

Indirect evidence of prey-switching in minks: empirical evidence, theoretical modeling, and spatial drivers

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A spatial gradient in the interactions between American minks (*Neovison vison*) and muskrats (*Ondatra zibethicus*) occurs in the Hudson's Bay Company fur harvest returns of Canada. Evidence for strong dependence of minks on muskrats exists in northwestern Canada, whereas evidence for weaker interactions exists in central and eastern Canada. We tested the hypothesis that minks consume fewer muskrats and more alternative prey in some areas, using fur records from 56 Hudson's Bay posts. Both muskrats and small microtines were found to explain mink dynamics, with small microtines and other alternative prey gaining importance in the eastern portion of our study area. Mink fur returns exhibited a range of cycle lengths from 2.6 to 13 years encompassing typical small microtine periodicities of 3–5 years and typical muskrat periodicities of 8–13 years. A time lag of 0 years occurred between mink and muskrat harvest data frequently in the eastern portion of our study area, hypothesized to be a result of minks consuming alternative prey. To biologically verify small microtines as a potential prey source, we modeled mink and muskrat population dynamics assuming small microtines were an alternative prey by modifying the Turchin and Hanski (1997) model. Simulated mink and muskrat time series replicated observed periodicity and time-lag range, suggesting that minks can be generalist predators and consume alternative prey. Finally, we examined species richness and land cover as potential drivers of mink prey-switching, but were unable to find support for either hypothesis, suggesting that additional environmental- or competition-related interactions influence mink population dynamics.

Key words: alternative prey, Canada, microtine, *Neovison vison*, *Ondatra zibethicus*, population dynamics, prey-switching, spatial variation

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Evidence of periodic population fluctuations has been found in long-term data sets and has largely been attributed to predation (Elton and Nicholson 1942; Erlinge et al. 1983; Hansson and Henttonen 1988; Korpimäki and Krebs 1996). Predator and prey populations commonly exhibit coupled oscillations, where predators follow prey population fluctuations with a time lag (e.g., Tapper 1979; Korpimäki and Krebs 1996; Viljugrein et al. 2001). Because the predation-related, regulatory drivers differ between specialist and generalist systems, different cyclical characteristics are observed in different systems (Errington 1963; Andersson and Erlinge 1977).

Empirical evidence of coupled oscillations has been found in both specialist predator–prey (Korpimäki et al. 1991) and generalist predator–prey (Erb et al. 2001) relationships. Specialist predators, such as least weasels (*Mustela nivalis*), tend to respond numerically to prey density and exhibit a

temporal lag in response to changes in prey population (Korpimäki et al. 1991). The lagged response of the predator induces a delayed, density-dependent structure in prey populations and leads to destabilization and high-amplitude fluctuations (Korpimäki 1993; Klemola et al. 2002). In contrast, generalist predators such as the red fox (*Vulpes vulpes*) respond both numerically and behaviorally to changes in prey density, allowing for stabilization of prey populations (Andersson and Erlinge 1977; Erlinge et al. 1984). Furthermore, behavioral strategies including spatial aggregative responses to local prey densities allow predators to track a given prey population with a lag period of 0 years (Korpimäki and Norrdahl 1989).



The American mink (*Neovison vison*) is a generalist predator (Errington 1943) known to exhibit both 4- and 10-year periodicities (Holmengen and Seip 2009) and is considered to be a major predator of muskrats (*Ondatra zibethicus*—Errington 1963; Shier and Boyce 2009). Accordingly, mink population fluctuations follow muskrat populations (Viljugrein et al. 2001). In western Canada, muskrat population dynamics significantly influenced mink dynamics with mink populations following muskrat population fluctuations by a lag of 2–3 years. In contrast, a weaker degree of interaction occurred between mink and muskrat populations in eastern Canada, where the species exhibited a lag of 0 years, relative to muskrat populations (Erb et al. 2001), possibly due to minks' consumption of alternative prey (Holmengen et al. 2009).

Mink populations exhibit a wide temporal range in periodicities, which may suggest that minks utilize alternative prey to muskrats. The typical 8- to 9-year muskrat periodicities occur at low latitudes, whereas 4-year cycle lengths occur in the higher-latitude arctic and subarctic ecozones likely due to predation by red foxes that switch between consuming muskrats and small microtines (Erb et al. 2000). Additionally, 4-year periodicity is characteristic of small microtines (Oksanen and Oksanen 1992) and their predators, least weasels (*M. nivalis*), short-tailed weasels (*Mustela erminea*—Korpimäki et al. 1991; Johnson et al. 2000), and red foxes (*V. vulpes*—Kjellander and Nordstrom 2003). Therefore, we suggest that the range in periodicities observed in mink populations in eastern Canada may be a result of minks switching between muskrats, small microtines, and other prey.

One hypothesis for the reduced dependence on muskrats in eastern Canada is increased species richness compared to western Canada, and therefore increased alternative prey availability in eastern Canada (Shier and Boyce 2009), which would reduce the time lag between mink and muskrat populations (Holmengen et al. 2009). Across Canada, areas of high prey species richness were correlated with a lower percentage of muskrats in mink diets (Shier and Boyce 2009). The pattern of prey species richness documented by Shier and Boyce (2009) could not explain all of the geographical variation in lag periods between mink and muskrat populations. In particular, mink populations were found to fluctuate ahead or at the same time as muskrat populations at a group of locations in eastern Canada where prey species richness was low (Shier and Boyce 2009). To our knowledge, the hypothesis of consumption of specific alternative prey and subsequent influence on mink dynamics has not been tested. Voles and insectivores (*Microtus* sp., *Peromyscus* sp., *Sorex* sp., and *Synaptomys* sp.) together comprised a large portion of prey species identified in the stomach and intestine of minks (Korschgen 1958; Shier and Boyce 2009) and represent possible alternatives to muskrats.

