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MUSKRAT HABITAT USE IN QUEBEC

by

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October 1995

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements of the degree of doctor of philosophy

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ISBN 0-612-12446-0

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ABSTRACT

A study of muskrat population variables in southern Quebec did not allow differentiation between the quality of ditches bordered by corn fields and those bordered by hay fields. Annual turnover of adults and juveniles was very high in both ditch types. The average maximum density of muskrats was the second highest recorded in the literature. Muskrat activity was not predictive of activity of other co-occurring vertebrates. The direct relationship between the logarithm of the number of burrows and the number of muskrats showed the usefulness of this sign of presence as an indicator of population size. Within given ditches, we failed to detect different genetic proximity between adults from successive years between corn and hay ditches. We failed to show that adult genetic proximity within ditches and within years differed between hay and corn ditches. Analyses of adult genetic proximity within and among ditches within a year confirmed the limited dispersal of female muskrats. Muskrat DNA fingerprinting analyses supported the general usefulness of spatiotemporal associations to determine kinship. Habitat use models based on muskrat signs of presence in southern Quebec high clay bank farm ditches showed that muskrat presence was positively associated with water depth, water velocity, and pulpy plant cover (excluding cattail), but was negatively associated with dredging. The type of crop was not important in explaining muskrat presence. In various habitats of the James Bay area, the habitat use models identified a positive relationship with percentages of submerged and floating plant cover, width of the shore herbaceous belt, bank slope and dominance of clay-loam soil on banks. Such models could be used to assess the potential of boreal wetlands to harbour burrow-dwelling muskrats.

RÉSUMÉ

Une étude des variables de populations de rat musqués réalisée dans des canaux de drainage du sud du Québec n'a pas permis de différencier la qualité de ceux bordés par des champs de maïs de ceux bordés par des champs de foin. Les taux de renouvellement des adultes et des juvéniles étaient très élevés dans les deux types de canaux. La moyenne des densités maximum de rats musqués était la deuxième plus élevée enregistrée dans la littérature. L'activité du rat musqué n'a pas permis de prédire l'activité des autre vertébrés sympatriques. La relation directe entre le logarithme du nombre de terriers et le nombre de rats musqués a démontré l'utilité de cet indice de présence comme indicateur de la taille de la population. À l'intérieur de canaux donnés, nous n'avons pu montrer que la proximité génétique entre adultes d'années successives était différente entre les canaux bordés par des champs de maïs et ceux bordés par des champs de foin. Nous n'avons pu démontrer de différence entre les canaux-foin et les canaux maïs quant à la proximité génétique entre adultes de même canaux pour une année donnée. L'analyse de la proximité génétique entre adultes occupant un même canal et entre adultes de canaux différents pour une même année a confirmé le degré de dispersion limité des femelles. L'analyse des empreintes génétiques des rats musqués a démontré l'utilité générale des associations spatio-temporelles des individus pour établir les liens parentaux. Les modèles de l'utilisation de l'habitat par le rat musqué dans les canaux de drainage à hautes berges argileuses du sud du Québec ont permis de démontrer que la présence du rat musqué était positivement associée à la profondeur d'eau et à la vitesse du courant, au recouvrement par les plantes charnues (excluant les quenouilles), et négativement liée au dragage des canaux, le type de culture n'ayant pas d'effet significatif. Une méthode similaire utilisée dans des habitats variés de la région de la Baie James a démontré une relation positive entre la présence du rat musqué et les pourcentages de recouvrement par les plantes submergées et flottantes, la largeur de la bande de végétation herbacée riveraine, la pente de la berge et la dominance de loam argileux sur les rives. De tels modèles pourraient être utilisés pour évaluer le potentiel de milieux humides boréaux à accueillir des rats musqués habitant des terriers.

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LIST OF ABBREVIATIONS

al.	alii
BSI	band sharing index
C	index of rank correlation
cm	centimetre
cm/s	centimetre per second
df	degree of freedom
DNA	deoxyribonucleic acid
E	east
e.g.	for example
EDTA	ethylene-diamine-tetra-acetic acid
F	Fisher F
Fisher's	Fisher's exact test
g/m^2	gram per square meter
g/day	gram per day
G	Goodness of fit value
G_c	Goodness of fit value with Williams correction
ha	hectare
HSI	Habitat Suitability Index
ind./ha	individual per hectare
K-W	Kruskal-Wallis non-parametric analysis of variance
km	kilometre
Log L	logarithm of likelihood
m	meter
m/min	meter per minute
mg/l	milligram per litre
min.	minute
mm	millimetre
mM	millimolar
N	sample size

LIST OF ABBREVIATIONS

(CONTINUED)

N_A	number of bands in individual A
N_{AB}	number of bands shared by individuals A and B
N_B	number of bands in individual B
NSERC	Natural Science and Engineering Research Council
NWT	Northwest Territories
°C	degree Celsius
°N	degree north
$\underline{P}$	probability
pers.comm.	personal communication
P_{jj}	expected proportion of shared bands between littermates
P_{pj}	expected proportion of shared bands between parent and offspring
P_{pp}	expected proportion of shared bands between unrelated adults
q	mean allele frequency in a population
R^2	Square of the multiple correlation coefficient
S	south
SDS	sodium dodecyl sulphate
SSC	solution of sodium citrate
τ_b	Kendall correlation tau b
TPE	Tris-phosphoric acid-EDTA
Tris	Tris-Hydroxymethylaminomethane
μg	microgram
W	west
x	mean probability of band sharing between individuals
χ^2	chi square
♂	male
♀	female

PREFACE

Candidates have the option of including, as part of the thesis, the text of a paper(s) submitted or to be submitted for publication, or the clearly-duplicated text of a published paper(s). These texts must be bound as an integral part of the thesis.

If this option is chosen, **connecting texts that provide logical bridges between the different papers are mandatory.** The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.

The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". **The thesis must include:** A Table of Contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a comprehensive review of literature, a final conclusion and summary, and a thorough bibliography or reference list.

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis.

In the case of manuscripts co-authored by the candidate and others, **the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent.** Supervisors must attest to the accuracy of such statements at the doctoral oral defense. Since the task of the examiners is made more difficult is these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of the co-authored papers. **Under no circumstances can a co-author of any component of such a thesis serve as an examiner for that thesis.**

For all the chapters presented in this thesis, the Ph.D. candidate has designed the studies, carried out the field work with the help of field assistants, performed the statistical analyses and has written the papers with advice provided by Dr. J.R. Bider for the papers entitled: "Muskrat habitat use in farm ditches", and "Comparison of muskrat (Ondatra zibethicus) population variables, and of muskrat and other stream dwelling vertebrates activity, in ditches bordered with corn and hay fields". Dr. Urs Kuhnlein provided lab facilities and advice for the paper entitled: "Effect of habitat quality on genetic proximity among muskrats". Robert Décarie, Daniel Lambert, and Mario St-Georges helped with the field work logistics, data entry, and provided advice for the paper entitled "Nonlinear modelling of muskrat use of habitat". This paper was published in the Journal of Wildlife Management, and the reference is: **NADEAU, S., R. Décarie, D. Lambert, and M. St-Georges. 1995. Nonlinear modelling of muskrat use of habitat. J. Wildl. Manage. 59(1):110-117.**

Co-authors of papers to be submitted will be: Dr. J. R. Bider for the papers entitled "Muskrat habitat use in farm ditches" and "Comparison of muskrat (Ondatra zibethicus) population variables, and of muskrat and other stream dwelling vertebrates activity, in ditches bordered with corn and hay fields"; Dr. J. R. Bider and Dr. Urs Kuhnlein for the paper entitled: "Effect of habitat quality on genetic proximity among muskrats". All papers will be submitted to the Journal of Wildlife Management.

STATEMENT OF ORIGINALITY

Despite the numerous studies on muskrat, few tools other than the time-consuming trapping, expensive radio-telemetry, and aerial surveys of lodges have been used. Aerial survey of lodges is not applicable to burrow-dwelling muskrat populations. In this thesis, I successfully used muskrat signs of presence, a non-intrusive, rapid, and relatively inexpensive method, to identify, for the first time, habitat variables important to muskrat presence in a boreal forest region and across a variety of wetlands where muskrats are mainly burrow dwellers. I also showed that rivers with slow current represented the best type of wetland, while muskrat was absent from bogs.

This thesis describes one of the very few reported studies dealing with muskrats in farm ditches, and the only one aimed at investigating the effects of crops bordering ditches on muskrat population dynamics. The prevalence of this type of wetland in agricultural landscapes renders useful, for the wildlife manager, the identification of important factors affecting habitat quality for muskrat. We used muskrat signs of presence, including burrows, to build habitat use models. Although univariate tests showed that muskrat presence was positively associated with the presence of alfalfa fields along ditches, the type of crop bordering ditch sections was not selected by the models to explain muskrat presence or absence. Moreover, the presence of alfalfa fields was only weakly correlated with only one variable selected by the models. I did not detect either any difference among alfalfa, cereal, and corn crops in the frequency of ditch sections showing signs of muskrat crop consumption. On the other hand, I showed for the first time that, within a range of low water velocity, muskrat presence was positively related to current speed. The confirmation of the positive relationship between muskrat presence and water level, combined with the first confirmed negative relationship between muskrat presence and dredged ditches, highlighted the importance of managing dredging to minimize its impact on muskrat populations.

This study has also documented a significant positive relationship between the number of muskrat burrows and muskrat abundance, thus confirming the usefulness of this sign of presence as an indicator of the size of muskrat populations. This tool should constitute an inexpensive and useful indicator for the importance of muskrat populations in areas where muskrats are mainly burrow dwellers.

The comparison of variables describing muskrat population dynamics in ditches bordered by perennial hay fields versus annual corn fields, never described before, did not allow the detection of important significant differences. These results would indicate that consideration of the crop factor is not warranted when managing habitat for muskrat. A modified tracking technique allowed me to show that muskrat activity between corn and hay ditches during the growing season could not be used as an indicator of the activity of other co-occurring vertebrates. The detection of muskrat density at the high end of recorded values and the almost complete summer-to-spring population turnover would indicate that the establishment of a fall trapping season would be of no concern, at least in small ditches.

Finally, use of DNA fingerprinting technique to compare the effect of an environmental factor (corn versus hay fields bordering drainage ditches) on the genetic proximity between individuals (adults of a given ditch within a year, and adults of a given ditch in two successive years) was innovative. A difference in genetic proximity could be due either to a difference in philopatry, or a difference in the rate of population turnover. We did not detect any significant important effect of the crop factor from either analyses, and this is in concordance with results of the study of muskrat population variables and habitat use based on signs of presence and trapping data. The higher genetic proximity between muskrats within the same ditch, as compared with muskrats from different ditches (for male-female and female-female pairs), showed that the effect of limited female migrations could be detected at the genetic level. The results of this study generally support the use of trapping data to infer relatedness between juvenile muskrats and between juvenile and adult muskrats. Trapping data must however be used with caution, since spatio-temporal proximity did not always mean kinship, and true parents were not always detected by trapping.

ACKNOWLEDGEMENTS

All my life, my parents have been supportive of my work and studies, and I want to particularly thank them. I am most indebted to my beloved wife and greatest source of inspiration, Anne-Christine Bonfils, for her encouragement, stimulation, and help in reviewing various versions of the manuscript. I want to thank my three field assistants, Kateri Lescop-Sinclair, Heather Cunningham and Jean-Guy Ladouceur for their patience and hard work. The patience of Magdalena Volkov in teaching a neophyte the basics of molecular biology has also to be acknowledged. I would also like to thank Patrick Galois, Joël Bonin and Ciro Rico for their friendship and good advice. Robert Décarie (Grebe Inc.) and Hydro-Québec provided the logistics for the study in the north. Daniel Lambert, Mario St-Georges, M. J. Lacki, G. J. Doucet, M. R. Julien, S. Novak, and an anonymous reviewer reviewed the paper entitled "Nonlinear modelling of muskrat use of habitat". I want to express my gratitude to all the farmers who allowed me to work on their land, and particularly Gilles Queneville, Jacques Leblanc and M. St-Onge for sharing with me their insights and knowledge of the country. Finally, I want to acknowledge the support and logistics provided by Dr. Urs Kuhnlein and my supervisor Dr. J. Roger Bider for the realization of this Ph.D.

GENERAL INTRODUCTION

Traditionally, studies of muskrat populations have been done in marshes or ponds (Bellrose and Brown 1941, Beshears and Haugen 1953, Mathiak 1953, Arata 1959, Olsen 1959, Erickson 1963, Donohoe 1966, Earhart 1969, Boyce 1977, MacArthur 1980, Parker and Maxwell 1980, 1984, McDonnell and Gilbert 1981, Blanchette 1985, Kangas and Hannan 1985, Proulx and Buckland 1986, Caley 1987, Clark 1987, Proulx et al. 1987, Simpson 1987, Boutin et al. 1988, Messier et al. 1990, Clark and Kroeker 1993), lakes (Aldous 1947, Schmitke 1959, Neal 1968, Danell 1977, 1978a, 1978b, Thurber et al. 1991), rivers and streams (Shanks and Arthur 1952, Smith 1954, Dauphiné 1965, Vincent and Quéré 1972, Brooks 1980, 1985, Brooks and Dodge 1981, 1986, Clay and Clark 1985, Proulx and Buckland 1986, Neves and Odom 1989, Halbrook 1990), and river delta and estuaries (Fuller 1951, Stevens 1953, Ambrock and Allison 1972, Wesworth 1974, Jelinski 1984, Simpson 1987, Kinler and Kinler 1990) . Studies of muskrat populations in farm ditches are not numerous (Errington 1937, 1938, Stewart and Bider 1974, Vincent and Quéré 1972, Bider et al. 1976, Chulick 1979, Proulx and Buckland 1986), and none have tried to test effects of human activity on ditch-dwelling muskrat populations.

The effects of crops on muskrat behaviour and population parameters have been described by various authors (Errington 1937, 1938, 1940, 1963, Chulick 1979, R. Foley, pers. comm.), but it has never been tested. While it has been suggested that creeks bordered by corn fields are preferred by muskrats, mainly for feeding purposes (Errington 1937, 1938, 1940, 1963, Chulick 1979), a negative association between the number of muskrat burrows and the presence of corn fields has also been observed in New-York State farm ditches (R. Foley, pers. comm.). The different types of crops bordering ditches may contribute differently to the food available to muskrats, both in quality or availability in time. Different crops may also be associated with different farming practices that could affect muskrats directly or indirectly, such as ploughing frequency, use of chemicals, such as fertilizers, herbicides and insecticides, and drainage conditions through the use of steeper and deeper ditches for certain crops than for others, thus requiring a higher dredging frequency.

