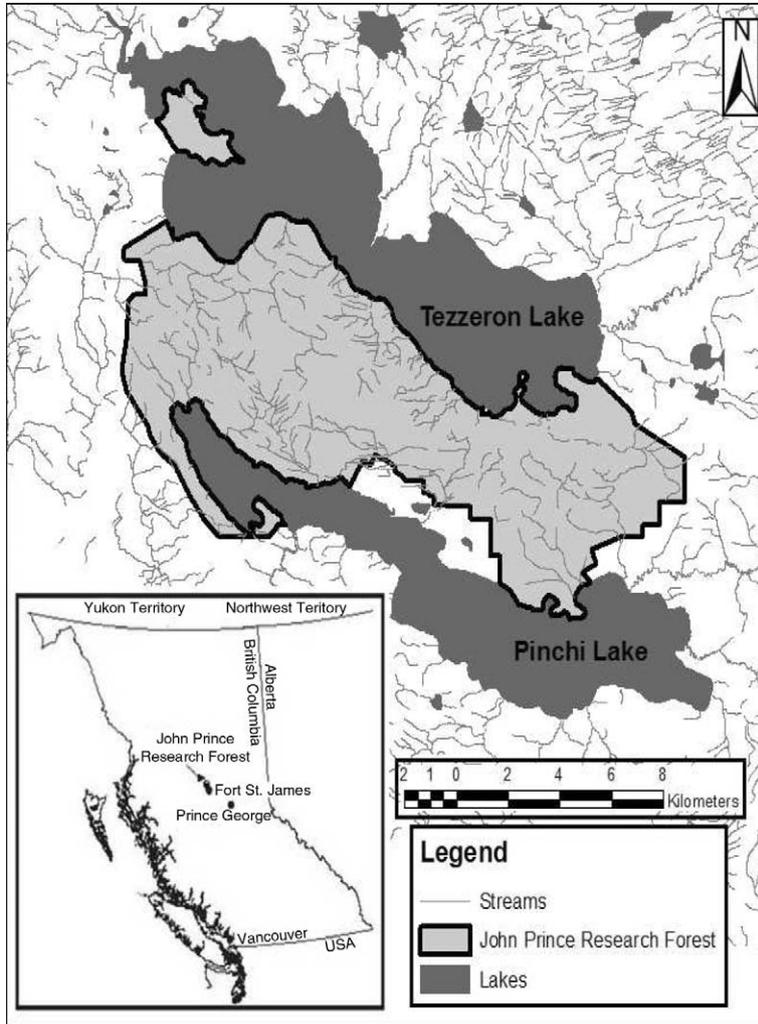
Figure 1. Our river otter study site and John Prince Research Forest (JPRF) in central British Columbia, Canada.

weight) using a ventral midline incision and marked with a 12 × 2 mm passive integrated transponder (PIT) tag inserted under the skin. Male otters were considered adult (> 2 years old) if their body weight was > 8 kg and/or zygomatic arch was > 8 cm (Stephenson 1977). Females were considered adult if there was evidence of lactation as determined by the presence of milk and/or enlarged nipples (Hamilton & Eadie 1964). The amount of teeth wear and staining was used as additional information to support age delineations for both genders. All handling protocols for river otters were approved by both the UNBC Animal Care and Use Committee and the British Columbia Ministry of Environment.

We located five radio-collared river otters (one juvenile male, two adult male, one juvenile female and one adult female) in the area from January to March 2008 using standard triangulation and hom-

ing radio-telemetry techniques (i.e. follow signal directly to otter and circle at short distance to verify location; Gorman et al. 2006). However, we only recorded snow-track information on otters that were located using homing methods. We approached otters approximately 30-50 m from their actual location. A range finder was used to estimate distances to the otter's location. The majority of otter locations were adjacent to the shoreline, and objects (i.e. rocks or trees) in the terrestrial environment were used as markers for laser placement. Otter locations were estimated to be accurate within ± 5 m based on visual landmarks and close-range telemetry information. We maintained a 30-50 m distance from the otter while searching a 100-m radius around the otter's location on snowshoes. We travelled a concentric search pattern at 15-20 m intervals outwards from the otter's location until we reached 100 m. We