Theoretical models of mink populations in Canada have been unable to describe the observed wide range of periodicities (Holmengen and Seip 2009). Time series of mink fur harvest records in the Hudson's Bay Company archives are characterized by 3.7- to 12.8-year cycle lengths; Holmengen

and Seip (2009) analyzed these data to evaluate the capacity of 3 different models in replicating the cyclic characteristics of minks and muskrats. The most complex model tested (Turchin and Hanski [1997] model) included effects of specialist predation, generalist predation, noise, and seasonality. The Turchin and Hanski model (1997) was found to be the best fit, replicating a range of mink cycle lengths from 3.6 to 5.6 years. Nevertheless, no models were able to replicate both the 3- to 5-year cycle lengths and 8- to 13-year cycle lengths, indicating that current models do not accurately reflect the mechanisms of the mink–muskrat system (Holmengen and Seip 2009).

In this study, we suggest that minks consume alternative prey to muskrats, allowing for decoupling between mink and muskrat populations in the eastern portion of our study area. To test the hypothesis, we evaluated prey as potential variables to explain recruitment of minks. If small microtines are an alternative prey for mink populations in our study area, we expect population fluctuations in both muskrats and small microtines to explain mink recruitment. We also expect a wide range of cycle lengths, from 3 to 13 years, because that would indicate that minks are tracking the 3- to 5-year small microtine periodicities and the 8- to 13-year muskrat periodicities. Last, we expect to find a lag of 0 years between mink and muskrat populations, implying that minks consumed alternative prey. To evaluate theoretical models in light of prey-switching and validate small microtines as viable prey items, we modified and parameterized the Turchin and Hanski (1997) model allowing minks to be generalist predators consuming both muskrats and small microtines. If our model can predict the dynamics in the empirical data set, then the hypothesis of alternative prey gains additional support because it indicates that the complex dynamics of minks can be temporally sustained. Finally, we evaluate the potential drivers of the observed mink–muskrat–alternative prey population dynamics with respect to prey species richness and quantification of land cover.

MATERIALS AND METHODS

Prey-switching: empirical data analysis.—We obtained data collected between 1916 and 1941 from 56 fur harvest posts of Hudson's Bay Company across Manitoba, Ontario, and Quebec, Canada. Selected posts had 16–26 years of continuous annual fur harvest returns, which is sufficient to detect periodicity (Swanson 1998). For our analyses, we assumed that there was no variation in harvest effort (Moran 1953; Swanson and Johnson 1996), and that the furs harvested reflect relative population sizes (Viljugrein et al. 2001). Prior to analyses, we transformed the data as $\ln(N_t + 1)$, where N_t is the harvest level in year t .

We used 3 statistical approaches to evaluate if minks exhibit prey-switching in the empirical data set: linear regression analyses, spectral analyses, and cross-correlation analyses (Table 1). To perform the linear regression analyses, we replaced all values of 0 with the smallest value of $\ln(N_t + 1)$ because the presence of zeros would hinder some of the calculations. Cook's distance metric was calculated for each

TABLE 1.—Breakdown of analyses performed and output generated. Objectives are marked by roman numerals, and associated hypotheses are listed below each objective. Methods utilized include linear regression (LR), spectral analysis (SA), cross-correlation analysis (CCA), and linear discriminant analysis (LDA).

Objectives and hypotheses	Method	Outcome	Conclusion
I. Prey switching: if minks are muskrat specialists			
a. Muskrat-based variables should be significant	LR	Muskrat significant: 30 posts; alternative prey significant: 26 posts	Minks consumed alternative prey
b. Minks' cycle length should range from 8 to 13 years	SA	Cycle 8–13 years: 33 posts; other cycle lengths: 23 posts	Minks consumed alternative prey
c. Minks should lag behind muskrats by 1 or 2 years	CCA	Lag 1–2 years: 25 posts; lag 0 years: 31 posts	Minks consumed alternative prey
II. Sustaining population fluctuations: if models support observed dynamics			
a. Simulated cycle length should range from 3 to 13 years	SA	Cycle 8–13 years, 3–6 years, and mixed	Model supports observed dynamics
b. Simulated lag period should range from 0 to 3 years	CCA	Lag 0, 1, and 2 years	Model supports observed dynamics
III. Driving population fluctuations: if the driver of observed dynamics is			
a. Species richness, alternative prey consumption should increase from north to south	LR	North to south: not significant; east to west: significant	Species richness is not the only driver in this system
b. Land cover, posts with the same dynamics should form discrete groups	LDA	Land cover not sufficient to discriminate major prey	Land cover is not the only driver in this system

observation to ensure that the replaced observations did not influence the results of our regression analyses (Cook 1977). Because ermines are mustelids that specialize on small microtines and follow the population dynamics of small microtines closely (Korpimäki et al. 1991; Johnson et al. 2000; King and Powell 2007), we used harvest returns of ermines as an index of small microtine populations. The harvest records do not identify the fur pelts to species. We assumed the majority of pelts were short-tailed weasels or least weasels because there is minimal range overlap with the long-tailed weasel (*Mustela frenata*—Simms 1979). Populations of short-tailed weasels are believed to follow small microtine populations with no lag, while a 0.5- to 1-year lag is observed with least weasel populations (Korpimäki et al. 1991). In addition, an outfit year in the Hudson's Bay fur harvest records runs from 1 June to 31 May in the next year (Cross 1940), and the peak breeding season for both the short-tailed weasel and the least weasel occurs in June (Amstislavsky and Ternovskaya 2000). Therefore, we incorporated a 1-year time lag in ermine records, and consider the resulting data set representative of small microtine populations.