The first three chapters of this thesis focus on one major question: does the presence of different crops along farm ditches influence muskrat habitat use and population variables ?

If crops bordering ditches were shown to affect muskrat habitat use, important changes in the surface covered by each crop in a given region could have an impact on muskrat populations.

The literature provides numerous examples of how to test the effect of one factor on a species' life history traits. Applied to the question asked above, one method would be to perform experimental tests of food preferences and requirements, in conjunction with analyses of the nutritive value and presence of secondary compounds in different crops. The problem with this method is that food preference may not necessarily correspond with habitat selection because it does not include factors such as the costs/benefits associated with the search for a given food item, and more importantly, biophysical habitat variables, other than the quality of food, associated with different crop types, that would influence muskrat selection of habitat and population variables. Another method would be to study muskrat population dynamics in the wild where all possible types of crops bordering farm ditches could be encountered. Parameters such as reproductive rate, growth rate, survival/mortality rate, emigration/immigration rate, population density, and health indices would be studied. The manpower required to answer the above question using this study design could be enormous. A similar study, in conditions where the number of crop types would be limited, and where values for variables known to be important for muskrat would be as similar as possible, could give an indication of the importance of crop type for muskrat populations. Such a study is the subject of chapters 3 and 4. In Chapter 4, we used the DNA fingerprinting technique to test the differential effect of crop type on the genetic proximity between adults, and to verify results obtained from trapping data. A difference in the rate of philopatry and population turnover could, over time, affect the genetic proximity between adults.

One of the available methods to study muskrat use of habitat along ditches bordered by a variety of crops is based on the use of signs of presence. This method allows the collection of data over a greater area than would a method requiring trapping of individuals. When performed in an area where a few of the important abiotic habitat variables are optimal, it may allow the detection of less important habitat variables in muskrat habitat selection. This approach has the disadvantage of reducing the range of habitat conditions under which the resulting conclusions would apply, but at the same time, it increases the sample size in such conditions for the same level of effort, thereby increasing the stability and strength of the model. Aldredge and Ratti (1986), among others, showed the statistical advantages of limiting the number of habitat types when studying resource selection by a species. This approach was used in Chapter 2 to determine the most important habitat variables influencing muskrat probability of presence in the studied ditch sections, with a special emphasis on crops bordering ditches, and assuming that muskrat signs of presence were equally detectable in all habitat types.

Habitat variables used to build the habitat use models fall into the categories used in Habitat Suitability Index (HSI) models, i.e. variables: (1) that can be selected for or against by a species, (2) that can be measured or estimated easily, (3) whose values can be predicted for future conditions, (4) that could change during the course of the study, (5) and that can be controlled by the manager. However, unlike typical HSI variables, (1) important variables were not inferred, but selected by the models, (2) index of habitat quality was calculated using a non-linear multivariable equation instead of summing and averaging linear univariate indices of habitat suitability, and (3) we used data on presence/absence of muskrat instead of density of muskrats to build the habitat suitability models.

Despite the impressive array of published literature on muskrats (see Errington 1963 and reviews by Perry 1982 and Boutin and Birkenholtz 1987), habitat use models identifying muskrat key habitat factors have not been satisfactorily developed from field data. In this manuscript, such models were developed using data recorded from a variety of wetlands of the pristine area of southeastern James Bay (Chapter 5). The approach used in the James Bay study area was generally similar to the one described above for chapter 2, although data were collected in a larger study area, where the density of muskrats, as indicated by the density of burrows, was much lower than in southern Quebec farm ditches. The use of presence/absence data, in a study area where muskrat occurrence was low, allowed to identify the most important variables influencing muskrat presence. However, a model designed to assess potential presence/absence conditions should not be expected to predict population densities over a wide range of habitat values (Schamberger and O'Neil 1986). The conditions for building a model representative of muskrat habitat use were optimal in many ways: (1) independent data points were collected over a study area several times the size of the average species home range that represented a wide range of habitat biophysical conditions, (2) the data set used was large, (3) models were tested using a dataset not used for model building, and (4) intraspecific competition pushing individuals into marginal habitats was unlikely due to the low occurrence of the species. A methodology is also suggested to use habitat use models developed from signs of presence data in the context of environmental assessments.

The following chapters aimed at understanding the relationship between the muskrat and its environment, in order that better tools can be developed for the management of muskrat populations.

CHAPTER ONE

Literature review

I. Theoretical background related to muskrat distribution and habitat use.

Krebs (1978) defined habitat very broadly as "the range of environments in which the species occurs." Ricklefs' (1973) definition is more precise, stating that these environments include "the surroundings of an organism (abiotic factors), plants and animals with which it interacts (biotic factors)." In his book entitled *"Ecology: The Experimental Analysis of Distribution and Abundance"*, Krebs (1978) wrote, in a short seven-page chapter, that " habitat selection is one of the most poorly understood ecological processes...". Since then, many scientific papers have been published on this topic.

In the 1970's and 1980's, the study of habitat selection by small mammals became very popular (Rosenzweig 1974, McCloskey and Fieldwick 1975, McCloskey and Lajoie 1975, McCloskey 1976, Meserve 1976a, Lemen and Rosenzweig 1978, Price 1978, Stamp and Ohmart 1978, Dueser and Shuggart 1978, Munger and Brown 1981, Vickery 1981, Kincaid and Cameron 1982, Thompson 1982, Harris 1984, Brown and Munger 1985, Harney and Dueser 1987). Habitat structure, rather than its specific composition, has been shown to be critical to small mammal communities (McCloskey 1976, Grant et al. 1982) and to bird communities (MacArthur et al. 1962). Habitat selection was believed to result from competition among species (Galindo and Krebs, 1986), although it was acknowledged that individuals also competed for resources within the same species. Intraspecific competition for resources, such as food, shelters, breeding sites or mates, is probably more likely to occur than interspecific competition, since individuals from the same species share the same niche while individuals from sympatric species have niches that may overlap, but not completely. Porter and Dueser (1982) confirmed experimentally the existence of intraspecific competition for food in small mammals. Supplemental feeding resulted in increased population growth, immigration and survival, decreased home range size, greater production of young and earlier sexual maturity (Gilbert and Krebs 1981, Taitt 1981, Taitt and Krebs 1981, Briggs 1986). DeAngelis and Waterhouse (1987) reedited the island biogeography theory of MacArthur and Wilson (1967) as the "patch theory" to explain the maintenance of populations at the landscape level. As to habitat, the patch theory states that the population dynamics in each habitat patch will vary with the quality of the patch. A habitat patch would be an area allowing individuals to perform all or part of their life cycle. The difference in patch quality would be attributed to factors such as differential predation rates, stochastic spatiotemporal distribution of resources within patches, or the residual variance due to the environment or to the demography and affecting the density of species (Strong 1986). Under the patch theory, the environment is a mosaic of patches where a population, which is not necessarily part of a stable ecological community, can survive long enough to send colonists to other patches before local extinction (DeAngelis and Waterhouse 1987). Muskrats must have access to patches of different quality before they can select habitat. Among suitable patches, muskrats may encounter patches in which the risk of mortality is too high to transit through. The colonization of good patches surrounded by such adverse patches (Rosenzweig 1974) may thus be prevented. The observation by Stewart and Bider (1974) that muskrat activity increases during rainy nights could support the assumption that rain changes the quality of patches, maybe through a reduction of predation. This could be due to reduced activity of predators on rainy nights, or reduced predation success.

Habitat selection by muskrats could be influenced by population density and intraspecific competition (Krebs and Davies 1979). According to the ideal free distribution theory of Fretwell and Lucas (1970), the distribution of muskrats living in a mosaic of habitat patches should be such that each individual will obtain the same fitness prospects. Fitness is here defined as the inclusive fitness of an individual and its kin (Hamilton 1964), i.e. the number of copies of its genes that will be passed to the next breeding generation. If muskrat distribution complies with the ideal free distribution model, then the density of muskrats in optimal patches will be higher than in suboptimal patches. However, if muskrat distribution follows more closely a despotic habitat use model (i.e. a situation where some individuals secure better territories through aggressive behaviour), as found by Messier et al. (1990), factors such as reproductive success, growth rate, adult weight and percentage of fat should be higher in optimal habitat patches. Intraspecific competition results in a lower average fitness of individuals at density D, than the average fitness of individuals at density D-1. Aggressive behaviour may, at least in early spring when intraspecific interactions are maximal, create a lower density of animals in better habitats. Van Horne (1983) presented cases in which the density of animals may be higher in low-quality habitat due to social interactions.

Ultimate factors used by muskrats to assess habitat suitability may be different depending on the season. Although muskrats are reluctant to leave their territory when conditions deteriorate (Errington 1963), severe droughts could force them to migrate. On the other hand, since the extent of summer and fall migrations by muskrats is limited (Errington 1963), we can postulate that spring migrations and associated habitat selection reflect most suitable patches year-round. However, the cues used by muskrats to identify the most suitable patch are not known.

Individual differences in habitat selection may reduce the level of correlation between a species and key habitat features, and intraspecific competition. Conversely, it is possible that in a stable and predictable environment, individual differences in habitat selection would be selected against. Environmental stochasticity due to unpredictable weather affecting the biophysical environment and unpredictable variance due to factors such as human-induced disturbances could favour a larger spectrum of phenotypes. The variance in individual habitat selection may be a key element that allows a species to thrive in a varying unpredictable environment. Such an environment would favour generalists rather than specialists.

Seasonal environments are characterized as being less stable (Cody 1966) and imposing higher levels of density-independent effects (Roughgarden 1971, Pianka 1970). Simpson (1987), when comparing weather data between Old Crow Flats (Yukon) and Tiny Marsh (southern Ontario), showed that the latter was more variable for the predictability of precipitation and temperature during the growing season. The number of days outside the thermoneutral zone of muskrats was also more predictable at Old Crow Flats. Simpson (1987) showed that survival of juvenile muskrats was higher in the Yukon (35.9%) than in Ontario (19.1%). On the other hand, Jelinski (1984) noted that only 4 of the 155 muskrats marked the first year in the Mackenzie Delta were recaptured the second year. In an analysis of published literature on muskrats, Boyce (1977) obtained an increasing proportion of young per adult female with increased latitude, which could be explained by the lower survival of adults in the North. Another contradictory observation was that females produced more young per year in the South (Boyce 1977). Thus, the analysis of the above data does not give a clear indication of the effect of latitude on female fitness.

One could postulate that the greater predictability of the environment at higher latitudes would make it more advantageous to select habitat within a narrower range of habitat variables at such latitudes than at lower ones. The reduction in muskrat density at higher latitudes could also reduce the effects of intraspecific competition in habitat use. The reduction of biodiversity at higher latitudes (Wilson 1992) also contributes to the likelihood of a simpler habitat structure, that could allow increased predictability of muskrat habitat use. In North America, habitat use models constructed for northern latitudes could therefore produce better predictions than models built for southern latitudes.

Habitat variables selected in habitat use models could be influenced by the degree of resource management performed by species through the year. Although long-term benefits accrued from territory ownership have not been demonstrated in mammals (Gordon and Lindsay 1990), the taxonomic group in which resource management is the most likely to have evolved is the rodentia, such as prairie dogs (*Cynomys* spp.; Hoogland 1981), marmots (*Marmota flaviventris*; Armitage 1986), squirrels (*Tamiasciurus*; Smith 1968), and naked mole rats (*Heterocephalus glaber*; Jarvis and Sale 1971). Animals such as muskrats, with access to a variety of plant types supplying a steady food source across different seasons within a relatively small geographic area, might also be capable of resource management. It is possible that muskrats manage grazing in late summer-early fall in order to maximize the availability of hydrophytes within a short distance of their burrows in the winter. Maximal use of peripheral home range in the fall and early winter may be an adaptation in muskrat populations occupying shallow water habitats that are subject to extensive freezing during late winter, when movements are restricted to the vicinity of burrows (MacArthur 1978). Exploiting resources that would not be available later during the winter, and maintaining resources that will be available at that time is a form of resource management. Such management would make it advantageous to overwinter in the summer/early fall territory. Moreover, in a situation where families maintain territories over the years (Caley 1987), the management of resources by an individual could increase its inclusive fitness. In a variable environment, resource management would operate if the cost of leaving and colonizing another territory was higher than the cost of maintaining occupancy of a territory through periods of low benefit (Davies and Houston 1983). These conditions could prevail during severe droughts when muskrats are known to maintain burrow occupancy (Errington 1963).

The burrowing and feeding activities of mammalian species, such as black-tailed prairie dog (*Cynomys ludovicianus*; King 1955, Coppock et al. 1983), woodchuck (*Marmota monax*; Swihart 1991), pocket gopher (*Geomys bursarius*, *Thomomys bottae*; Tilman 1983, Hobbs et al. 1988, Inouye et al. 1987), and Arctic ground squirrel (*Spermophilus parryi*; Mallory and Hefferman 1987) have been shown to modify the abundance and growth rate of plants and their nutrient content. We do not know if habitat management exists in muskrats, but its simple feeding activities do reduce cover and density of preferred species (Errington 1963, Danell 1977). Muskrats also influence the structural composition of the marsh vegetation through the building of houses. Kangas and Hannan (1985) have shown that the biomass of plant species on muskrat mounds was thirty-five times greater than in the surrounding marsh. Habitat transformation by the species under study can distort the analysis of habitat selection. Such transformation may give the impression that the species prefers certain habitat types, while the initial biophysical characteristics of the chosen site may have been subsequently altered.

The effect of soil excavation on vegetation abundance and quality will depend upon the nutrient content of the excavated soil, the change in competitive interaction due to habitat modification (Williams et al. 1986, Inouye et al. 1987), and possibly the difference in soil compaction or moisture (Swihart 1991). Muskrat burrowing activity is likely to increase water turbidity and may influence aquatic plant communities, particularly where the density of burrows is high and the volume of water is small.

Economically, muskrats do more damage to agriculture through burrowing activities (Lynch et al. 1947, Beshears and Haugen 1953, Cook 1957, Erickson 1966, Miller 1974, Gosling and Baker 1989) than through the consumption of crop species (Errington 1938, 1963). In the Netherlands, muskrat burrowing is considered so important that a control program worth seven million pounds per year is considered cost-effective (Gosling and Baker 1989). The muskrat has been eradicated from the U.K. for similar reasons (Gosling and Baker 1989). However, muskrat consumption of aquatic plants in shallow creeks or ditches may contribute to maintain the stream flow (Bider et al. 1976), thus reducing the intervals between ditch improvements by dredging.

II. Muskrat habitat use models

Muskrat habitat use models have been developed for riverine ecosystems of the northern United States (Brooks and Dodge 1981, 1986), with habitat variables measured on geological topography maps. Variables selected by the model to explain the number of muskrat burrows were: (1) number of islands, (2) number of coves, (3) percentage of open land, (4) percentage of forest, and (5) dominant class of the river section. The model underestimated the number of burrows by 53% when tested on external data.