used 10×50 binoculars to aid in the detection of tracks. We recorded the presence or absence of otter tracks within a 100-m search radius centered in the otter's location. Tracks were sketched in a field notebook to help differentiate old from new tracks, and presence was recorded only for tracks that were made since the previous visit. Estimates of track age based on known weather events were used to investigate the repeated use of track trails and corroborate information from field sketches. Although there was potential for detecting tracks of unmarked otters at the locations of the studied otters, this was most likely limited for several reasons: 1) a study of otters at a similar latitude demonstrated smaller home ranges and limited overlap between otters when lake systems were ice covered (Reid et al. 1994), 2) observations of marked otters in our study support the findings of Reid et al. (1994), 3) we rarely (< 5 times) detected tracks in the vicinity of marked otters that could not be linked to known movements by the same individuals, and 4) when marked otters were observed they were rarely (< 5 times) accompanied by other individuals.

We recorded the presence of tracks as unknown when visibility was very poor (i.e. sun angles or blowing snow). Days with wind speeds > 10 km/hour were very rare in our study area and typically did not reduce visibility or cover tracks unless combined with a snowfall event. Snow depth and conditions throughout our study caused otters to leave behind tracks that were easily detected and identified (i.e. shallow body imprint), but were not deep enough to excessively restrict otter movement above the surface of snow (i.e. confining otters to the use of repeated trail networks). Tracks identified previously were examined closely on consecutive days to determine repeated use. Changes in environmental conditions (i.e. snowfall or snowmelt) between location events generally allowed us to easily distinguish between old and new tracks. Data were not collected in late winter

when hard snow and ice conditions prevented otters from leaving behind detectable tracks.

Binary model analysis

We used a mixed-effect logit model to identify factors that explained variation in occurrence of snow tracks by river otters. The presence (1) or absence (0) of snow tracks at a known otter location was the dependent variable in the model. We included a random effect for individual otters to account for discrepancies in sample sizes among individuals and non-independence of relocations for each individual (Hurlbert 1984, Gillies et al. 2006, Hebblewhite & Merrill 2008). Mixed-effect models were estimated in Stata (version 9.2, Statacorp 2006) using the GLLAMM procedure with adaptive quadrature (Rabe-Hesketh et al. 2004).

We used five environmental, demographic and behavioural variables to model the presence of snow tracks by river otters. Environmental variables representing the weather included mean daily temperature (°C) and the number of days since the last snowfall event (> 1 cm). Weather data were taken from Environment Canada's National Climate Data and Information Archive. Demographic variables included gender (male or female) and age classified as juvenile (< 2 years) or adult (> 2 years). Lastly, the distance which was moved from the otter's previous location (m/day) was used to examine the influence of movement distances on the detection of otter tracks in the snow.

We used eight biologically plausible models as hypotheses to explain the presence of snow tracks by river otters (Table 1). We included weather, demographic and global models to explain the presence of otter tracks. The global model contained all demographic, movement distance and environmental variables. We hypothesized that demography influenced the presence of tracks and that the majority of the remaining models were a combination of demo-

Table 1. Summary of AIC$_c$ model selection statistics for candidate binary models predicting the presence of river otter snow tracks on Tezzeron and Pinchi Lakes in central British Columbia, Canada, based on data collected from January to March 2008.

Model structure	Binary model name	Rank	AIC$_c$	ΔAIC$_c$	AIC$_{cw}$
gender + movementdistance	gender/movement distance	1	142.4	0.0	0.885
age + gender + meantemp + snowdays + movementdistance	global	2	147.3	4.9	0.077
age + gender	demography	3	150.8	8.4	0.013
gender + meantemp + snowdays	gender/weather	4	151.4	9.0	0.010
meantemp + snowdays + movementdistance	weather/movement distance	5	151.8	9.4	0.008
age + meantemp + snowdays	age/weather	6	152.5	10.1	0.006
meantemp + snowdays	weather	7	155.2	12.8	<0.001
age + movementdistance	age/movement distance	8	157.2	14.8	<0.001

//Xinet/production/w/wbio/live_jobs/wbio-18-01/wbio-18-01-05/layouts/wbio-18-01-05.3d
Allen Press, Inc. ■ Tuesday, 31 January 2012 ■ 9:30 am