We used linear regression analyses to identify the best model explaining the detrended series (Royama 1977), or rate of change of minks, at each post (Table 1; Berryman 1991). We lagged all independent variables, including rate of change of muskrats, rate of change of small microtines, ratio of minks to muskrats, ratio of minks to small microtines, and ratio of muskrats to total prey items (sum of muskrats and small microtines) by 0, 1, and 2 years. The entire set of models formed our set of candidate models for evaluation with Akaike information criterion (AIC) values. All models were considered competing models if they were significant ($\alpha = 0.05$) and had change in AIC corrected for small sample size (ΔAIC_c) values ≤ 2 . Posts were then classified into 2 categories. The category "muskrat" included posts where the rate of change of muskrats

(lagged by 1 or 2 years) or the ratio of minks to muskrats (lagged by 0, 1, or 2 years) were the only competing models. Muskrats were presumed to contribute to mink recruitment strongly at these posts. The category "alternative prey" included posts where muskrats lagged by 0 years was the only model with $\Delta AIC_c \leq 2$, because a lag of 0 years is indicative of consumption of alternative prey (Viñjugrein et al. 2001). If a small microtine model was a competitive model, then the alternative prey was considered to be small microtines. At posts where small microtines do not influence mink recruitment, other prey such as crabs or frogs (Korschgen 1958; Shier and Boyce 2009) were presumed to be important. Posts where no significant model was obtained also were included in the "alternative prey" category. At these posts, nonsignificance of all linear regression models could be obtained only if mink dynamics are strongly influenced by prey items other than muskrats or small microtines. Finally, the "alternative prey" category also included posts where small microtines were a competing model. Mink recruitment at these posts was presumed to be influenced by small microtines to some degree.

We performed spectral analyses with the Proc Spectra function in SAS 9.2 (SAS Institute Inc. 2009) to determine period length from periodograms. Periodograms are plots of spectral density versus period length (Bjørnstad and Grenfell 2001) and test the null hypothesis that the periodogram is white noise using the Bartlett Kolmogorov–Smirnov test statistic. All period lengths with spectral density peaks within 50% of the highest peak were considered to be important. We used this evaluation criterion to include all period lengths that explain at least 50% of the variation characterized by the best period length at each of the 56 posts. Period lengths greater than 15 years were disregarded given that the maximum length of time series was 26 years of continuous data. Similarly, period lengths of 2 years were considered to be a result of density dependence rather than true periodicity (Stenseth 1999). We

expected 4 possible outcomes. First, posts where minks exhibited 8- to 13-year periodicities were presumed to be a result of minks consuming muskrats. Second, posts where minks showed 3- to 5-year periodicities were presumed to be a result of minks consuming small microtines. Third, posts where minks exhibited both 8- to 13- and 3- to 5-year periodicities were presumed to be a result of minks consuming both prey types. Finally, we considered posts where mink dynamics exhibited white noise to be reflective of no true periodicity and suggestive of abiotic disturbance events or perturbations to the system (Halley 1996).

Finally, we performed cross-correlation analyses using SAS 9.2 (SAS Institute Inc. 2009) to determine the lag period between mink and muskrat populations (Ranta et al. 1995). Mink dynamics at posts were defined as being influenced by muskrats if a lag period > 0 years was found. Alternatively, if a lag period of 0 years or a nonsignificant lag period was found, we labeled this post as influenced by alternative prey.

Sustaining population fluctuations: theoretical models.—We modeled annual mink and muskrat numbers over multiple years to determine if theoretical models could replicate cyclical properties identified in the empirical data. Similar to Holmengen and Seip (2009), we based our models on the Turchin and Hanski (1997) model, using the equations describing rate of change of predator (equation 1) and prey (equation 2) populations:

$$\frac{dP}{dt} = vP \left(1 - \frac{qP}{N} \right) \quad (1)$$

and

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - \frac{g \times N^2}{H^2 + N^2} - \frac{c \times P \times N}{N + D}, \quad (2)$$

where v and r are the intrinsic rates of increase of the predator and prey populations, respectively; q is the ratio of prey to predator at equilibrium; K is the carrying capacity of prey; g is the intensity of generalist predation (a product of the number of prey killed by the predator, c , and the number of predators, P —Turchin 2003); H is a threshold prey density above which the predator actively searches for the prey item; c is the maximum per capita predation rate; and D is the half-saturation constant (Turchin and Hanski 1997). The equation describing the rate of change of prey (equation 2) incorporates losses that occur as a result of generalist and specialist predation (type III and type II functional responses, respectively).

To account for the consumption of alternative prey by minks, we modified the Turchin and Hanski (1997) model (equations 1 and 2) so that minks were treated as generalist predators and small microtines were considered alternative prey to muskrats. To incorporate small microtines in the modified models we assumed, based on their relative masses, that a muskrat is approximately equal to 37 small microtines (Anderson 1947; Heit 1949; Chitty 1952; Rose and Gaines 1978; Simpson and Boutin 1993; Schulte-Hostedde et al. 2001). Hence, our modified forms of equations 1 and 2 were:

$$\frac{dP}{dt} = vP \left(1 - \frac{qP}{N_m + \frac{N_v}{37}} \right) \quad (3)$$

and

$$\frac{dN_m}{dt} = rN_m \left(1 - \frac{N_m}{K} \right) - \frac{cP \times (N_m)^2}{H^2 + (N_m)^2}, \quad (4)$$

where N_m represents number of muskrats and N_v is the number of small microtines. Our model assumes that population cyclicity is driven by predator–prey interactions, the discrepancy in caloric benefits between muskrats and small microtines can be explained by discrepancy in weights, growth occurs in a discrete fashion, and the parameter estimates are constant. Finally, the model assumes that small microtine population dynamics are unaffected by predation by minks. Although some evidence exists that minks located on islands limit small microtine abundances during peak phases of cyclicity creating a stabilizing effect on populations, this evidence is based on simple island models (Banks et al. 2004). Additionally, large predators (e.g., foxes and badgers) have a greater impact on rodent populations compared to smaller predators (Andersson and Erlinge 1977), which means that the role of minks alone as predators of small microtines is minimal in comparison to the effect of multiple, larger predators (Korpimäki and Norrdahl 1989).