A habitat use model was also developed for managed marshes along the St. Lawrence river in southern Quebec (Blanchette 1985). Variables selected by the model were: (1) slope of the bottom, (2) emergent plant cover, (3) emergent plant height, (4) terrestrial plant cover, (5) distance from the shore to a water depth of 50 cm, and (6) water depth at 50 cm from the shore. However, the methodology followed artificially increased the sample size and did not conform to test assumptions. As a result, the model selected some variables that were not significantly correlated with burrows per km, and variables that have a high likelihood of being correlated with each other (e.g. distance from the shore to a water depth of 50 cm, and water depth at 50 cm from the shore).

The only other habitat model developed for muskrats is the Habitat Suitability Index (HSI) model built by Allen and Hoffman (1984) for the management of muskrats in coastal U.S. ecosystems. HSI models are based on the assumption that individual habitat variables can be linked to the habitat suitability for a given species. A combined index of suitability for a given habitat patch can be obtained by summing, weighing, and averaging the suitability indices for the retained habitat variables (Laymon and Barrett 1986). The combined index of suitability does not predict the species density in a given patch. Instead, it predicts the relative habitat quality for the species in question. Variables used in HSI models are limited to those (1) that are selected for or against by a species, (2) that can be measured or estimated easily, (3) whose values can be predicted for future conditions, (4) that could change during the course of the study, and (5) that can be controlled by the manager. Factors such as predation, competition or weather are thus generally not included in HSI models (Schamberger and O'Neil 1986). HSI models are planning models designed to assess impacts of change (Schamberger and O'Neil 1986). Some of the underlying assumptions of HSI models have sometimes been shown to be misleading, such as: (1) the linear relationship between wildlife density and individual habitat variables, (2) the superiority of univariate indices over multivariate ones, (3) the similar habitat use among age classes and seasons, (4) the use of species density as a reliable measure of habitat quality, and (5) the negligible effect of predators and competitors on the abundance of their prey (Laymon and Barrett 1986). The model developed by Allen and Hoffman (1984) did not result from the analysis of new data, but was rather the result of an inferential approach in the analysis of published data. Variables selected in the HSI model were: (1) percentage of canopy cover of emergent herbaceous vegetation, (2) percentage of a year with presence of surface water, (3) percentage of stream gradient, (4) percentage of the river channel with presence of surface water during minimum flow, (5) percentage of the river channel dominated by emergent herbaceous vegetation, (6) percentage of the herbaceous canopy cover within 10 m of the water's edge, and (7) percentage of emergent herbaceous vegetation consisting of persistent species.

Muskrat signs of presence could be useful for the production of muskrat habitat use models. Brooks and Dodge (1981, 1986) attempted to build such a model by counting the number of active muskrat burrows. At our latitude, it is relatively easy to distinguish between a muskrat burrow from the burrows of other animals. Muskrat burrows are 10-15 cm in diameter and the underwater depth of their openings can be up to 58 cm (Beshears and Haugen 1953, Earhart 1969). Other species inhabit burrows with submerged entrances (e.g. *Castor canadensis*, *Condylura cristata*, *Mustela vison*), but only the mink (*Mustela vison*) will occupy burrows of sizes similar to muskrat burrows. Mink, however, do not dig their own burrows underwater, and use the ones dug by muskrats (Murie 1974). Muskrat breeding burrows typically have two entrances, while feeding burrows may only have one opening (Errington 1963). Some authors have distinguished between active and inactive burrows by the presence of muddy water near a burrow opening (Brooks and Dodge 1981, 1986). However, muddy water is not always observed around active burrows (personal observation), and is likely to vary with stream flow and the size of sediment particles. Muskrat droppings are quite distinctive, being about 2 cm in length, ovoid and slightly curved, often agglutinated and showing a pinkish colour when fresh. Muskrat droppings are used for marking and are often laid on prominent objects (Errington 1963). Some of the muskrat feeding signs cannot be confused with feeding signs of other vertebrates. Muskrats often cut aquatic plant stems into small pieces that can be seen floating, or accumulated in piles on the shore or in the entrance of a muskrat burrow. Aquatic plant shoots with their basal portion eaten is also another muskrat feeding sign. Muskrats have been shown to feed on freshwater clams (Convey et al. 1989, Neves and Odom 1989, Chatelain and Chabot 1983). Bivalves consumed by muskrats have characteristic scratches on the periostracum of one valve, and the unbroken valve stays attached by the hinge ligament (Neves and Odom 1989). About nine centimetre wide runways (Murie 1974), that go from a water body to a nearby terrestrial food source (e.g. crop field), are a good indicator of muskrat presence (Errington 1963).

While few studies have produced muskrat habitat use models, many have been published on population dynamics of muskrats in various types of habitat. Most of these studies were descriptive, but few had experimental designs. Errington (1963), Perry (1982) and Boutin and Birkenholtz (1987) provide a good literature review. The following section is a review of the biotic and abiotic factors affecting muskrat distribution and movement.

III. Abiotic factors affecting muskrat distribution and movement

Abiotic factors have a considerable influence on muskrat ecology. They can be grouped under three main types: weather, water and substrate.

III.1. Weather

Air temperature is very important for muskrats, as is the case for any terrestrial mammalian species. The thermoneutral zone of muskrats lies between 10°C and 32°C (McEwan et al. 1974). Outside this range, muskrats spend extra energy to maintain physiological and physical activities. Air temperature seems also to be linked to spring dispersal and the onset of breeding (Olsen 1959, Erickson 1963, Danell 1978a). Time spent in lodges in the winter has been shown to be inversely related to air temperature (MacArthur 1980). Air temperature also has indirect effects on muskrat activity, behaviour, and population parameters, through its correlation with ice thickness, length of the growing season and vegetation.

Rainfall affects water level fluctuation, turbidity and vegetation, and has been shown to be positively correlated with muskrat activity in ditches (Stewart and Bider 1974). However, rainfall did not influence summer muskrat activity at Delta Marsh (MacArthur 1980).

In large water bodies, waves resulting from windy situations may have a negative influence on muskrat movement during the ice-free season. Wind may also have an indirect impact through its negative effect on aquatic vegetation (Errington 1963, Bergeron 1977, MacArthur 1977). Time spent in lodges by muskrats in the summer was inversely correlated with wind speed (MacArthur 1980).

III.2. Water

Although a minimum water level is required to maintain burrow entrances or house openings under water, muskrats are reluctant to leave their territories when water is almost absent (Errington 1963). Water depths of 30-90 cm in autumn were considered optimal values in marshes along the St. Lawrence River (Bélanger and Léveillé 1984). Water level under the ice in the winter should allow movements between shelter and feeding stations (Errington 1963; Hamerstrom and Blake 1939; Revin 1975). Freezing of wetlands is a major cause of mortality in temperate regions (McLeod et al. 1951, Olsen 1959, Errington 1963). In the Prairies, Yukon and Northwest Territories, optimal water depth in the fall would be 0.6-0.9 m between 53°N and 55°N, and around 1.8 m at 67°N (McLeod et al. 1947, Stevens 1953, Ambrock and Allison 1972). However, a water depth superior to the euphotic zone would not be suitable for the development of emergent vegetation (Environment Canada 1979). Ice thickness is maximal in small water bodies where water velocity is low (Adams and Roulet 1980), and in the winter, muskrats dig their burrows in deeper waters than in the summer (Jelinski 1984). When water levels decrease, muskrat density increases in areas where water is still present (Proulx and Gilbert 1983), which produces a greater negative impact on aquatic vegetation and modifies the vegetal succession (Fuller 1951). Droughts make muskrats more susceptible to predation (Proulx et al. 1987). On the other hand, flooding of burrows in the spring forces muskrats outside where they may suffer from frost and are more likely to be killed by predators (Bellrose and Brown 1941). The frequency of tidal flooding in a brackish marsh has been negatively associated with the number of litters and the number of young per litter (Kinler and Kinler 1990). Water level is also important due to its effect on vegetation. It is generally recognized that a water level of a few inches is necessary for good germination of emergent plants (Weller and Spatcher 1965, Weller 1978), that are important muskrat food items (see section IV.2.D). Emergent plants are the principal food resource for muskrats in the central and southern portion of their range from late fall to early spring. Hutchinson (1975) showed that the seeds of many species of aquatic plants are unable to withstand total desiccation. However, too high a water level will cause a decline of emergents (Errington 1963, Weller 1978). In an experimental study of flooding effects at Delta marsh, Manitoba, muskrat populations increased to more than 30 per hectare after the second growing season (Clark and Kroeker 1993). Many authors have observed the same phenomenon (Errington et al. 1963, Danell 1978a, Kroll and Meeks 1985). However, densities declined to less than one per hectare a year later after emergent vegetation cover had drastically declined. Many authors suggested that, at a given latitude, denser populations of muskrats occur in habitats with stable water levels (Bellrose and Brown 1941, Donohoe 1966, Thurber et al. 1991).

Crawford (1950) and Errington (1963) stated that muskrats prefer lentic water. In rivers, Brooks (1980) found 60% of the burrows where water velocity was < 16 cm/s. A river flow over 30 m^3/s would represent a poor habitat (Brooks and Dodge 1981). Chulick (1979) did not observe any difference in population density for streams varying in stream flow by up to 1600%, but his data still suggest a negative effect of water velocity.

The effect of water turbidity on muskrats, if it exists, is probably indirect, through effects on aquatic vegetation. High water turbidity would reduce the depth of the euphotic zone. While Crawford (1950) mentioned that turbid water was positively linked to muskrat abundance, others have observed an inverse relationship (Hunter and Bonds 1955, Errington 1963). The cause of water turbidity has to be detected before it can be used to predict muskrat abundance, as muskrat can create turbidity through its burrowing activities.

III.3. Substrate

Earhart (1969) found that fine-grained sediments composed of less than 43% sand represented good material for the maintenance of burrows. Danell (1978a) also observed more burrows where the substrate was made of fine-grained sediments than where coarse-grained sediments dominated. Brooks (1985) noted an absence of muskrat burrowing activity where sand and gravel exceeded 90%. Bider et al. (1976) showed that muskrat activity was higher in clay and muckland ditches than in sand ditches, while stony till ditches were not used. Errington (1937) mentioned that the presence of high clay banks is a requirement of stream muskrats. Particle size can also be correlated with vegetation type or density, and affect muskrat presence indirectly (Danell 1978a).

Banks need to be relatively steep (>30% in Ohio rivers, Gilfillan 1947; 20% in California ponds, Earhart 1969; 156% in rivers of Massachusetts, Brooks 1980) to allow muskrat to dig burrows higher than the mean high water mark. In northern latitudes, muskrat occupy burrows on steeper slopes in the winter than in the summer, as steep slopes accumulate more snow and thus have a thinner ice cover (Jelinski 1984). Gilfillan (1947) mentioned that bank height should always exceed 50 cm, while Brooks (1980) observed a mean value of 0.99 ± 0.65 m.

IV. Biotic factors affecting muskrat distribution and movement

Muskrat interactions with other living organisms could influence its distribution. These interactions can be grouped under three major headings: Intraspecific interactions, interactions with other animal species, and interactions with plant species.

IV.1. Intraspecific interactions

IV.1.A. Breeding

Several authors have presented convincing evidence that muskrats exhibit a certain level of monogamy (Stevens 1953, Sather 1958, Erickson 1963, Errington 1963, Mathiak 1966, Earhart 1969). However, this relationship has not been established with certainty. In mammals, polygyny is the most common mating system (Kleiman 1977).

Clay and Clark (1985) and Clark (1987) have shown that reproduction in adults and survival of juveniles were density dependent. Beer and Truax (1950) found that there was a significantly greater proportion of young males in a low density population than in a high density population of muskrats. Male muskrat breeding behaviour is likely to be influenced by habitat quality, the density of females, female behaviour and kinship (inbreeding avoidance), territorial male aggressiveness and the risks of being killed by a predator when travelling between female territories (Bengtsson 1978, Caley 1987). Barnard and Fitzsimons (1989) have shown that house mouse *(Mus musculus)* litter size at birth and post weaning increased with a decrease in parents kinship. For these reasons, and due to the possible costs of meiosis and breaking of co-adapted gene complexes, Caley (1987) has suggested that muskrats should optimally breed within a few home range diameters of their natal site.

Myllimaki (1977) suggested that overlap of home ranges also varied with density. Territorial behaviour, or the active defense of a home range (Burt 1943), has been inferred for Luther Marsh muskrats because of the non-overlapping nature of their home ranges (McDonnell and Gilbert 1981). Sather (1958) and Westworth (1974) also observed non-overlapping family home ranges, and Shanks and Arthur (1952) observed that stream-dwelling muskrats in Missouri were territorial. Erickson (1963) on the other hand, reported slight overlapping of home ranges in central New York, and Neal (1968) did not observe any evidence of territorial behaviour in muskrats. Although intraspecific aggression has been reported among muskrats in marsh populations (Errington 1963, Le Boulengé and Le Boulengé -Nguyen 1981), active defense and marking of territories (scat piles, scent posts) in rivers have not been observed (Brooks 1985). Minimal distances between muskrat dwellings were observed by Danell (1978b), but their distribution did not follow a regular distribution model. Errington (1963) noted that breeding territories expanded with decreasing population densities, but that in years of peak population, their centres could be separated by only 18 to 37 m. Messier et al. (1990) showed a distribution of dwellings that followed a despotic model under which some individuals seemed to inhabit a better quality habitat than others.