Page 4
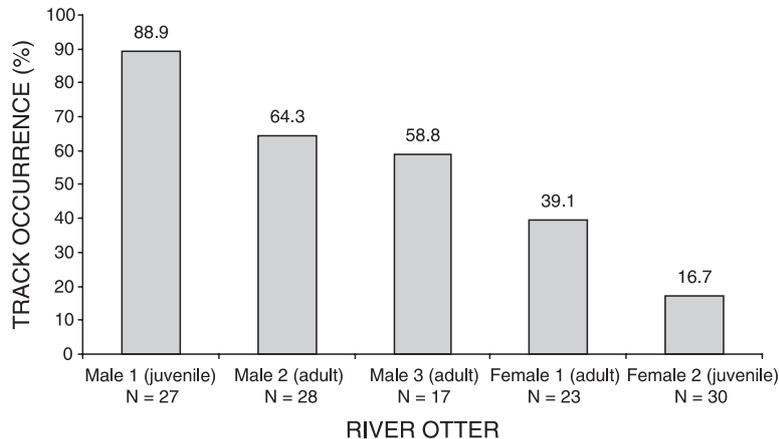
Figure 2. Percent occurrence of snow tracks at locations of radio-transmitted river otters on Tezzeron and Pinchi Lakes, central British Columbia, Canada, from January to March 2008.

graphic variables with either movement distance or environmental variables. We used 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 et al. 2000). However, none of the models used in this analysis had high levels of multicollinearity.

We used Akaike's Information Criterion for small sample sizes (AIC_c) to identify the most parsimonious explanatory models of the presence of snow tracks by otters (Burnham & Anderson 2004). The 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_{cw}) 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. However, a model with a ΔAIC_c < 2 was considered to be equivalent to the model with the minimum score (Burnham & Anderson 2002). An AIC_{cw} is a value from 0-1 that represents the approximate probability that a model is the best among a set of candidate models. We used beta-

coefficients and z-statistics to assess the importance of model parameters.

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

Results

We recorded information on the presence or absence of snow tracks for 125 locations based on five individual otters during winter 2008. The percent occurrence of snow tracks varied among otters, but was lowest for females (Fig. 2). The average daily movement distances varied considerably among monitored individuals (Fig. 3).
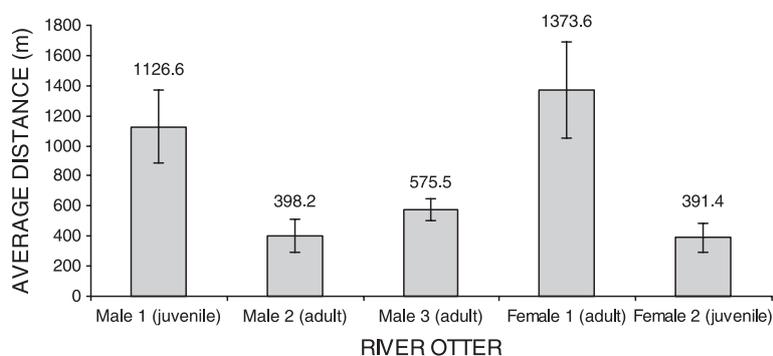
Figure 3. Average distance traveled per day (m ± SE) by radio-transmitted river otters on Tezzeron and Pinchi Lakes, central British Columbia, Canada, from January to March 2008.

//Xinet/production/w/wbio/live_jobs/wbio-18-01/wbio-18-01-05/layouts/wbio-18-01-05.3d
Allen Press, Inc. ■ Tuesday, 31 January 2012 ■ 9:30 am

Page 5

Table 2. Estimated coefficients and 95% confidence intervals for the best binary model (gender/movement distance; see Table 1) predicting the presence of snow tracks by river otters on Tezzeron and Pinchi Lakes, central British Columbia, Canada, from January to March 2008.

Parameter	Coefficient	SE	95% CI
Male	2.222	0.453	1.334 - 3.110
Female	-2.222	0.453	-3.110 - -1.334
Movement distance	0.698	0.276	0.157 - 1.239
Constant	-0.542	0.384	-1.294 - 0.212

The presence of snow tracks at river otter locations was best explained by a model that contained covariates for gender and daily movement distance (see Table 1). The global model was the second-ranked model, but had an AIC_c score of 4.9 points higher than the top-ranked model and was not considered equivalent. The three highest-ranked models all contained the gender variable. The top-ranked model received an Akaike's weight of 0.89, which was 11.5 times higher than the second-ranked model. The ROC score showed that the top-ranked model had good predictive accuracy ($AUC = 0.801$). The ability to detect track occurrence given otter presence was higher for males compared to females, and increased with daily movement distance of the radio-marked otter (see Table 2).