We used an intrinsic rate of increase of 1.39 per year (r) for muskrats (Williamson and Brown 1986) and 0.5 per year (v) for minks (Tanner 1975). The intrinsic rates used were estimated for healthy populations of minks and muskrats, that is, low mortality rates and high fecundity (Tanner 1975; Williamson and Brown 1986). We estimated the maximum per capita predation rate (c) based on the energetic requirements of a mink and the caloric benefits of a muskrat. For captive minks, the daily resting metabolic rate is approximately 20.2 kcal/100 g in outdoor temperatures (Farrell and Wood 1968b). Hence, the daily resting metabolic rate of an average 1.15-kg male muskrat (Mitchell 1961) is 232.3 kcal. Assuming a rest to activity ratio of 2:1 (Gerell 1969) and an energetic cost of activity of 1.7 resting metabolic rate (Taylor et al. 1970), the annual energetic requirement of a male mink is $\sim 100,000$ kcal. Applying the same assumptions to a nonlactating female with a mass of 0.6 kg (Mitchell 1961), the annual energy requirement is approximately 54,000 kcal. We assumed that a lactating female has an energetic requirement equal to double the amount of a nonlactating female or approximately that of a male. The average interbirth interval calculated for 4 mustelid species (including minks) is 375 days, or approximately 1 year (Ferguson and Larivière 2002). Thus, the energetic requirement for a single mink, regardless of sex, is approximately 100,000 kcal. We calculated the caloric benefit of a single muskrat based on the assumption of a mean mass of 1 kg (Simpson and Boutin 1993). Assuming a caloric density value of 1.5 kcal/g (Schreiber and Johnson 1975), an ingestion efficiency of 0.75 (Powell 1979), and an assimilation efficiency of 0.71 (Farrell

and Wood 1968a), the energy provided by a single muskrat is ~ 800 kcal. Thus, the minimum predation rate, assuming muskrats are the only food source for minks, is approximately 125 muskrats per year. Seasonal variations occur in the diet of a mink with low consumption of muskrats in winter (Korschgen 1958). A study performed in southern Michigan indicated that muskrats represent about 31% of the diet of a mink by volume (Sealander 1943). Prey base, however, becomes smaller at higher latitudes and it is estimated that in the study areas of this project, muskrats will represent about 50% of the diet. Thus, the maximum per capita predation rate (c) is 62.5 muskrats per year. In addition, muskrat populations tend to possess a larger proportion of juveniles (Schofield 1955) and surplus killing by minks is commonly observed (Breault and Cheng 1988; Craik 1997). Therefore, the predation rate can be assumed to be higher than biomass intake. We used a range of values to represent c (45–75 muskrats per mink evaluated over intervals of 5) to assess sensitivity of our model to chosen parameter estimates.

Carrying capacity of muskrats (K) was set to 2,000, at a density of 38 muskrats/ha (Butler 1940). We did not find any values for the ratio of muskrats to mink at equilibrium (q) in the literature, but assumed the value to be close to c . A range of 30–500 muskrats per mink (evaluated over intervals of 5) was used in the simulations to assess the sensitivity of the model to the parameter. We found no data for prey threshold density and performed sensitivity analyses using the range of $H = 0.76$ – 7.6 muskrats/ha (evaluated over intervals of 0.1). We used an initial population size of 1,500 muskrats and 10 minks. The 5-, 4-, and 3-year small microtine cycles, iterated over time, were defined as having sequential population sizes of 1,000, 3,000, 6,000, 6,000, 3,000, and 1,000; 1,000, 3,000, 6,000, 3,000, and 1,000; and 1,000, 3,000, 6,000, and 1,000; respectively. Time series were simulated using equations 3, 4 in R (R Development Core Team 2012).

Period length and lag of the simulated time series were analyzed using identical methods as the empirical data. Values from simulated and empirical time series were compared with respect to range of period lengths and range of lag periods between mink and muskrat populations.

Driving population fluctuations: spatial analysis.—In order to identify spatial trends in mink dynamics, we identified the locations of posts of Hudson's Bay Company fur harvests that occurred within the study area between 1915 and 1940 by compiling the years of operation for all posts within Manitoba, Quebec, and Ontario, as well as 5 posts located near the border of Manitoba and Saskatchewan, from records in the Archives of Hudson's Bay Company (Archives of Manitoba, Winnipeg, Manitoba, Canada). Additionally, images of post locations from the archives were georeferenced in ArcMap 10 (Environmental Systems Research Institute 2010), and post locations were digitized from the image. Finally, we determined geographic coordinates of each post and performed logistic regressions in R to look for north-south and east-west gradients of mink dynamics across our study area. We performed 3 logistic regressions, based on the results

of regression analyses, spectral analyses, and cross-correlation analyses (Table 1) to explain occurrence of posts where alternative prey were significant, using latitude and longitude as covariates.