IV.1.B. Dispersal

Muskrat migratory movements, from 200 to 400 m, occur mainly in the spring (Coulter 1948, Erickson 1963, Dauphiné 1965, Caley 1987), although fall movements also occur (Errington 1963). Errington (1963) believed that spring dispersal was more a population adjustment phenomenon rather than any desire to travel, since individuals that find satisfactory breeding locations close to their wintering locations will usually remain there for the summer. The low availability of suitable habitats could probably explain long distance movements (Errington and Errington 1937, Wragg 1955). Muskrat home range is generally within a diameter of 200 m (Aldous 1947, Shanks and Arthur 1952, Krear 1953, Mathiak 1953, Sather 1958, Schmitke 1959, Mallach 1971, Westworth 1974). However, Stewart and Bider (1974) reported that female ditch-dwelling muskrats needed, on average, 365 m of ditch sections to maintain themselves. Several authors have observed that males migrate longer distances in the spring than females (Sather 1958, Errington 1963, Caley 1987). As the costs of pregnancy and lactation in rodents have been shown to double rodent energy requirements (Kaczmarski 1966, Migula 1969, Randolph et al. 1977, Millar 1978), a female migrating a short distance from its mother's territory to obtain a breeding territory would likely increase its reproductive output. This short distance dispersal would reduce the likelihood of incestuous breeding and reduce energy costs. Dispersal will be density dependent among mature animals although home range size would decrease, or overlap would increase, with increased muskrat density. In the spring, individuals born the previous year have two choices: (1) remain as non-reproductive floaters in the patch, wait for a home range owner to die, then compete for that home range with other floaters (Brown 1969), or (2) disperse in search of available space elsewhere. Mature animals that allow their offspring to remain on their breeding home range, as long as they remain sexually immature, will potentially have higher fitness: young should survive better on their natal home range than if they moved off, and eventually they will get their parents' breeding home range or home ranges of adjacent individuals as they die (Bondrup-Nielsen 1985). Juvenile muskrats generally stay near their mother's territory until the following spring (Errington 1963, Le Boulengé and Le Boulengé-Nguyen 1981, Caley 1987). In the winter, several adult muskrats may occupy the same burrow system (Errington 1963, MacArthur 1977). In the summer, adult females are highly intolerant to young other than their own while males are relatively tolerant (Le Boulengé and Le Boulengé-Nguyen 1981). Young muskrats are sometimes killed by congeners during the summer, most likely by adult females (Caley and Boutin 1985).

If, as observed by a few authors, the sex ratio in the spring is imbalanced in favour of males (Erickson 1963, Neal 1968, Parker and Maxwell 1980), males should disperse more than females to find a mate. In an experimental study, Wolff et al. (1988) showed that young male white-footed mice (*Peromyscus leucopus*) were preprogrammed to disperse, independently of density. This behaviour was thought to have evolved to avoid inbreeding. Caley (1987) has also shown that inbreeding avoidance between siblings is potentially responsible for the dispersal of young male muskrats. Muskrats could avoid inbreeding through a combination of short dispersal and kin recognition (Caley and Boutin 1987).

IV.2. Interactions with other animal species

IV.2.A. Competition

In the central and northern portion of their North American range, muskrat and beaver (*Castor canadensis*) are the only two semi-aquatic mammalian herbivores. Beavers eat aquatic plants, as do muskrats, but the relationship between both species is believed to be one of commensalism in favour of muskrats, probably because (1) their feeding habits do not overlap significantly (Boutin and Birkenholtz 1987), (2) beaver damming activities contribute to provide stable water levels, and (3) muskrats use both abandoned and active beaver dwellings (Hodgdon and Hunt 1955, Dauphiné 1965).

Within the last 50 years, wild populations of nutria (*Myocastor coypus*), a caviomorph rodent native to South America, have been established in Europe and North America where they occur in sympatry with muskrats (Aliev 1967). Since both muskrats and nutria prefer aquatic plants (Errington 1963), and because nutria are responsible for damage to native plant communities (Boorman and Fuller 1981), both species are likely to compete for food. However, nutria are not likely to extend their range into Canada because of their susceptibility to cold weather (Doncaster and Micol 1990). The absence of competing species or sympatric species reduces the necessity for muskrats to perform narrow habitat selection. Stewart and Kantrud (1972) observed that in periods of low water, grazing ungulates may trample stands of cattail, thereby lowering habitat quality for muskrats.

IV.2.B. Muskrats as predators

Although muskrats are mostly herbivorous (Perry 1982), they can sometimes consume clams, mussels, fish, and other available animal food (Errington 1963). The conditions under which muskrats become predators have not been the object of specific studies, but Errington (1963) believed that it was more likely to happen when the availability of adequate plant food items was reduced. In this case, predation would be more common in the winter and early spring. Muskrat predation rate on clams was shown to vary with clam size (Convey et al. 1989), and was identified as a cause of endangerment for some clam species (Neves and Odom 1989). On the other hand, accumulation of clam shells at muskrat feeding stations was shown to provide good spawning substrate for lake trout (*Salvelinus namaycush*) in gravel deficient habitat (Chatelain and Chabot 1983).

Caley and Boutin (1985) found evidence that adult muskrats could kill new born muskrats. However, killed animals were not consumed, which would indicate that they were not killed for food, but probably to decrease intraspecific competition.

IV.2.C. Predation and parasitism on muskrats

IV.2.C.1. Non-human predators

In its native range, the muskrat is preyed upon by mammalian, avian and reptilian predators (Errington 1963, Boutin and Birkenholtz 1987). However, the most important non-human predator is certainly the mink (*Mustela vison*) (Errington 1963, Boutin and Birkenholtz 1987), particularly when droughts reduce the possibility of muskrat escape and increase their density (Proulx et al. 1987). Bulmer (1975) even proposed that the mink's cycle was dependent on muskrat fluctuations, following it by 2.3 years. Danell (1985) has found that red fox predation on muskrats in Sweden increased when the cyclical population of voles was at a low level. Predation may exert an influence on the distribution of muskrats if it is not equal between different habitat types. For example, predation may explain why the use of upland habitats by muskrats has been documented only once (Clough 1987), in the isolated conditions of an island. Lacki et al. (1990) found that predator avoidance was likely to influence muskrat habitat use.

IV.2.C.2. Human predation

Trapping is probably the most important predatory agent on muskrat populations of agro-forested ecosystems, particularly when the price of a pelt is high. Muskrat is considered the most important furbearer in North America, because of the number of animals harvested each year and the species' widespread distribution (McCabe and Wolfe 1981). In the province of Quebec alone, the number of muskrats harvested in 1986 exceeded 350 000 (Mathieu, 1991). However, despite the high trapping pressure, muskrat populations appear relatively stable. This could be due to a combination of compensatory reproduction (Errington 1951, Olsen 1959), precocial breeding (Errington 1963) and increased survival in low density populations. Clark and Kroeker (1993) demonstrated that the per capita rate of increase at Delta Marsh, Manitoba, was negatively related to the density of animals in May. However, at Old Crow flats, Yukon, Simpson et al. (1989) did not observe any of the three mechanisms that would allow populations to remain stable after extensive mortality. This may be due to the relatively low density of the northern populations and the short growing season. The intensity of trapping in years of high pelt price is probably higher in easily accessible areas and in areas of dense muskrat populations, and may thus have an influence on muskrat distribution by reducing survival rate in better habitats (Chulick 1979).

IV.2.C.3. Parasitism

Extensive mortality in muskrats has occurred as a result of tularaemia (*Pasteurella tularensis*) and the haemorrhagic disease (Errington 1963). Chulick (1979) observed that the incidence of *Cysticercus fasciolaris*, a larval stage of *Taenia taeniaeformis* present in the liver, was greatest in muskrats in the vicinity of a golf course, where higher occurrence of the parasite may have been due to recipient waters from a sewage system.

IV.2.D. Interactions with plant species

During the summer months, muskrats eat almost any kind of herbaceous plants, reflecting the floristic composition of the surrounding stands (Gashwiler 1948, Smith 1954, Dauphiné 1965, Proulx and Gilbert 1983) and seasonal choices (Butler 1940; Takos 1947). Mousseau and Beaumont (1981) listed 167 species eaten by muskrats. Lacki et al. (1990) showed that broadleaf cattail (*Typha latifolia*) was present in food beds in proportions almost equal to its availability, while other species such as sedges (*Carex* spp. and *Cyperus* spp.) and *Potentilla palustris* were present in proportions lower than their availability. Dauphiné (1965) observed that sedge was the main summer food item in bog-like marshes, alder-choked creeks and barren glacial lakes. According to Errington (1963), muskrats of northern United States usually showed the greatest responsiveness to cattails, while bulrushes (e.g. *Scirpus olneyi*) were preferred in southern coastal marshes. These two species can be used as food items or to build lodges. Other species that may attract muskrats to a particular wetland area include: American water plantain (*Alisma* spp.), burreed (*Sparganium* spp.), arrowhead (*Sagittaria* spp.), sago pondweed (*Potamogeton* spp.), and wild rice (*Zizania aquatica*) (Mousseau and Beaumont 1981). Food was shown to be determinant in summer habitat selection (Jelinski 1984). In northern latitudes, during the summer, muskrat burrows were closer to emergent stands than in the winter months when muskrats relocalized in deeper water where they relied more on submerged plants (Westworth 1974, Jelinski 1984). Boyd (1978) showed that freshwater plants generally contained large amounts of proteins that could be required in winter to allow year-old muskrats to breed the following spring (Errington 1941). In 1937, Errington reported that shallow creeks abounded with muskrats when stream banks and margins of adjacent fields were covered with dense vegetation. Jelinski (1984) observed that muskrat dwellings were not located in large, dense, monotypic stands of emergents, despite their value as a good food source. This may have been due to the modification of the plant community structure by muskrats (see section I.1).

According to Errington (1963), the best all-around food for midwestern muskrats was cultivated ear corn. Errington (1963) reported that stream-dwelling muskrats selected areas with a high abundance of corn. Chulick (1979) suggested that the presence of corn attracted muskrats to habitat with coarse-textured soil and sparse aquatic vegetation. Corn was heavily utilized in the summer and fall, when corn fields were within 10 m of a stream (Chulick 1979). However, Robert Foley (pers comm.) found fewer active burrows in ditches adjacent to corn fields in New York State than in more natural ditches.

Seasonal changes in muskrat feeding habits are expected since nutrient extraction by herbivores was shown to be inversely related to the fibre content of the plant, and that lignin content was shown to increase with the age of plant tissues (Lacki et al. 1990). Muskrat digestion of fibres is comparable to digestion by many ruminants and pseudoruminants, and is more efficient than digestion in other rodents (Campbell and MacArthur 1994).

V. Effects of the environment on muskrat morphology and health

Muskrats were smaller when the quantity and quality of available foliage was reduced (Dozier et al. 1948, Cook 1952, Alexander 1955, Errington 1963, Dauphiné 1965). McCullough (1951) observed a decrease in body size in response to intraspecific food competition. Chulick (1979) found that the largest animals occupied streams flowing within 50 m of corn fields. In these streams, muskrats exhibited the highest body weight/body length and percentage of kidney fat, and the lowest ratios of adrenal weight/body weight, heart/body weight, and liver/body weight (Chulick 1979). The adequacy of food supply has been related to the maturation of testis, quality of pelage, and physical development of the young (Errington 1941, Grimm 1941, Chulick 1979). Pankakoski (1985) and Pankakoski et al. (1987) showed that poor muskrat growth index, probably related to environmental factors, was related to increased variability in skull morphology. Crawford (1950) observed a positive correlation between soil fertility and muskrat body size, and quality and size of pelt. Conversely, Chulick (1979) did not observe a greater abundance of muskrats or individuals with better physical condition where soil was more fertile, although soil fertility could affect muskrats through its effect on vegetation.

Boyce (1977) found that muskrat body size was largest in regions of high annual precipitation and low seasonality in rainfall patterns. Boyce (1977) further hypothesized that small body size, being correlated with lower energy requirements, allows muskrats to survive in periods of food shortage. Winter is not necessarily a period of food shortage since Jelinski (1984) showed that the percentage of adult muskrat body fat was higher in the winter than in the summer. Dauphiné (1965) also found that small body size in Adirondack muskrats was associated with pronounced water level fluctuations and poor food quantity and quality.

A few studies have tested the usefulness of the muskrat as an indicator of environmental pollution. The results of these studies are conflicting and vary with the pollutant (Everett and Anthony 1976, Sheffy 1977, Chulick 1979, Erickson and Lindzey 1983, Radvanyi and Shaw 1981, Blus et al. 1987, Halbrook 1990). Only Halbrook (1990) studied the effects of pollutants (14 polynuclear aromatic hydrocarbon and 33 heavy metals) on muskrat physiology, body condition and population parameters. No effect on density and reproductive rates and no overt signs of toxicity were detected, but the mean total carcass and spleen weights were lower in the most polluted area. The incidence of disease may also have been higher in this area. However, the author concluded that the influence of contaminants on muskrats appeared minimal, and that the values for over 80% of the heavy metals detected in both sediments and muskrat tissues were not correlated (Halbrook 1990). The concentrations of heavy metals were found to be higher in plants than in muskrats of the same area, suggesting that biomagnification of heavy metals did not occur in muskrats (Everett and Anthony 1976).

VI. Effect of the environment on muskrat population parameters

While the density of muskrats in creeks, streams, and rivers bordered by crop fields has been reported to range from 23 to 40 per kilometre (Errington 1940, Chulick 1979, Brooks and Dodge 1986), it was observed to range from only 8 to 14 per kilometre in inferior habitats (Byrd 1951, Smith 1954, Dauphiné 1965). The density of muskrat burrows varies greatly between habitats (see Table 1.1), probably due to the associated biophysical characteristics.

Juvenile mortality during the growing season has been shown to vary from 20% to 57.5% in various habitats (Smith 1954; Dauphiné 1965; Proulx and Buckland 1986; Clough 1987) and annual survival of juveniles to vary from 8.5% to 35.9% (Stewart and Bider 1974; Le Boulengé and Le Boulengé-Nguyen 1981; Proulx and Gilbert 1983; ; Clark 1987; Simpson 1987; Boutin et al. 1988). Summer juvenile mortality was greater in creeks, then in ditches, ponds, and rivers (Proulx and Buckland 1986). Survival of juvenile muskrats was shown to be higher in Yukon than in Ontario (Simpson 1987). Annual survival of adult muskrats has also been shown to vary from 5.8% to 20% in riverine environments (Le Boulengé and Le Boulengé-Nguyen 1981; Clay and Clark 1985; Clark 1987). Clay and Clark (1985) have reported that the annual mortality rate was higher in adults than in juveniles. The proportion of juveniles versus adults in a population was shown to vary between 66 and 91% at different times of the year (Donohoe 1966; Mathiak 1966; Parker and Maxwell 1980; Dauphiné 1965). Much lower values were obtained for strip-mine ponds (43% - Arata 1959) and untrapped rivers exhibiting low quality habitat (41% - Halbrook 1990). Errington (1943) and Beer and Truax (1950) found low percentages of young after years of light trapping. In normal conditions of water level at Delta Marsh, annual survival of muskrats of all ages was shown to be as low as 3.1% (Clark and Kroeker 1993).

Erickson (1963) obtained an average growth rate value of 5.34 ± 0.1 g/day from captive muskrats, while a value of about 5 g/day was obtained by Vincent and Quéré (1972) in drainage ditches and ponds of Belgium, and a value of 4 g/day was obtained by Simpson (1987) in lakes of northern Yukon. Higher values were obtained in Ontario (7.1-8.84 g/day; Simpson 1987) and New Brunswick marshes (7.1-7.5 g/day; Parker and Maxwell 1984).

However, a growth rate value of 4.2 g/day has also been reported for an Ontario marsh (Simpson 1987).