Discussion

Our study was the first to examine the role of demographic, behavioural and environmental factors in interpreting findings from inventory methods that use tracks to document otter distribution and absolute or relative abundance. We found that the gender of otters and the distances they moved influenced the presence of observable tracks during the winter. Track surveys are thought to be an efficient method for monitoring otter populations. However, differences in track presence between demographic groups or individuals within a population could bias the interpretation of these surveys. Based on our findings, population numbers or distribution would be underestimated during track counts if the sample contained females that are relatively less detectable.

To limit disturbance effects when searching for tracks, we maintained a minimum distance from the known locations of radio-transmitted otters and we approached otters quietly. Individual animals demonstrated minor reactionary behaviour to our presence. Furthermore, repeated locations of individual otters in similar areas suggested that they were not displaced by our survey activities. Regardless of our influence on otter behaviour, observer effects were likely consistent among the various categories of bias addressed in our study.

Although the sample size of individual animals for our study was small ($N = 5$), we did represent the primary demographic groups in a balanced fashion. We also had sufficient relocations for each demographic group to generate robust logit models that showed good predictive ability. However, the effects of demographic variables should still be approached with caution as our sample sizes make it difficult to differentiate demographic from individual otter influences. Regardless of the ultimate source of variation (i.e. gender vs individual), our results strongly suggest that caution should be exercised when using track surveys that do not correct for detection biases related to the behavioural characteristics of the population.

In studies of another mustelid species, the wolverine *Gulo gulo*, variation in detection rates was attributed to differences in movement distances and habitat selection between genders (Krebs et al. 2007, Lofroth et al. 2008). Although movement distance influenced track presence in our study, it was not correlated with gender and, thus, not a function of differences between male and female movement distances. The variation in track presence between genders is most likely explained by differences in how otters move in their environment. Behavioural strategies by females did not involve long-distance movements in exposed areas on top of the snow. In contrast, males often left more detectable tracks above the surface of the snow and ice when making both short- and long-distance movements.

Although environmental variables did not influence the presence of otter tracks relative to demographic and behavioural variables, they most likely still play a role in the detection of tracks. Previous studies have documented the influence of the number of days since the last snowfall on track detection (Becker 1991, Becker et al. 1998, Beauvais & Buskirk 1999). Although tracks may still be present, they may be more difficult to detect if only a short interval of time has passed and animals have not had a sufficient time to travel. In our study, we knew the exact location of the otter and could detect both large and small amounts of tracks, which most likely reduced the effects of detection bias.

//Xinet/production/w/wbio/live_jobs/wbio-18-01/wbio-18-01-05/layouts/wbio-18-01-05.3d
Allen Press, Inc. ■ Tuesday, 31 January 2012 ■ 9:30 am

Page 6

Estimates of otter distribution, relative abundance and habitat selection derived from track surveys may be misinterpreted if the influences of behavioural biases are not considered. Occupancy models are used with increasing frequency to determine species distribution where the probability of detection is < 1 (MacKenzie et al. 2002, O'Connell et al. 2006, Bailey et al. 2007). Our results not only demonstrate the importance of estimating the detection probability, but also considering specific sources of observation heterogeneity such as behavioural differences among individuals. In addition, temporal (i.e. survey length and frequency) and spatial (i.e. survey length, shape and pattern) elements of survey design may have to be adjusted to take into account demographic differences in detection probability (Kendall et al. 1992, Stanley & Royle 2005). Incorporating such variation in study design and analysis will decrease bias and increase the power of the survey to detect spatial and temporal trends or patterns in distribution and abundance.

Population estimates based on data collected from mark-recapture studies may also be affected by heterogeneity in track presence among individuals (Lukacs & Burnham 2005). Mark-recapture estimates can take into account unequal capture probabilities by stratifying age and gender classes with different risks of capture. However, the biological causes of heterogeneity are often unknown (Wilbur & Landwehr 1974). Studies that combine track detection with known individuals in the population can provide insight into the causes of capture heterogeneity. Knowledge of mechanisms affecting the presence of animal tracks and other signs in the landscape is critical to developing sampling designs that minimize heterogeneity in capture or animal detectability. Track surveys of river otters that do not have knowledge of potential demographic or behavioural factors should be interpreted with caution until further research can quantify or correct the associated level of bias.