For each post, we analyzed land cover over 4 spatial extents: immediate area, local area, regional area, and nonoverlapping fur collection zones, using the Geospatial Modeling Environment (Beyer 2012). Immediate, local, and region areas were defined by 50-, 100-, and 200-km buffers from each post location, respectively. To define the nonoverlapping areas from which furs were likely collected for each post, we used a series of Thiessen polygons. Once created, Thiessen polygons contain 1 focal point, or post, and encompass the area closer to the focal post than to any other post. We created 1 Thiessen polygon per post for each year to define the nonoverlapping fur collection zones around each post per year. The files were then separated by post, converted to a raster format, and then reclassified such that the collection zone around each post was assigned a value of 1 and all other zones were assigned a value of 0. Finally, the raster files for each post were summed to generate a composite collection zone extent. Only cells contained within the collection zone 75% of the total number of years the post was operational between 1916 and 1941 were retained. Thus, the resulting shape was an approximation of the extent of the nonoverlapping collection zone for each post in the study. Land-cover data were obtained as vector files (Center for Topographic Information of Natural Resources Canada, Sherbrooke, Quebec, Canada) with an estimated accuracy of 30 m. We used the Geospatial Modeling Environment isectpolypoly tool (Beyer 2012) to extract the proportion of each land-cover class that occurred within each post polygon over the 4 spatial extents. Land-cover variables selected for use in subsequent analysis were percentage of wetland, shrubland, grassland, forest, and barren land, because these environments are suitable for minks (Arnold and Fritzell 1990). We used a discriminant analysis to identify land-cover variables that best delineated posts where minks consume mainly muskrats and posts where muskrats are less important in mink diets. The analyses were performed in R using the package MASS (Venables and Ripley 2002).

RESULTS

Prey-switching: empirical data analysis.—Linear regression analyses showed that the best model explaining mink dynamics varied across posts of the Hudson's Bay Company. Muskrat-based models were strong explanatory variables of mink dynamics at 53.6% of the posts (30 of 56 posts; Table 2). The influence of alternative prey was detected at the remaining 46.4% of the posts (26 of 56 posts; Table 2). In particular, posts in the far western portion of the study area ($n = 13$) showed strong evidence of muskrats being an important prey, because minks to muskrats ratio lagged by 0 years was a consistent best model explaining mink dynamics (Fig. 1; Table 2). Of the 26 alternative prey posts, 15 showed evidence of small microtines being an important alternative prey either as the best model or as a competitive model.

TABLE 2.—Best model, slope of variable (*SE*), Akaike weight of best model, period length of mink (*Neovison vison*) time series (in years), and lag period between mink and muskrat (*Ondatra zibethicus*) series (in years) for $n = 56$ posts. The best model is “Muskrat” if mink dynamics were explained by rate of change of muskrats, “Mink/Muskrat” if explained by ratio of minks to muskrats, “Microtines” if explained by rate of change of small microtines, “Mink/Microtines” if explained by ratio of minks to small microtines, and “Muskrat/Prey” if explained by ratio of muskrats to total prey. L0, L1, and L2 indicate lag of 0, 1, and 2 years, respectively. NS indicates no significant models or lag periods were obtained. WN indicates that mink series was white noise.