While the review by Smith et al. (1981) describes how litter size could be affected by cyclic patterns, habitat quality, age and time of year, Clay and Clark (1985) detected no influence of habitat type on litter size. Evidence is also conflicting as to whether or not muskrat litter size increases with latitude (Boyce 1977; Simpson 1987). The percentage of adults and the number of litters per adult female were shown to decrease with latitude, while the number of young per adult female was shown to increase with latitude (Boyce 1977; Simpson 1987). The average reported number of litters per adult resident female in populations experiencing a cold winter season is around two (See reviews by Clough 1987 and Dauphiné 1965), whereas muskrats occupying terrestrial habitats had a much lower average of 1.4 litters per adult female (Clough 1987). Litter size, and the number of litters per adult female, were shown to be low in low-quality habitats (Arata 1959; Errington et al. 1963; Proulx and Buckland 1986; Dauphiné 1965). Boutin et al. (1988) showed that there was no trade-off between litter size and juvenile survival.

According to Chulick (1979) and Halbrook (1990), female productivity is not related to habitat quality. On the other hand, the difference in muskrat reproductive efforts between Tiny Marsh (Ontario) and Old Crow Flats (Yukon Territory) was believed to be due to a difference in habitat quality (Simpson 1987).

A number of studies show that the sex ratio of juveniles ranges from 54.5% to 71.4% males, and the sex ratio of adults from 45.5% to 65.0% males (Mathiak 1966; Parker and Maxwell 1980; Caley 1987; Halbrook 1990; review by Dauphiné 1965). Several explanations have been put forward for these unbalanced sex ratios, such as a difference in the probability of capture between sexes, although this was denied by studies of Beer and Truax (1950) and Caley (1987); and a difference in mortality and/or migration rates between males and females. The study by Caley (1987) also suggests that more males are produced, for unknown reasons. Other studies have shown conflicting evidence that the frequency of males could be higher in poorer habitats or in habitats where density was low (Beer and Truax 1950; Neal 1968; Chulick 1979) as well as in early born litters (Gashwiler 1950; Olsen 1959).

In brief, within its semi-aquatic habitat, muskrat life history traits are mostly influenced by genetically determined requirements of the species, and by a range of biotic and abiotic factors. However, the general distribution of the species reflects its ability to thrive in a multitude of environmental conditions.

Table 1.1 Number of muskrat burrows per kilometre of shoreline in various wetland types.

Wetland	Number of burrows/km	Area	Reference
creek	27.9 ± 24.7[1]	Pennsylvania	Chulick 1979
farmland stream	28-38	Iowa	Errington 1940
river in glaciated area	5.96 ± 0.63	Northern Massachusetts	Brooks 1985
river in unglaciated area	5.7 ± 0.73	Northern Massachusetts	Brooks 1985
river	14	Sweden	Danell 1978b
shallow lake and sheltered seashore	5	Sweden	Danell 1978b
shallow lake summer 1982	4.7 ± 4.0	Northwest Territories	Jelinski 1984
shallow lake winter 1982	5.9 ± 3.5	Northwest Territories	Jelinski 1984
shallow lake summer 1983	6.0 ± 3.8	Northwest Territories	Jelinski 1984
strip mine pond	7.9	Illinois	Arata 1959
marsh	11 - 23	Saskatchewan	Messier et al. 1990
marsh	11.4	Southern Ontario	Proulx & Gilbert 1983
flooded sand pit	23.3 ± 7.8	Southern Quebec	Blanchette 1985
pond	18.4 ± 10.5	Southern Quebec	Blanchette 1985
artificial island	4.3 ± 4.5	Southern Quebec	Blanchette 1985
exposed seashore	0	Sweden	Danell 1978b

[1] In this thesis, "number ± number" represents Mean ± Standard Deviation

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As shown in the first chapter, a variety of environmental factors may affect muskrat populations. But the question *Does the presence of different crops along ditches influence muskrat habitat use ?* has not been answered. The second chapter of this thesis presents a habitat use model built with muskrat signs of presence data collected along southwestern Quebec farm ditches. I tested the influence of adjacent crops on muskrat habitat use. Conditions of soil and bank slope were optimal and were assumed not to influence muskrat habitat use. Bordering crops can provide food to muskrats, but different crops could require different farming techniques implying a different frequency of dredging, use of herbicides, timing of ploughing and erosion rate, etc... The importance of crops to muskrats has been reported by a few authors (Errington 1937, 1938, 1940, 1941, 1963; Chulick 1979; R. Foley, Pers. comm.) but has never been tested. Frequency of muskrat consumption of different crops was also examined.

CHAPTER TWO

Muskrat habitat use in farm ditches

ABSTRACT

We studied how crop types adjacent to farm ditches in southwestern Quebec influenced muskrat (*Ondatra zibethicus*) habitat use. Conditions of soil and bank slope were optimal and similar in all ditches. Muskrat signs of presence were used to build logistic regressions on biophysical characteristics. The density of burrows (37.4/km) was among the highest recorded in the literature. Muskrat signs of presence were positively linked to water depth and to surface covered by pulpy hydrophytes, excluding cattail, although pulpy vegetation cover was not selected in models that were based on the presence of burrows only. An unexpected positive relationship between muskrat presence and water velocity was observed, that could be explained by a lower mean velocity (2.8 ± 4.5 m/min) than the maximal value for muskrat presence of 10 m/min established by Brooks and Dodge (1981). Dredging of ditches was negatively linked to muskrat presence. Despite a positive association between muskrat presence in ditches and the presence of alfalfa (*Medicago sativa*) in adjacent fields, muskrat probability of presence was not significantly influenced by the type of crop bordering ditches. Muskrat consumption of crop plants (in 10.2% of the sections) did not vary significantly when compared among alfalfa, cereal and corn (*Zea mays*) crops.

Key words: farm ditches, habitat use, logistic regression, muskrat, *Ondatra zibethicus*, Quebec.

INTRODUCTION

Drainage ditches are often the dominant component of hydrographic systems in agricultural landscapes. In previously published studies of muskrat populations, farm ditches have received little attention (Errington 1937, 1940, Vincent and Quéré 1972, Stewart and Bider 1974, 1977, Chulick 1979, Proulx and Buckland 1986). Drainage ditches are often temporary wetlands, from which sufficient reliable data on associated transient animal populations are difficult to acquire. To date, models of muskrat habitat use have been published for rivers only (Brooks and Dodge 1981, 1986). In such models, the percentage of open and agricultural land per site was significant (Brooks and Dodge 1981, 1986). Moreover, Errington (1937) stated that farm ditches may abound with muskrats if stream banks and margins of adjacent fields are covered with dense vegetation.

In terms of the type of vegetation, Errington (1937) hypothesized that corn fields may be essential constituents of Iowa's best muskrat streams. Chulick (1989) observed a higher density of muskrat burrows in creek sections bordered by corn fields than in sections bordered by a golf course, grazed pastures, or forested lands, and these differences could not be accounted for by the proportion of clay in bank soil. Bordering crops can provide food to muskrats, but different crops can require different farming techniques including different frequencies of dredging, use of herbicides, timing of ploughing, and influence on erosion rates. Even though the importance of crops to muskrats has been reported by a few authors (Errington 1937, 1938, 1940, 1941, 1963, Chulick 1979, R. Foley, Pers. comm.), this factor has never been tested.

In this study, we investigated the importance of biophysical characteristics of farm ditches of the mid-northern hardwoods eco-zone on muskrat habitat use, based on muskrat signs of presence, with special emphasis on adjacent crops. The frequency of muskrat consumption of different crops was also examined.

METHODS

STUDY AREA

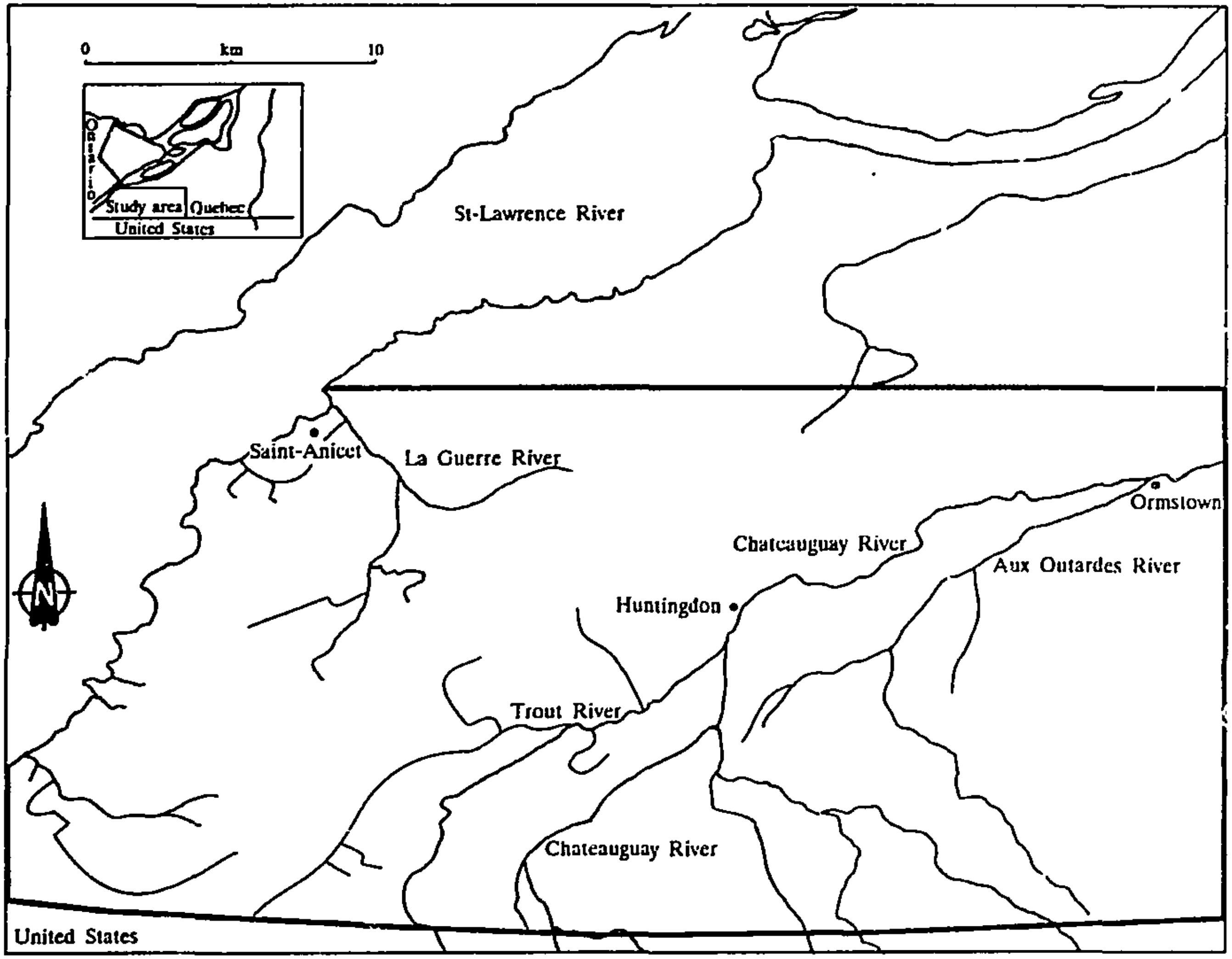
The study area was located in the southernmost part of Quebec, 60 km southwest of Montreal, along the New York State border (Figure 2 1). It extended from latitudes of 45°00' to 45°10' and from longitudes of 74°00' to 74°30'. The study area covered 648 km^2. Two main river systems drain the area: the Trout, Chateauguay, and Aux Outardes system, and the La Guerre River. A few ditches drain directly into the St. Lawrence River. While corn fields were dominant along ditches, other crops such as wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), soya (*Glycine max*), alfalfa (*Medicago sativa*) and hay were common. Crop rotation was observed a few times. Vegetation cover adjacent to ditches varied with the type of crop, and whether it was annual or perennial. Very few ditches were bordered with small trees and shrubs.

FIELD WORK

Sampling periods extended from 16 May to 16 August, 1989, and from 22 May to 23 August, 1990, after the macrophyte communities were judged to be well developed. From the northernmost and southernmost points of the study area, farm ditches with a water depth exceeding 10 cm were selected as encountered. As annual crops were dominant in the study area, ditches bordered by perennial crops were searched in particular.

The presence of muskrat burrows was determined on ditch sections of 75 m by two observers probing both submerged banks with their feet. Other muskrat signs recorded visually were droppings, browsing, tracks, runways or the animal itself (as in Murie 1974). We also recorded the number of 15 m long segments within each 75-m ditch section that showed other vertebrate signs of presence.

Figure 2.1 Study area in southwestern Quebec, where 468 ditch sections of 75 m length, from 56 different ditches, were sampled for muskrat signs and biophysical muskrat habitat variables, in the summers of 1989 and 1990.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Aux Outardes River
Huntingdon
Trout River
Chateauguay River
United States

These were: tracks or droppings for raccoon (*Procyon lotor*), mink (*Mustela vison*), and canidae (*Canis familiaris*, *Canis latrans*, *Vulpes velox*), and dams, burrows, cut trees and barkless limbs and with rodent tooth marks for beaver (*Castor canadensis*)(as in Murie 1974). A two-day training period at the beginning of each year allowed familiarization of the new observer with muskrat and other vertebrate signs of presence. The author regularly verified the validity of the signs recorded by the other observer. Each successive 75 m section was sampled until 150 m beyond the point where water level was lower than 5 cm or when the ditch joined a river.

Habitat variables were measured or estimated by the author only, and included physical characteristics directly measured at the central point of the section. These were: (1) water depth at the centre of the main channel (cm), (2) width of the waterway (m), (3) mean bank height of both shores from water level (m), (4) mean width of the non-cultivated belt on both shores from water edge (m), and (5) water velocity at the centre of the main water channel (m/min). Water velocity was measured using a five cm long wood cylinder of one cm in diameter, removing any object that could have altered the course of the floating wood cylinder, and measuring the distance travelled by the cylinder in one minute..

As rainfall can influence water level and velocity, we did not sample ditches if there were obvious signs that water level had recently increased after rainfall. Water level is likely to decrease during the course of the summer due to lower precipitation and increased temperatures. We chose to measure water level only once, at the same time as data on presence indices were taken. Due to limited resources, it was not feasible to measure water level in all sections used in the analysis over a short period of time, and we preferred to record habitat data, including water level data, and animal sign data, simultaneously.