References

Bailey, L.L., Hines, J.E., Nichols, J.D. & MacKenzie, D.I. 2007: Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. - Ecological Applications 17: 281-290.

Beauvais, G. & Buskirk, S.W. 1999: An improved estimate of trail detectability for snow-trail surveys. - Wildlife Society Bulletin 27: 32-38.

Becker, E.F. 1991: A terrestrial furbearer estimator based on probability sampling. - Journal of Wildlife Management 55: 730-737.

Becker, E.F., Spindler, M.A. & Osborne, T.O. 1998: A population estimator based on network sampling of tracks in the snow. - Journal of Wildlife Management 62: 968-977.

Boulanger, J., Stenhouse, G. & Munro, R. 2004: Sources of heterogeneity bias when DNA mark-recapture sampling methods are applied to grizzly bear (*Ursus arctos*) populations. - Journal of Mammalogy 85: 618-624.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and inference: a practical information theoretic approach. 2nd edition. - Springer, New York, New York, USA, 488 pp.

Burnham, K.P. & Anderson, D.R. 2004: Multimodel Inference: Understanding AIC and BIC in model selection. - Sociological Methods and Research 33: 261-304.

Chatterjee, S., Hadi, A.S. & Price, B. 2000: Regression analysis by example. 3rd edition. - Wiley, New York, New York, USA, 359 pp.

Gallant, D., Vasseur, L. & Berube, C.H. 2007: Unveiling the limitations of scat surveys to monitor social species: A case study on river otters. - Journal of Wildlife Management 71: 258-265.

Gallant, D., Vasseur, L. & Berube, C.H. 2008: Evaluating bridge survey ability to detect river otter *Lontra canadensis* presence: a comparative study. - Wildlife Biology 14(1): 61-69.

Gehrt, S.D. & Fritzell, E.K. 1996: Sex-biased response of raccoons (*Procyon lotor*) to live traps. - American Midland Naturalist 135: 23-32.

Gillies, C., Hebblewhite, M., Nielsen, S.E., Krawchuk, M., Aldridge, C., Frair, J.L., Saher, D.J., Stevens, C. & Jerde, C. 2006: Application of random effects to the study of resource selection by animals. - Journal of Animal Ecology 75: 887-898.

Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A. & Cryan, J.R. 2006: A comparison of noninvasive techniques to survey carnivore communities in Northeastern North America. - Wildlife Society Bulletin 34: 1142-1151.

Gorman, T.A., Erb, J.D., McMillan, B.R. & Martin, D.J. 2006: Space use and sociality of river otters (*Lontra canadensis*) in Minnesota. - Journal of Mammalogy 87: 740-747.

Hamilton, W.J., Jr. & Eadie, W.R. 1964: Reproduction in the otter, *Lutra canadensis*. - Journal of Mammalogy 45: 242-252.

Hebblewhite, M. & Merrill, E. 2008: Modelling wildlife-human relationships for social species with mixed-effects resource selection models. - Journal of Applied Ecology 45: 834-844.

Hurlbert, S.H. 1984: Pseudoreplication and the design of ecological field experiments. - Ecological Monographs 54: 187-211.

Kanda, L.L., Fuller, T.K. & Friedland, K.D. 2005: Temperature sensor evaluation of opossum winter activity. - Wildlife Society Bulletin 33: 1425-1431.

Kendall, K.C., Metzgar, L.H., Patterson, D.A. & Steele, B.M. 1992: Power of sign surveys to monitor population trends. - Ecological Applications 2: 422-430.

Krebs, J., Lofroth, E.C. & Parfitt, I. 2007: Multiscale habitat use by wolverines in British Columbia, Canada. - Journal of Wildlife Management 71: 2180-2192.

Linnell, J.D.C., Fiske, P., Herfindal, I., Odden, J., Broseth, H. & Andersen, R. 2007: An evaluation of structured snow-track surveys to monitor Eurasian lynx *Lynx lynx* populations. - Wildlife Biology 13(4): 456-466.

Lofroth, E.C., Klafki, R., Krebs, J.A. & Lewis, D. 2008: Evaluation of live-capture techniques for free-ranging wolverines. - Journal of Wildlife Management 72: 1253-1261.

Long, R.A., Martin, T.J. & Barnes, B.M. 2005: Body temperature and activity patterns in free-living arctic ground squirrels. - Journal of Mammalogy 86: 314-322.