Posts	Best model	Slope ($\pm SE$)	Akaike weight	Period length	Lag period
Beren's River	Mink/MuskratL0	-5.026 (± 1.46)	0.877	WN	0
Cross Lake	Mink/MuskratL0	-6.233 (± 1.81)	0.621	6.5	1
God's Lake	Mink/MuskratL0	-7.689 (± 1.76)	0.782	WN	1
Island Lake	Mink/MuskratL0	-6.456 (± 1.26)	0.998	8.7	2
Little Grand Rapids	Mink/MuskratL0	-5.658 (± 1.18)	0.869	8.7, 13	1
Nelson House	Mink/MuskratL1	-4.574 (± 1.22)	0.674	8.7, 6.5	0
Norway House	Mink/MuskratL0	-6.031 (± 1.48)	0.407	13, 6.5	2
Oxford House	Mink/MuskratL0	-4.642 (± 1.58)	0.688	13, 6.5	0
Pukatawagan	Mink/MuskratL0	-6.605 (± 1.33)	0.978	11	1
Split Lake	Mink/MuskratL0	-6.045 (± 1.15)	0.995	WN	0
York Factory	Mink/MuskratL0	-3.910 (± 0.90)	0.957	WN	0
Nipigone House	Mink/MuskratL2	-2.120 (± 0.80)	0.338	10	NS
Pine Ridge	MuskratL1	0.758 (± 0.28)	0.328	8, 5.3	1
Fort Severn	MuskratL0	0.585 (± 0.21)	0.455	10	1
Osnaburgh	Mink/MuskratL0	-5.322 (± 2.02)	0.419	10	1
Attawaspiskat	Mink/MuskratL0	-6.988 (± 2.90)	0.234	10	0
Fort Hope	Mink/MuskratL0	-7.309 (± 2.13)	0.503	10	0
Sioux Lookout	Mink/MicrotineL0	-4.399 (± 1.20)	0.519	9.5	0
Moose Factory	Mink/MicrotineL2	-2.483 (± 0.58)	0.876	10	1
Lac Seul	Mink/MuskratL1	-4.297 (± 1.33)	0.424	10	2
Minaki	Mink/MuskratL0	-4.845 (± 1.68)	0.566	WN	NS
Long Lake	Mink/MuskratL1	-5.307 (± 2.04)	0.296	10	0
Mobert	Mink/MuskratL0	-6.163 (± 1.63)	0.718	10	0
English River	Mink/MuskratL0	-3.741 (± 1.41)	0.269	10	1
Hudson	Mink/MuskratL0	-4.475 (± 1.21)	0.532	8	1
Grassy Narrows	MuskratL1	1.043 (± 0.23)	0.930	10	NS
Temagami	MuskratL1	0.355 (± 0.13)	0.461	11	1
Fort Albany	MuskratL0	0.497 (± 0.12)	0.668	WN	0
Mattic Post	MicrotineL0	-0.540 (± 0.12)	0.478	4	1
Gogama	Mink/MuskratL0	-4.260 (± 0.80)	0.990	10	1
Missanabie Post	Mink/MuskratL0	-4.334 (± 1.27)	0.448	10, 5	1
Weenusk Post	Mink/MuskratL0	-2.599 (± 1.43)	0.183	10	1
Cat Lake Post	Muskrat/PreyL2	-7.095 (± 3.02)	0.211	WN	2
Trout Lake	Mink/MuskratL0	-8.743 (± 1.81)	0.990	WN	0
Ogoki Post	Mink/MuskratL0	-5.762 (± 1.46)	0.438	10	1
Deer Lake Post	Mink/MuskratL0	-4.332 (± 1.34)	0.597	10	2
Dinorwic Post	Mink/MicrotineL0	-1.340 (± 0.59)	0.161	3.3, 4, 5	0
Nipigon Post	Mink/MuskratL2	-2.392 (± 0.86)	0.324	10	NS
St. Augustine	MuskratL0	0.507 (± 0.10)	0.993	4.3, 8.7	0
Barriere	MicrotineL0	-0.681 (± 0.20)	0.347	WN	0
Bersimis	MuskratL0	0.544 (± 0.09)	0.959	8.3	0
Eastmain	MuskratL0	0.775 (± 0.23)	0.476	8.7	0
Fort George	Mink/MuskratL0	-5.826 (± 1.65)	0.415	WN	0
Grand Lac	MuskratL0	0.757 (± 0.10)	0.999	8.7	0
Great Whale River	MuskratL0	0.718 (± 0.14)	0.997	8.7, 4.3, 13	0
La Sarre	Mink/MuskratL0	-4.014 (± 1.19)	0.730	13, 8.7, 6.5, 3.7	1
Manuan	MuskratL0	0.741 (± 0.14)	0.787	8.7	0
Mistassiny	Mink/MicrotineL2	-1.253 (± 0.37)	0.848	8.7	0
Obijuan	MuskratL0	0.721 (± 0.14)	0.977	8.7	0
Pointe Bleue	MuskratL0	0.718 (± 0.14)	0.990	8.3	0
Romaine	MuskratL0	0.671 (± 0.14)	0.994	4.3	0
Rupert's House	Mink/MuskratL0	-5.407 (± 1.18)	0.902	WN	1
Senneterre	Mink/MuskratL0	-2.645 (± 0.72)	0.641	13, 8.7	1
Seven Islands	Mink/MicrotineL0	-6.877 (± 1.04)	1.000	8.7, 4.3	0
Woswonaby	Mink/MuskratL0	-2.899 (± 0.58)	0.954	8.7, 6.5	2
Nemaska	Mink/MicrotineL0	-1.891 (± 0.48)	0.683	WN	0

TABLE 3.—Results of logistic regression analysis using latitude and longitude to explain occurrence of alternative prey consumption by minks (*Neovison vison*). Consumption of alternative prey at a post was defined from the results of linear regression, spectral, and cross-correlation analyses as outlined in Table 1. An asterisk (*) denotes significance.

	Latitude		Longitude	
	<i>P</i>	β coefficient ($\pm SE$)	<i>P</i>	β coefficient ($\pm SE$)
Linear regression	0.72	0.05 (± 0.14)	< 0.01*	0.15 (± 0.05)
Spectral analyses	0.80	0.05 (± 0.18)	0.03*	0.09 (± 0.04)
Cross-correlation	0.41	0.10 (± 0.12)	0.04*	0.08 (± 0.04)

muskrat cycle lengths were observed, despite negligible changes occurring in mink numbers. At very high numbers of small microtines (> 60,000), mink and muskrat populations were driven to extinction.

Using our modified Turchin and Hanski (1997) model (equations 3 and 4), simulated mink time series produced periodicities ranging from 2.8 to 13 years as determined by spectral analyses. Cross-correlation analyses indicated lag periods of 0, 1, 2, and 3 years between mink and muskrat populations. Simulations with small microtines as an alternative prey produced mixed 2.8- to 5.2-year and 8.5- to 13-year cycle lengths in mink populations with a 0- to 3-year lag period between minks and muskrats. Simulations without small microtines resulted in 8.7- to 13-year cycle lengths and lag periods of 1 and 2 years. Only the set of parameter combinations $q = 45$, $c = 55$, and $H = 5.7$ produced 5-year cycle lengths in minks in the absence of small microtines.

Driving population fluctuations: spatial analyses.—The logistic regression indicated that, regardless of which analyses were used to define the groups, post longitude explained the occurrence of minks consuming alternative prey (Table 3). Moreover, the β coefficients associated with longitude ranged from 0.08 to 0.15, indicating that an increase in longitude resulted in an increase in occurrence at posts where alternative prey were important for minks. In contrast, the latitude of posts was never a significant variable explaining occurrence of mink prey items (Table 3). Linear discriminant analyses, performed using land-cover variables collected over 4 spatial scales, was not able to differentiate between posts where muskrats were an important prey and posts where alternative prey items influenced mink dynamics (Fig. 3).

DISCUSSION

The empirical data analyses provided evidence that minks in Canada were consuming alternative prey species, and these trends were replicated in our simulated results using the modified Turchin and Hanski (1997) model. Moreover, land cover and species richness did not appear to be the sole drivers that influenced spatial variation in dependence on muskrats observed from the west to east across the study area.