Habitat variables describing the whole 75 m section were: (1) presence or absence (p-a) of water pools, (2) recent dredging of the ditch (p-a), (3) evidence of herbicide application on ditch vegetation (p-a), (4) presence of shrubs or trees (p-a) and (5) adjacent crops or land use (corn, pasture, oat, wheat, soya, barley, hay, alfalfa, perennial crop, fallow land, road, railway recorded in 3 categories: 0 = absent, 1 = present on one side of the ditch, 2 = present on both sides). The variables evaluated on the whole central 15 m section were: (1)

plant cover on banks and in channel (ditch plant cover), (2) total hydrophyte surface cover (hydrophyte cover), and (3) surface covered by various plant species in five categories (0 = 0%, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%). These included: cattail (*Typha latifolia*), reed grass (*Phragmites communis*), great bulrush (*Scirpus validus*), arrowhead (*Sagittaria* spp.), American water plantain (*Alisma* spp.), wild rice (*Zizania aquatica*), flowering-rush (*Butomus umbellatus*), giant bur-reed (*Sparganium eurycarpum*), rice cut-grass (*Leersia oryzoides*), purple loosestrife (*Lythrum salicaria*), river horsetail (*Equisetum fluviatile*), pondweed (*Potamogeton* spp.), smartweed (*Polygonum* spp.), climbing nightshade (*Solanum dulcamara*), cape touch-me-not (*Impatiens capensis*), spearmint (*Mentha spicata*), swamp spike-rush (*Eleocharis smallii*), common duckweed (*Lemna minor*), macroscopic algae, and unidentified graminaceous plants. We also created a variable, hereafter referred as "pulpy plant cover", representing the sum of the surface cover indices by the following plant species: reed grass, great bulrush, arrowhead, American water plantain, wild rice, flowering-rush, and giant bur-reed. These species, known to be used by muskrat (see review by Mousseau and Beaumont 1981), were grouped since individually they rarely covered more than 25% of the water course section, but they often did altogether. In the sections sampled in May (less than 5% of the sample), wild rice (*Zizania aquatica*, a plant species considered rare in Quebec according to Fleurbec (1987) may not have been detected due to its slow development. However, this situation was not believed to have occurred for other species, and using broad categories of cover should reduce considerably the chance that recorded values are affected by seasonal changes in vegetation development. In the literature, the recorded habitat variables were found to be significant to muskrat in farm ditches, or were thought to be potentially important (see sections II, II.2, and IV.2.D in Chapter one).

Bank slope was always greater than 45° and was similar among ditches; this variable was therefore not considered. Soil was almost always composed of clay or clay-loam, an optimum substrate for the maintenance of burrows (Earhart 1969). The few ditches encountered that were in gravel soil were discarded. Only one section every 150 m was used to build muskrat habitat use models, to minimize the effect of autocorrelation between sections (Legendre and Legendre 1983).

STATISTICAL ANALYSES

We followed the methodology proposed by Brennan et al. (1986) in order to generate a habitat use model using a minimum number of significant variables. We ran all the quantitative habitat variables (water depth in centre of main channel, width of waterway, mean bank height of both shores from water level, mean width of non-cultivated belt on both shores from water edge, and water velocity in centre of main water channel) through Wilcoxon two-sample tests, using muskrat presence/absence as the dependent variable.

Categorical habitat variables were tested for muskrat presence/absence using Chi-square tests for multiple category variables, and Fisher's exact tests for 2 X 2 frequency tables (habitat variable in presence/absence, and muskrat presence/absence). The variables "ditch plant cover", "hydrophyte cover" and "cattail cover" were tested using the five cover categories in which they were recorded. The variable "pulpy plant cover" was tested using three categories representing the sum of cover indices (0, 1-4, 5-8). Cover by rice cut-grass was tested using four categories (0, 1, 2-3, 4). Cover by American water plantain and macroscopic algae were each tested using three categories (0, 1, 2-3-4). The effect of presence of adjacent corn field, alfalfa field and perennial crop (hay, alfalfa, clover *Trifolium* spp.) were each tested with a Chi-square test, using the three categories in which the crop variables were recorded. Presence of raccoon was also tested using a Chi-square test (4 categories: 0, 1, 2, 3-5 15-m long sections with raccoon presence), with presence-absence of muskrat signs of presence as the dependent variable. The effects of other habitat variables on muskrat presence/ absence were tested using 2 X 2 frequency tables, due to insufficient sample size in many categories (to respect statistical requirements of the Chi-square test - Scherrer 1984). Presence of mink, canidae and beaver were each tested using 2 X 2 frequency tables and Fisher's exact tests ("other vertebrates" variable in presence/absence, and muskrat presence/absence). Only significant variables at $\underline{P} < 0.15$ were kept for further investigation. The elimination of insignificant variables using univariate tests at a probability threshold greater than 0.05 prior to developing the logistic regression model was recommended by Hosmer and Lemeshow (1989). Kendall correlations were then calculated between the remaining variables. Two variables were considered redundant when showing a significant ($P < 0.05$) $\text{tau}_b > 0.40$. Between each pair of redundant variables, we retained only the variable that showed the lowest probability in previous univariate tests. A stepwise logistic regression model ($p=0.05$ for entry in and for exclusion from the model) was then produced using the remaining habitat variables and muskrat presence/absence. The form of a logistic regression is the following: $E(Y|x) = (e^{Bo+B1x}/1+e^{Bo+B1x}) + e$ where e = error or deviation from the conditional mean, and follows a binary distribution. In a linear regression, the method to identify the unknown parameters Bo and B1 is the least squares between the regression line and data points. In the logistic regression, the method is called maximum likelihood = -2 log likelihood = the summation of the probability that each observation is predicted by the regression curve multiplied by the weight of each observation. This statistic follows a chi-square distribution, and the probability is used to test the difference between model in step t and model in step t+1. In addition, a variable can be added to the model only if its Wald Chi-square is significant (square of the parameter estimate divided by its standard error) at the significance threshold. A variable entered at a given step can be deleted in ulterior steps if it is no longer significant for the model (Hosmer and Lemeshow 1989).

In order to assess the descriptive power of the model, we used the Index of rank correlation C between observed responses and predicted probabilities (SAS Institute Inc 1990). We verified the classification stability of the model by calculating the predicted probabilities of muskrat presence in ditch sections that were not used to generate the model. A probability over 0.5 was considered as muskrat presence, and the percentage of correct predicted probabilities was computed.

We repeated all the above steps, using the presence-absence of muskrat burrows as the dependent variable, to investigate the effect of an index of longer-term use on the variables selected in a model of habitat use.

The presence of muskrats was compared among crops using a Chi-square test. Due to insufficient sample size, and to the presence of different crops on both sides of ditch sections, five categories were used: (1) alfalfa or hay on both sides, (2) alfalfa or hay on one side and corn or cereals on the other side, (3) alfalfa or hay on one side and either a railway, a road or fallow land on the other side, (4) corn or cereal on both sides, and (5) corn on one side and either a railway, a road or fallow land on the other side. The abundance of muskrat burrows between perennial and non-perennial crops was compared using an univariate analysis of variance. Presence/absence of muskrat consumption of crop species in 75-m long ditch sections was compared among alfalfa, cereal and corn fields using a Chi-square test. Hay fields were not included in the analysis because we could not differentiate consumption of plants in hay fields from the consumption of plants on the banks.

RESULTS

Data on muskrat habitat use were collected in 56 ditches over a linear distance of 35.1 km. Water depth averaged 20.5 ± 20.8 cm and channel width averaged 2.4 ± 1.8 m in the sampled sections (Table 2.1). Water velocity was low at 2.8 ± 4.5 m/min, with 94% of the sections showing a water velocity below 10 m/min (Table 2.1). Bank height was characteristic of good drainage ditches, averaging 1.47 ± 0.45 m. The mean width of the non-harvested belt from the edge of the water channel was 3.70 ± 1.42 m (Table 2.1).

ALL SIGNS OF PRESENCE

Signs of muskrat presence were detected in 76% of the 75-m sections used for model building. Muskrat presence did not change with adjacent crop type (chi square test, $\chi^2 = 2.579$, 4 df, $\underline{P} = 0.631$). Of the 47 variables tested with univariate tests, 17 were significantly related to muskrat presence (Table 2.2). Four variables were not considered for the logistic regression, because of their correlation with other variables that showed higher significance in univariate tests on muskrat presence. These four variables were: total hydrophyte cover (correlated with cattail cover: Kendall $\tau_b = 0.4726$ $\underline{P} = 0.0001$), arrowhead cover (correlated with pulpy plant cover: Kendall $\tau_b = 0.4159$ $\underline{P} = 0.0001$), width of non-cultivated belt (correlated with bank height: Kendall $\tau_b = 0.4227$ $\underline{P} = 0.0001$) and width of the water channel (correlated with water depth: Kendall $\tau_b = 0.5182$ $\underline{P} < 0.0001$). Beaver presence was positively associated with muskrat presence, but since biophysical variables measured are thought to represent all important biophysical conditions modified by beaver activity, the "presence of beaver" variable was not considered for the regression. All other significant variables (Table 2.2) were included for consideration by the model. Four variables were selected by the logistic regression to explain the presence-absence of muskrat: dredging of the ditch, water depth, water velocity, and pulpy plant cover (Table 2.3).

Table 2.1 Range of values for variables recorded in ditch sections.

Variable	Min.	Max.	Mean	Standard deviation
Water depth (cm)	0	240	20.51	20.80
Water channel width (cm)	0	1060	239.04	181.89
Width of the non-cultivated belt (cm)	30	925	370.57	141.77
Bank height (cm)	40	405	147.56	44.73
Number of pools	0	2	0.05	0.23
Dredged ditch (p/a)	0	1	0.04	0.20
Herbicide (p/a)	0	1	0.01	0.11
Water velocity (m/min)	0	24	2.80	4.47
Hydrophyte cover[1]	0	4	2.79	1.29
Pulpy plants cover	0	8	1.91	1.76
Cattail[1]	0	4	1.26	1.44
Reed grass[1]	0	4	0.06	0.42
Great bulrush[1]	0	3	0.14	0.40
Other graminaceous[1]	0	4	0.60	1.07
Rice cut-grass[1]	0	4	0.77	1.27
Arrowhead[1]	0	4	0.40	0.65
Purple loosestrife[1]	0	1	0.13	0.34
River horsetail[1]	0	3	0.09	0.35
Pondweed[1]	0	3	0.10	0.43
Tree (p/a)	0	4	0.31	0.73
Smarthweed[1]	0	1	0.02	0.15
Climbing nightshade[1]	0	2	0.05	0.27
Cape touch-me-not[1]	0	1	0.05	0.22
Alisma water plantain[1]	0	4	0.51	0.70
Spearmint[1]	0	3	0.11	0.40
Swamp spike-rush[1]	0	3	0.06	0.35

Table 2.1 Cont. Range of values for variables recorded in ditch sections.

Variable	Min.	Max.	Mean	Standard deviation
Wild rice[1]	0	4	0.13	0.57
Flowering-rush[1]	0	4	0.16	0.58
Giant bur-reed[1]	0	4	0.32	0.79
Common duckweed[1]	0	4	0.13	0.57
Algae[1]	0	4	0.77	1.35
Ditch plant cover[1]	0	4	2.90	1.20
Corn (p/a)	0	1	0.52	0.50
Pasture (p/a)	0	1	0.01	0.08
Hay (p/a)	0	1	0.36	0.48
Alfalfa (p/a)	0	1	0.24	0.43
Oat (p/a)	0	1	0.02	0.15
Wheat (p/a)	0	1	0.09	0.29
Soybean (p/a)	0	1	0.01	0.11
Barley (p/a)	0	1	0.09	0.29
Road (p/a)	0	1	0.07	0.26
Railway (p/a)	0	1	0.03	0.18
Fallow land (p/a)	0	1	0.01	0.11
Mink[2]	0	4	0.09	0.48
Raccoon[2]	0	5	0.66	1.26
Canidae[2]	0	5	0.06	0.43
Deer[2]	0	3	0.10	0.37
Beaver[2]	0	3	0.07	0.35
Woodchuck[2]	0	1	0.03	0.17
Turtle[2]	0	1	0.02	0.15
Garter snake[2]	0	1	0.01	0.08

Table 2.1 Cont. Range of values for variables recorded in ditch sections.

Variable	Min.	Max.	Mean	Standard deviation
Frog[2]	0	5	0.25	0.71
Fish[2]	0	1	0.04	0.20
Subsections of 15 m showing muskrat browsing signs[2]	0	5	1.24	1.59
Number of muskrat browsing signs	0	17	2.19	3.14
Subsections of 15 m showing muskrat droppings[2]	0	4	0.28	0.71
Subsections of 15 m showing muskrat tracks[2]	0	5	0.34	1.02
Subsections of 15 m showing muskrat burrows[2]	0	5	1.39	1.52
Number of muskrat burrows	0	29	2.89	4.47
Subsections of 15 m showing muskrat runways[2]	0	5	0.19	0.80

[1] Data were recorded in five categories: 0 = 0%, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%

[2] Data represent the number of subsections of 15 m, within the 75-m section, that showed signs of presence for the species.

Table 2.2 Significance of habitat variables for muskrat presence (all signs) and presence of burrows in selected farm ditches of southern Quebec during summers 1989-1990.

	All signs of presence		Presence of a burrow	
Variable	Test	P*	Test	P*
Ditch plant cover	$\chi^2 = 4.082$	0.395	$\chi^2 = 7.806$	0.099 -
Hydrophyte cover	$\chi^2 = 8.8$	0.066 +	$\chi^2 = 11.7$	0.019 +
Pulpy plant cover	$\chi^2 = 10.6$	0.005 +	$\chi^2 = 5.0$	0.083 +
Cattail	$\chi^2 = 11.7$	0.019 –	$\chi^2 = 13.3$	0.010 –
Wild rice	Fisher's	0.298	Fisher's	0.016 +
Great bulrush	Fisher's	0.017 +	Fisher's	0.268
Arrowhead	Fisher's	0.005 +	Fisher's	0.016 +
River horsetail	Fisher's	0.072 +	Fisher's	0.001 +
Pondweed	Fisher's	0.072 +	Fisher's	0.763
Flowering-rush	Fisher's	0.014 +	Fisher's	0.129 +
Giant bur-reed	Fisher's	0.044 +	Fisher's	0.024 +
Smartweed	Fisher's	0.043 –	Fisher's	0.308
Reed grass	Fisher's	1.000	Fisher's	0.650
Rice cut-grass	$\chi^2 = 1.695$	0.638	$\chi^2 = 2.673$	0.445
Other graminaceous	Fisher's	1.000	Fisher's	1.000
Purple loosestrife	Fisher's	1.000	Fisher's	0.485
Tree	Fisher's	0.823	Fisher's	0.445
C. nightshade	Fisher's	0.672	Fisher's	0.701
Cape touch-me-not	Fisher's	1.000	Fisher's	0.737
A. water plantain	$\chi^2 = 0.230$	0.891	$\chi^2 = 0.358$	0.836
Spearmint	Fisher's	0.765	Fisher's	0.596
Swamp spike-rush	Fisher's	1.000	Fisher's	0.403
Common duckweed	Fisher's	0.734	Fisher's	0.763
Algae	$\chi^2 = 1.784$	0.410	$\chi^2 = 3.605$	0.165
Corn	$\chi^2 = 1.139$	0.566	$\chi^2 = 1.180$	0.554

Table 2.2 Cont. Significance of habitat variables for muskrat presence (all signs) and presence of burrows in selected farm ditches of southern Quebec during summers 1989-1990.