Lukacs, P.M. & Burnham, K.P. 2005: Review of capture-recapture methods applicable to noninvasive genetic sampling. - Molecular Ecology 14: 3909-3919.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. 2002: Estimating site occupancy rates when detection probabilities are less than one. - Ecology 83: 2248-2255.

Melquist, W.E., Polechla, P.J. & Toweill, D. 2003: River otter. - In: Feldhamer, G.A., Thompson, B.C. & Chapman, J.A. (Eds.); Wild mammals of North America: biology, management, and conservation. John Hopkins University Press, Maryland, USA, pp. 708-734.

Menard, S. 2001: Applied Logistic Regression Analysis. 2nd edition. - Sage University Press, Thousand Oaks, California, USA, 111 pp.

O'Connell, A.F., Jr., Talancy, N.W., Bailey, L.L., Sauer, J.R., Cook, R. & Gilbert, A.T. 2006: Estimating site occupancy and detection probability parameters for meso- and large mammals in a coastal ecosystem. - Journal of Wildlife Management 70: 1625-1633.

Patterson, B.R., Quinn, N.W.S., Becker, E.F. & Meier, D.B. 2004: Estimating wolf densities in forested areas using network sampling of tracks in snow. - Wildlife Society Bulletin 32: 938-947.

Pearce, J. & Ferrier, S. 2000: Evaluating the predictive performance of habitat models developed using logistic regression. - Ecological Modeling 133: 225-245.

Rabe-Hesketh, S., Skrondal, A. & Pickles, A. 2004: GLLAMM Manual. 2nd edition. - U.C. Berkeley Division of Biostatistics Working Paper Series, University of California, Berkeley, California, USA, 138 pp.

Reid, D.G., Bayer, M.B., Code, T.E. & McLean, B. 1987: A possible method for estimating river otter, *Lutra canadensis*, populations using snow tracks. - Canadian Field-Naturalist 101: 576-580.

Reid, D.G., Code, T.E., Reid, A.C.H. & Herrero, S.M. 1994: Spacing, movements, and habitat selection of the river otter in boreal Alberta. - Canadian Journal of Zoology 72: 1314-1324.

Squires, J.R., McKelvey, K.S. & Ruggiero, L.F. 2004: A snow-tracking protocol used to delineate local lynx, *Lynx canadensis*, distributions. - Canadian Field-Naturalist 118: 583-589.

Stanley, T.R. & Royle, J.A. 2005: Estimating site occupancy and abundance using indirect detection indices. - Journal of Wildlife Management 69: 874-883.

St-Georges, M., Nadeau, S., Lambert, D. & Decarie, R. 1995: Winter habitat use by ptarmigan, snowshoe hares, red foxes and river otters in the boreal forest-tundra transition zone of western Quebec. - Canadian Journal of Zoology 73: 755-764.

Stephenson, A.B. 1977: Age determination and morphological variation of Ontario otters. - Canadian Journal of Zoology 55: 1577-1583.

Sulkava, R. 2007: Snow tracking: a relevant method for estimating otter *Lutra lutra* populations. - Wildlife Biology 13(2): 208-218.

Swets, J.A. 1988: Measuring the accuracy of diagnostic systems. - Science 240: 1285-1293.

Thompson, I.D., Davidson, I.J., O'Donnell, S. & Brazeau, F. 1989: Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. - Canadian Journal of Zoology 67: 1816-1823.

Vashon, J.H., Meehan, A.L., Jakubas, W.J., Organ, J.F., Vashon, A.D., McLaughlin, C.R., Matula, G.J. & Crowley, S.M. 2008: Spatial ecology of a Canada lynx population in Northern Maine. - Journal of Wildlife Management 72: 1479-1487.

Wilbur, H.M. & Landwehr, J.M. 1974: The estimation of population size with equal and unequal risks of capture. - Ecology 55: 1339-1348.

Zimmerling, T.N. 2005: The influence of thermal protection on winter den site selection by porcupines, *Erethizon dorsatum,* in second-growth conifer forests. - Canadian Field-Naturalist 119: 159-163.

8

© WILDLIFE BIOLOGY 18:1 (2012)

//Xinet/production/w/wbio/live_jobs/wbio-18-01/wbio-18-01-05/layouts/wbio-18-01-05.3d
Allen Press, Inc. ■ Tuesday, 31 January 2012 ■ 9:30 am

Page 8