Linear regression analyses indicated that muskrat-based models explained mink recruitment particularly in the western portion of our study area. Toward the central and eastern portion, small microtine-based models (or models based on lagged ermine harvest abundances) were competitive models explaining mink recruitment or rate of change of minks resulting in reduced muskrat dependence (Fig. 1; Table 2).

The spectral density periodograms support the linear regression analysis and suggest that, at some posts, minks were muskrat specialists and at others minks consumed alternative prey. In the western portion of the study area, the best model explaining mink dynamics for 13 posts was the ratio of minks to muskrats (lag of 0 years; Fig. 1). Additionally, 8 of these posts had significant spectral density peaks, 7 of which occurred in the 8- to 13-year periodicity range, suggesting that muskrats were important prey for mink populations in the area. Conversely, at 9 other posts in the central and eastern portion of our study area, the spectral density suggested a periodicity of 3–5 years (Table 2). Because of the shift in periodicity from muskrat periodicity to small microtine periodicity, we interpreted these results as suggestive of decreased dependence on muskrats and, therefore, increased dependence on alternative prey. Previous diet studies suggest that voles and insectivorous mammals contributed strongly to mink diets (Shier and Boyce 2009). Voles belong to the cyclical small microtines group (Boonstra 1994), whereas shrews (Soricidae) exhibit a similar but weak cyclicity (Sonerud 1988). Therefore, it is likely that minks at the alternative prey posts were consuming small microtines, producing 3- to 5-year cycle lengths.

Finally, the cross-correlation analyses indicated a decoupling of mink and muskrat populations at some posts across the study area, supporting the alternative prey hypothesis. Although a lag of 1 or 2 years was observed in 25 posts, indicating high reliance of minks on muskrats, a lag of 0 years was observed between minks and muskrats at 31 posts (Table 1). The lag of 0 years suggests poor coupling of mink–muskrat dynamics (Viljugrein et al. 2001) and, therefore, decreased reliance of minks on muskrats. These results support the linear regression and spectral analysis results and suggest that, at some posts, minks consumed alternative prey such as small microtines.

Differential reliance on different prey items can subsequently affect mink recruitment (as seen in the linear regression analyses; Table 1), mink cyclicity (reflected by spectral analyses; Table 1), and time required for mink populations to respond to changes in muskrat populations (reflected by the cross-correlation analyses; Table 1). Although each of the statistical approaches used to analyze the empirical data suggests that minks were consuming alternative prey, the analyses were not always in agreement at a single post. We suggest that these results are reflective of different degrees of reliance of minks on muskrats at some posts compared to the reliance of minks on alternative prey sources at other posts, and that the statistical methods employed differ in their relative sensitivities to factors producing the population dynamic