	All indices of presence		Presence of burrow	
Variable	Test	P*	Test	P*
Pasture	Fisher's	1.000	Fisher's	1.000
Oat	Fisher's	1.000	Fisher's	0.308
Wheat	Fisher's	0.765	Fisher's	1.000
Soya	Fisher's	0.421	Fisher's	1.000
Barley	Fisher's	1.000	Fisher's	0.437
Road	Fisher's	0.736	Fisher's	0.562
Railway	Fisher's	0.630	Fisher's	1.000
Fallow land	Fisher's	0.421	Fisher's	1.000
Perennial crop	$\chi^2 = 1.057$	0.589	$\chi^2 = 1.652$	0.438
Hay	Fisher's	0.135 +	Fisher's	0.752
Alfalfa	$\chi^2 = 7.738$	0.021 +	$\chi^2 = 6.994$	0.030 +
Width of the non-cultivated belt	Z = -1.4	0.175	Z = −1.5	0.137 +
Water depth	Z = −5.0	< 0.001 +	Z = −6.1	< 0.001 +
Water channel width	Z = −4.2	< 0.001 +	Z = −4.7	< 0.001 +
Bank height	Z = -1.2	0.219	Z = 0.16	0.875
Water velocity	Z = −3.2	0.001 +	Z = −3.8	< 0.001 +
Dredged ditch	Fisher's	0.009 −	Fisher's	0.021 −
Herbicide	Fisher's	0.421	Fisher's	1.000
Pool	Fisher's	0.199	Fisher's	0.042 +
Raccoon	$\chi^2 = 2.241$	0.524	$\chi^2 = 2.245$	0.523
Canidae	Fisher's	0.338	Fisher's	0.403
Mink	Fisher's	0.201	Fisher's	0.142 +
Beaver	Fisher's	0.117 +	Fisher's	0.0825 +

(The + or − sign indicates the direction of the relationship with muskrat presence)

Table 2.3 Results of the Wald Chi-square (P) for each habitat variable included in the logistic regression models on the presence/absence of muskrat using all signs of presence and on the presence/absence of muskrat burrows in southern Quebec farm ditches.

	All signs			Burrows		
Variable	Coefficient	χ^2	P	Coefficient	χ^2	P
Intercept	-0.998	5.08	0.024	-1.638	20.04	0.0001
Dredged ditch	-2.493	6.41	0.011			
Water depth	0.074	11.17	0.001	0.088	23.74	0.0001
Water velocity	0.190	5.55	0.018	0.163	10.37	0.0013
Pulpy plant cover	1.003	6.91	0.009			
% of used data explained by model	75.6			70.5		
% of unused data explained by model	91.1			70.5		
Index of rank correlation C	0.824			0.796		

Presence of dredging was negatively correlated with macrophyte cover (Kendall τ_b = -0.1516 $\underline{P}$ = 0.029; 1.8 ± 1.1 in dredged ditches; 2.8 ± 1.3 in ditches not dredged). The index of rank correlation between observed responses and predicted probabilities, classification rate of used sections by the model, as well as classification rate of unused sections by the model were characteristic of a good descriptive model (Table 2.3).

BURROWS

Muskrat burrows were present in 58% of the 75-m sections, for an average density of 37.4 ± 31.9 burrows per kilometre. The presence of muskrat burrows did not change with the type of adjacent crop (Chi-square test, χ^2 = 0.907, 4 df, $\underline{P}$ = 0.924). Likewise, the abundance of burrows did not vary between perennial and non-perennial crops (ANOVA, $\underline{F}$ = 0.16, 1 df, $\underline{P}$ = 0.6921). The presence of mink (*Mustela vison*) was positively related to muskrat presence at $\underline{P}$ < 0.15, and therefore mink presence did not significantly affect the presence of muskrat, despite the predator-prey relationship between these two species. The variable "mink" was thus not included for consideration by the model. Total hydrophyte cover, cover by pulpy plant species, width of the non-cultivated belt and water channel width were not considered for the logistic regression, due to their correlation to other variables (see above section). All other variables found to be significant for the presence of muskrat burrows (Table 2.2) were included for consideration by the model. Only two variables, water depth and water velocity, were retained in the logistic regression model to explain the presence of muskrat burrow (Table 2.3). The index of rank correlation between observed responses and predicted probabilities, classification rate of used sections by the model, as well as classification rate of unused sections by the model were slightly lower than values obtained in the model using all signs of presence (Table 2.2). Muskrat consumption of crop species was detected in only 48 (10.2%) of the 468 sections sampled. However, the number of sections with crop damage due to muskrat was similar (Chi-square test, χ^2 = 2.282, 2 df, $\underline{P}$ = 0.319) in alfalfa (13.0%), cereal (14.4%) and corn fields (10.1%). Two occurrences of soybean consumption were also noted.

DISCUSSION

Earhart (1969) determined that breeding burrows often occur in pairs, 1 m to 18 m apart. The mean foraging distance from burrow was estimated to be within 126 ± 26 m (Mean ± SD) in Massachusetts rivers (Brooks 1985). Other authors have observed that muskrat home range was limited within a radius of approximately 100 m (Chu and Yien 1962, Erickson 1963, Errington 1963, Neal 1968). Given the above results, the distance of 150 m between sampled sections should have been sufficient to reduce spatial autocorrelation of data since the average of maximum distance covered by adult males in a four-day period, including spring movements, was (Mean ± SD) 190 ± 43.5 m, while for adult females this distance was reduced to 75 ± 70.5 m (see Chapter 3).

We used the stepwise logistic regression because it has the potential to be more robust than the discriminant function analysis and linear regression to the non-respect of multivariate normality and equal covariation (Efron 1975, Press and Wilson 1978), and since many ecological phenomena have an inherent non-linear nature, non-linear statistics could provide more realistic results than linear statistics.

Modelling (Hobbs and Hanley 1990) and field experiment (Van Horne 1983) have shown that species-habitat relationships may vary with the species density. Since the proportion of houses, and thus the relative density of muskrats, vary with overall muskrat density in various habitat types (Messier et al. 1990), the importance of variables best describing muskrat habitat use could also change with muskrat density. The density of muskrat burrows was among the highest recorded (see Chapter 1, Table 1.1). Since marginal habitats are more likely to be used when the density of muskrats is high, the present habitat models may have detected only the most critical habitat variables. No variable representing crop type or use of land adjacent to farm ditches were selected in our muskrat habitat use models. Although the presence of alfalfa fields was positively associated with muskrat presence and the presence of burrows, this variable was not selected in the habitat use models. In addition, the only significant relationship between the presence of alfalfa fields and one of the variables selected by both models (water velocity: Kendall $\tau_b = -0.132$ $\underline{P} = 0.048$) was weak and inverse. Water depth was of significant importance in both the model using all signs of presence and the model using only presence/absence of burrows. If water level is selected in the habitat use models despite its variation through the summer, it would mean that the importance of this variable is even greater than the one conferred by the models. Water level variation through the summer would not have influenced the test of bordering crops on muskrat habitat use as we systematically tried to sample in alternation ditch sections bordered by perennial and annual crops. Danell (1978) obtained a negative correlation between the number of burrows and the distance from the shore to a water depth of 0.5 m. Muskrat predation by mink was also shown to be dependent on water level (Proulx et al. 1987), and stable water levels were found to be critical during the rearing of young (Errington 1937). On two occasions, after heavy rain, we observed that water level had increased over 1 m in rivers receiving input from several ditches, while water level in ditches did not increase as much. Young muskrats could then be less exposed to drowning in small ditches than in rivers. A sufficient water depth allows under-ice movements and access to feeding areas, and is critical for muskrat in winter (Jelinski 1984). Water depth is also one of the limiting factors considered in the habitat suitability index (HSI) model for estuarine habitats (Allen and Hoffman 1984). In the present study, the estimated probability of muskrat presence in a section reaches 0.9 with a water depth equal to or greater than 30 cm. However, as previously noted by Errington (1937), we observed that muskrats preferred to stay in their burrow systems when water levels dropped to zero. At low water levels, we frequently (N = 35 sections of 75 m) observed that muskrats had dug channels in the mud. Dominant plant species in those channels were cattail, rice cut-grass and tall graminaceous plants, all of which provide good escape cover. It has been reported that muskrat burrowing causes more economic damage than their direct consumption of crops (Gosling & Baker 1989). However, erosion of steep banks, particularly during the spring and fall and during heavy rain, could contribute more to filling ditches than muskrat burrowing. Also, muskrat channels and the consumption of hydrophytes could contribute to maintaining the drainage of ditches.

Results obtained in the present study regarding the direction of the relationship between muskrat presence and water velocity seem contradictory to those of Brooks and Dodge (1981) and Nadeau et al. (1995). A possible explanation could be that the mean water velocity in ditches of the study area was low (2.8 ± 4.5 m/min) and most of the sections (94%) had a water velocity under the maximum value for muskrat presence of 10 m/min established by Brooks and Dodge (1981). In the present study, the relationship between muskrat presence and water velocity was observed under suitable conditions for muskrat presence, and does not represent relationships under a wide range of water velocities. Muskrats may select ditches with a water velocity that would reduce ice thickness in winter, while still allowing muskrat movement at reasonable energy expenditure levels. The positive relationship between muskrat presence and water velocity may also be the result of the reduced number of macrophyte stems following muskrat browsing and the presence of channels dug by muskrat. In sections with vegetation cover of 76%-100%, water velocity was, on average, higher where muskrat was present (2.3 ± 4.3 m/min) than where it was absent (0.1 ± 0.8 m/min). Danell (1977) showed how muskrats could create open areas in dense aquatic plant communities and induce short-term plant succession. Weller (1981) described the importance of muskrat for managing vegetation in freshwater marshes.

In theory, the impact of muskrats on vegetation should increase with population density (Errington 1963). We observed a negative relationship between the presence of burrows, or the presence of any muskrat sign, and cattail cover. This might reflect either: (1) the result from an active avoidance of cattail communities by muskrat, which would deny the results of other studies (Errington 1963, Smith and Jordan 1976, Blanchette 1985), although muskrat consumption of cattail has been shown to decrease from spring to summer as the content in lignin of the plant increases (Lacki et al. 1990); (2) the result of a high number of muskrats that would repeatedly feed upon cattail in winter and early spring, or (3) the possibility that dense stands of cattail may represent sites where water level drops to lower depths than at other sites, a condition known to be more favourable to cattail propagation (Weller 1975), but not so favourable to muskrat presence. Cattail cover was in fact negatively correlated with water depth (Kendall τ_b = -0.2157 $\underline{P}$ = 0.0002). Pulpy plant cover, which could have been negatively linked to cattail cover because of competition between the two groups of plants, was selected in the model on signs of presence. Pulpy plant species may thus benefit from muskrat grazing on cattail, as was shown for purple loosestrife (Thompson et al. 1987).

No relationship was found between muskrat presence-absence and purple loosestrife cover. This species is known to slowly replace native wetland species in southern Canada (Thompson et al. 1987). Evidence of muskrat grazing on loosestrife was only found in 5 of the 468 sections sampled, but none of the sampled sections were dominated by purple loosestrife. The presence of a herbaceous belt has been shown to be of significant importance during the summer in northern habitats (Jelinski 1984, Nadeau et al. 1995), but this was not the case in the present study possibly because of the abundance of emergent plants in the study area.

The importance of dredging was significant in the model, which could be explained by its effects in removing plants, seeds and sediments, and in reducing water depth through improvement of stream flow. Over time, dredging had more impact on the ditch vegetation than herbicide application, in the few where the latter was noted. Dense colonies of water plantain were found to grow on the exposed soft sediments after herbicide has been applied to the ditch vegetation.

Despite the high density of muskrat burrows, muskrat consumption of crop plants during the summer was not frequent, as was previously observed in Britain (Warwick 1940). The attraction effect of adjacent crop type as food for muskrat was thus negligible. Indirect negative effects, such as dredging and use of herbicide on the ditch vegetation which would reduce the availability of emergent plants, were not frequently observed, regardless of the type of bordering crop. The number of muskrat burrows per kilometre (37.4/km) in farmland ditches of the study area was higher than values recorded in other habitats (Danell 1978, Chulick 1979, Proulx and Gilbert 1983, Jelinski 1984, Brooks 1985, Messier et al. 1990; see Table 1.1 in Chapter one)). This value is higher than those recorded in cattail-bulrush marshes (Errington 1963, Perry 1982, Proulx and Gilbert 1983, Clark and Kroeker 1993). Chulick (1979) on the other hand, recorded a very high value of 51.7 burrows/km in two creek sections with dense aquatic vegetation and bordered by corn fields. A value of 25 burrows/km was obtained for streams bordered by cropland in New-York State (R. Foley, unpublished data). However, the comparison of the number of burrows/km among studies is questionable, as it does not include considerations of potential differences in stream width and pulpy plant availability, two variables identified in the present study as determining factors for muskrat presence.

The present paper demonstrates that within a favourable range of water velocity conditions, the relationship between water velocity and muskrat presence can be positive. With high densities of muskrat burrows, and in optimal conditions for bank slope and soil type, the type of crop bordering farm ditches was not found to be significantly related to muskrat probability of presence.

MANAGEMENT IMPLICATIONS

In agricultural landscapes representing a mosaic of different crop kinds bordering drainage ditches, changes in crop type did not influence muskrat probability of presence. Muskrat predation on crop species was also shown to be similar across three different crop types. The results of the present study do not support making changes in regulations to control muskrat trapping, or changes in control programs in areas where muskrat is considered a pest, for wetlands bordered by different crop types. On the other hand, if multiple use of resources in the agricultural landscape are considered, policies to maintain a minimum water level in ditches, reduce the occurrence of dredging and favour the development of stands of species such as reed grass, great bulrush, arrowhead, American water plantain, wild rice, flowering-rush, and giant bur-reed should contribute to maintain high muskrat presence.

ACKNOWLEDGEMENTS

We are grateful to Kateri Lescop-Sinclair and Heather Cunningham for their significant contribution to the field work. We thank all landowners of the St-Anicet and Huntingdon areas who allowed us to work on their land. This work was financed by NSERC grants to J.R. Bider and a NSERC Doctoral fellowship to S. Nadeau.