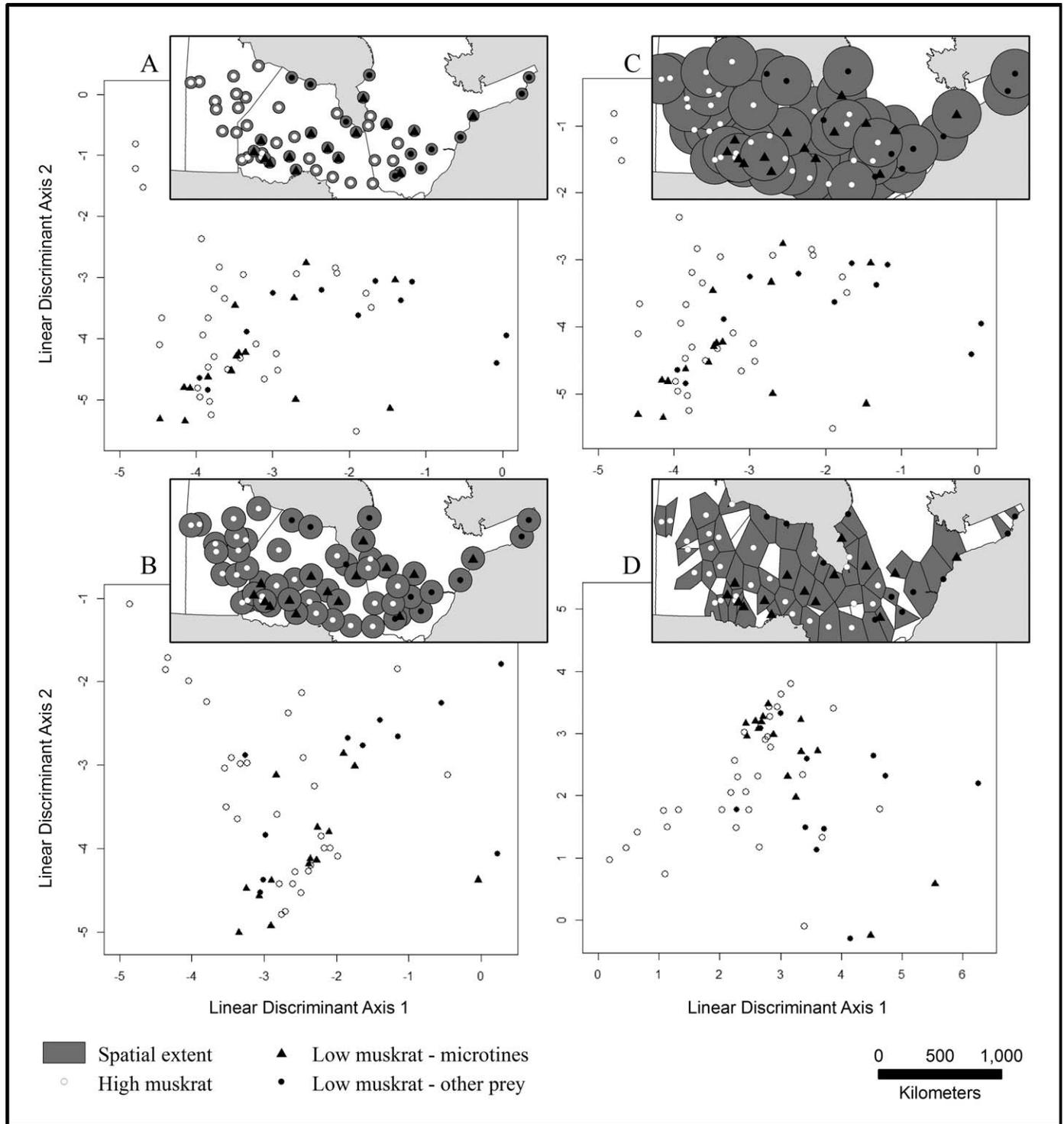


FIG. 3.—Linear discriminant plots by spatial extent. Land cover was analyzed at 4 different spatial extents: A) 50-km buffer from each post; B) 100-km buffer from each post; C) 200-km buffer from each post; and D) Thiessen polygons around each post. No significant land-cover pattern was found to group posts with similar mink (*Neovison vison*) diet across any of the spatial extents utilized.

patterns observed. We believe that it is unlikely that our results reflect spurious significances from testing a large number of posts of Hudson’s Bay Company because more recent diet analyses (Shier and Boyce 2009) suggest that complex mechanisms influence the gradient of mink–muskrat interac-

tions. Regardless of the differences, we found support, using at least 1 metric, for minks consuming small microtines at 20 posts across the entirety of our study area, which we validated by modeling mink and muskrat populations with existing ecological theory.

Using our modified Turchin and Hanski (1997) equations (equations 3 and 4), we found that a narrow set of biologically relevant and appropriate parameter estimates produced coupled oscillations (Fig. 3). At very low prey threshold densities ($H < 1.71$ muskrats/ha), characteristic of a specialized predator, cycle lengths greater than 15 years occurred that were not observed in the empirical data (Hanski et al. 1991). In order to allow cycle lengths to remain shorter than 15 years in a time series, the threshold density exhibited by minks must be high, indicating generalist predation. Coupled oscillations were generally obtained at $q:c$ ratios < 1 , which may be indicative of surplus predation where the predator does not cache carcasses for later consumption. Although minks exhibit surplus predation, they do cache carcasses for later consumption (Craik 1997), which should influence survival and recruitment of minks. Therefore, the parameter q must be close to if not greater than c , producing a $q:c$ ratio ≥ 1 . Very high $q:c$ ratios (> 1.33) produced 4-year muskrat periodicity with negligible changes in mink numbers; this situation was not found in the empirical time series. If the caloric benefit provided by a small microtine is one-thirty-seventh that of a muskrat, a mink diet where the number of small microtines consumed equals 33% of the total number of muskrats consumed seems unrealistically high. Introducing very high numbers of small microtines in the model resulted in a rapid increase in mink recruitment, followed by heavy predation on muskrats and extinction of mink and muskrat populations. This result suggests that minks are not able to survive on small microtines alone, and could provide an explanation for why degrees of reliance on alternative prey are observed in the empirical data. One set of parameter estimates produced a 5-year periodicity in the absence of small microtines. The $q:c$ ratio of 0.8 indicates that each mink would have to kill $\sim 22\%$ more muskrats than what is required for survival and recruitment. Because this is unlikely, the 5-year cycle length does not appear biologically relevant.

Our modified Turchin and Hanski (1997) equations generated coupled oscillations and replicated dynamics observed in the empirical data set using biologically realistic parameter estimates. Consumption of small microtines as alternative prey species was successfully included in the model as evidenced by the mixed 2.8- to 5.2-year and 8.5- to 13-year periodicities of simulated mink time series. A lag range of 0–3 years was simulated, whereas the empirical time series indicated a 0- to 2-year range. The lag period of 3 years occurred only in simulations run with a 3-year small-microtine cycle length, which could be an artifact of superimposing a 3-year subcycle on the 10-year periodicity that occurred in both mink and muskrat time series.

We examined factors that may be responsible for minks consuming alternative prey by looking at the relationship between the observed mink dynamics and species richness or land cover. Because prey species richness for minks across our study area increased from north to south (Shier and Boyce 2009), we expected a north–south trend in instances of prey-switching. Instead we found an east–west spatial pattern in the

degree of dependence of minks on muskrats (Fig. 1; Table 3). Additionally, we found no evidence that land cover was driving the observed spatial pattern (Fig. 3). Although the land-cover variables were obtained from aerial photographs collected between 1996 and 2001 and may not reflect land-use type in the study area between 1916 and 1941, we expect that major land covers outside of urban and agricultural areas have changed little, because they are supported by relatively stable abiotic factors. We suggest that additional variables, such as foxes, may influence mink–muskrat dynamics (Erb et al. 2001) and potentially interact with land-cover variables. It also is important to note that our study provides statistical evidence of minks consuming small microtines as an alternative prey, and the correlation observed is only indirect evidence. Therefore, field studies are necessary to confirm the population trends identified.

Our study is the 1st to provide evidence for the hypothesis of consumption of alternative prey (specifically small microtines) by minks using the Hudson's Bay Company fur harvest records. Future studies tracking mink, muskrat, and small microtine abundances along with diet of minks are important to confirm the existence of a prey threshold density in the system. Moreover, such studies can evaluate true parameters and potential for sustaining population fluctuations in the mink–muskrat system with the influence of small microtines. Finally, interactions of minks and muskrats with foxes, and the vulnerability of muskrats to minks in different land-cover types are worth investigating to identify spatial drivers of mink–muskrat interactions.

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