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Although it was shown in Chapter 2 that muskrat presence in drainage ditches was not affected by the type of crop bordering ditches, it could still be possible that different crops would confer different habitat quality for muskrat. I further tested this through the measurement of population variables. In the third chapter I studied the differential effects of ditches bordered by hay fields and ditches bordered by corn fields on muskrat population variables measured by livetrapping, killtrapping and mudtracking. Activity of co-occurring wildlife detected by mudtracking was also compared between both types of ditches.

CHAPTER THREE

Comparison of muskrat (Ondatra zibethicus) population variables, and of muskrat and other stream dwelling vertebrate activity, in ditches bordered with corn and hay fields

ABSTRACT

Muskrat population variables were compared in ditches bordered with corn or hay fields, using a combination of trapping and mudtracking data. Data were collected in six to ten ditch sections in farmlands of southwestern Quebec in the summers of 1989 and 1990 and in March 1991. We did not detect significant effects of crop type on the number of adult males, the number of adult females, the overall number of adults, the number of juveniles, the sex ratios in adults and juveniles, the number of litters, the number of litters per resident adult female, the number of young per litter, the weight of adult males, the weight of adult females, the juvenile birth-to-capture mortality rate, and the annual population turnover. Muskrat activity was found to be lower, and the average birth date earlier, in corn ditches than in hay ditches, in 1989. The statistical power of most tests was low due to limited sample size and high standard deviations. Muskrat activity was not predictive of raccoon (*Procyon lotor*), mink (*Mustela vison*), turtle, or frog activity. The highly positive relationship between the natural logarithm of the number of burrows and the number of residents ($F = 54.28$ $R^2 = 0.78$ $p=0.0001$) or the maximum number of muskrats ($F = 56.79$ $R^2 = 0.79$ $p = 0.0001$) confirmed the validity of using the number of burrows as an index of population size. Altogether, the studied ditches showed a high maximum muskrat population density, with an average of 85.83 ± 60.57 muskrats/ha in 1989, and an almost complete annual turnover ($\geq 95\%$). There was no indication from this study that corn or hay fields bordering ditches influenced muskrat populations.

Key words: farm ditches, habitat use, logistic regression, muskrat, *Ondatra zibethicus*, Quebec.

INTRODUCTION

Muskrat (*Ondatra zibethicus*) can adapt to various habitats, even to those that do not have water throughout the year (Errington 1963; Clough 1987). Proulx and Buckland (1986) showed that marshes generally represent the highest quality habitat for muskrat, followed by ditches and small creeks. While many authors have studied richer habitats represented by marshes (e.g. Errington 1963; MacArthur 1978, 1980; Parker and Maxwell 1980, 1984; McCabe and Wolfe 1981; Smith et al. 1981; Proulx and Gilbert 1983, 1984; Bélanger and Léveillé 1984; Caley 1987), ponds (e.g. Erickson 1963; Earhart 1969; Messier et al. 1990; Clark and Kroeker 1993), fens (Lacki et al. 1990), eutrophic lakes (e.g. Neal 1968; Danell 1978a, 1978b, 1985) and rivers (Snead 1950; Brooks and Dodge 1981, 1986; Le Boulengé and Le Boulengé-Nguyen 1981; Brooks 1985; Clay and Clark 1985; Proulx and Buckland 1986; Clark 1987), few have studied muskrat populations in farmland ditches (Errington 1937, 1963; Stewart and Bider 1974, 1977; Chulick 1979; Proulx and Buckland 1986).

The percentage of open and agricultural land per site has been shown to be significantly related to the abundance of muskrat burrows (Brooks and Dodge 1981). In 1937, Errington reported that shallow creeks abounded with muskrats when stream banks and margins of adjacent fields were covered with dense vegetation. Errington (1940) has stated: "Medium-small food-rich agricultural lands may accommodate six to eight breeding pairs per mile, but such water-courses, if bordered mainly by pasture, may be suitable only for half as many pairs or fewer." Errington (1963) has also stated: "stream-dwelling populations of the corn-belt may conspicuously reorient themselves according to the local accessibility of corn fields (Errington 1938; 1941)."

Bordering crops can provide food to muskrats, which may also be affected by crop-associated farming techniques through habitat modification due to dredging, use of herbicides and erosion. Since the type of crop cultivated in a region may change over time, it is important to understand the effects of these crop changes on muskrat populations. In this study, we investigated the possibility that ditches bordered by corn fields could present a habitat of different quality for muskrat than ditches bordered by hay fields. Consequently, we hypothesized that ditches bordered by corn or hay fields would present different values for muskrat life history traits such as: (1) adult weight, (2) population size (all muskrats), (3) rate of population turnover, (4) sex-ratio of young and adults, (5) number of adult residents, (6) number of litters, (7) the growth rate of juveniles and their birth date, (8) the number of young per litter and juvenile summer mortality rate, and (9) intensity of muskrat activity.

The activity of co-occurring vertebrates was compared between corn and hay ditches, in order to test whether muskrat activity in both types of ditches was similar to the activity of other species.

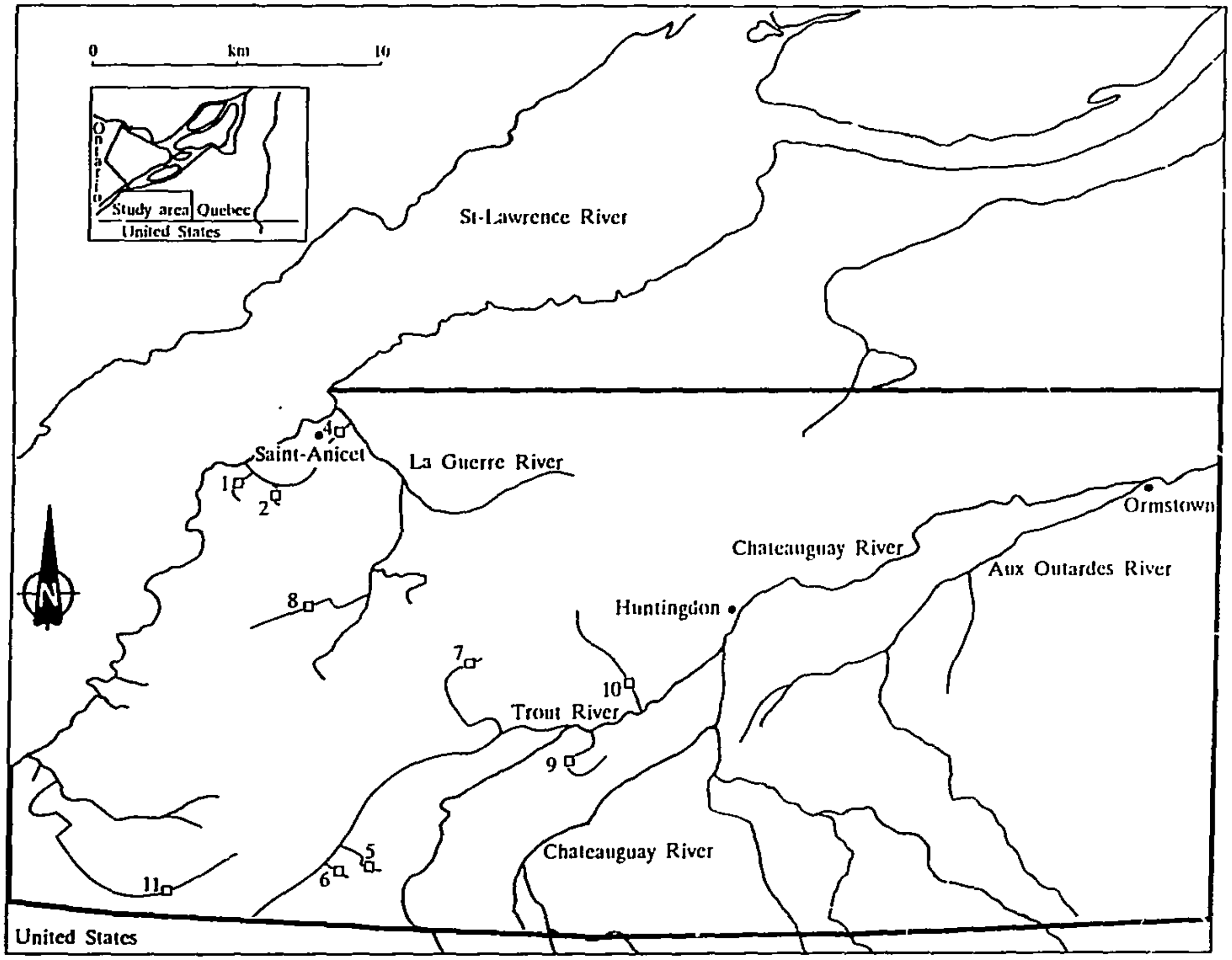
We also tested the relationship between muskrat population size and the number of burrows to evaluate the possibility of using this sign of presence as an index of population size.

METHODS

STUDY AREA

The study area was located in the southernmost part of Quebec, 60 km southwest of Montreal, close to the New-York State border (Figure 3.1). Six ditch sections were selected in the summer of 1989, of which three were bordered by corn fields, and three were bordered by hay fields. The ditches were selected to be as similar as possible for water level, emergent vegetation, soil type, bank height and slope, so that these parameters would not influence muskrat life history traits. In 1990 and 1991, two ditch sections bordered by hay fields, and two bordered by corn fields, were added to the six already studied. Average biophysical characteristics of the ten selected ditch sections were recorded every 75 m in July 1990 following the methodology outlined in Chapter 2.

Figure 3.1 Study area in farmlands of southwestern Quebec. Livetrapping of muskrats and mudtracking was conducted in 240 m to 270 m long ditch sections of selected ditches in 1989. In 1990, livetrapping was performed in 270 m long ditch sections. In 1991, killtrapping was performed in 270 m long ditch sections. The studied ditch sections are identified by an empty square. Ditch # 3 is missing because it was not sampled.


0
km
10
Ontario
Study area
Quebec
United States
St-Lawrence River
4
Saint-Anicet
La Guerre River
1
2
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8
Ormstown
Chateauguay River
Aux Outardes River
Huntingdon
7
10
Trout River
9
Chateauguay River
5
6
11
United States

TRAPPING AND TRACKING

In 1989, three livetrapping sessions were conducted in each ditch, from 2 May to 24 August (except for ditch #7, that replaced a ditch dredged after the first trapping session, and that was thus trapped only twice). In order to maximize the number of ditches studied, we limited the length of each section to 200 m, the average size of a home range (Aldous 1947, Shanks and Arthur 1952, Krear 1953, Mathiak 1953, Sather 1958, Schmitke 1959, Mallach 1971, Westworth 1974), plus a safety distance of 70 m. However, in 1989 low water levels after mid-July dropped under 5 cm in some of the upstream sections. To avoid the bias of comparing sections of different lengths, we created three paired groups of corn and hay bordered ditch sections of the same length: 240m (#1-corn and #4-hay), 255m (#2-corn and #7-hay), and 270m (#6-hay and #8-corn). In each ditch, starting from the downstream end of the studied section, a chicken wire-mesh fence with a gap in the middle was installed permanently across the ditch at 15-m intervals forcing muskrats to swim in the middle of the channel. During trapping sessions, a home-made multiple-catch family livetrap (as described in Snead 1950) was placed in the central opening of each fence for 4 days or until no new individual was caught. The underwater part of this type of trap takes the form of a tunnel with an oblique door at each end. Animals are caught when they push the door that falls back into place after the animal has gone through. The animal then goes to the aerial part of the trap to breathe; there, a similar door system maintains it in another compartment. The trap is then ready to catch another animal. The first time an animal was captured, it was sexed, weighed and one of its toes was cut at the first phalanx for identification when retrapped or when it crossed mudtracking boards. Each subsequent trapping of the same individual included only its identification, unless it was a juvenile (weighing less than 900 g), in which case the animal was weighed to evaluate its daily weight gain. The same juveniles were weighed only once during a given trapping session. All manipulations of trapped individuals, marking, and weight measurements, were done by the author. In 1989, between trapping sessions, we used the mudtracking technique, an adaptation of sandtracking (Bider 1968), to follow muskrat movements. A styrofoam tracking board 3 cm thick X 30 cm wide X 60 cm long was placed in the central opening of the wire-mesh barrier. The tracking medium spread over the board consisted of approximately 75% sand and 25% clay softened with water. This medium was kept soft by periodically reincorporating water. We placed a plastic tent over each board to prevent the erasing of tracks by heavy rain. In each ditch section, from June through August, we recorded tracks for 11 periods of 3-4 days each. Individually marked muskrats were identified by their tracks, otherwise tracks were qualified as produced by unmarked individuals or non-readable. The presence of tracks produced by animals other than muskrats was recorded to the lowest taxonomic level possible. Tracks were erased after readings. Reading of the signs on mudtracking boards were only done by the principal investigator. We used a log-linear analysis to compare muskrat activity (i.e. the number of boards with tracks versus the number of boards without tracks) between corn and hay ditches in June, July and August. Activity was also analyzed for four of the five most common taxa encountered, i.e. raccoon (*Procyon lotor*), mink (*Mustela vison*), frog (only *Rana pipiens* and *Rana clamitans were observed*) and turtle (only *Chelydra serpentina* and *Chrysemis picta* were observed). Since raccoon tracks often masked other species tracks, boards were considered free of tracks from a given species, only when raccoon tracks were also absent.

In 1990, modified livetrapping was performed to acquire information on muskrat movements. Mudtracking was abandoned due to the inconvenience of having to maintain the tracking medium in a soft state. Two livetraps separated by 15 m were placed at each end of a section, and each was moved by 15 m toward the centre of the section each day, until the entire section was covered. The marking and weighing of muskrats was done as in 1989. Three trapping sessions were performed per ditch, from 10 May to 30 August. Water level was higher in 1990 than in 1989, allowing us to compare sections of the same length for all ditches, i.e. 270m. In the third week of March 1991, Conibear kill traps #110 were set at the entrance of every muskrat burrow with presence indices, for a minimum of two days, or until no animal was caught. When burrows were separated by more than 15 m, killtraps baited with carrots or apples were set on the bank at 15 meter intervals, covering thus the entire 270 m section. Individuals were weighed and sexed, and female oviducts were examined for the presence of embryos.

In 1989 and 1990, birth dates for each juvenile were estimated by backdating the animal from its first capture, with a weight increase per day of 6.13 grams that was estimated from measurements of juvenile growth rate in both years, assuming that growth rates in corn and hay ditches were similar. This growth rate value was compared with the one produced by regressing values from Erickson (1963). Weight at birth was considered to be 23.5 grams (Erickson 1963). Within a ditch, potential members of the same litter were identified by associating the two juveniles with the closest birth dates and adding new juveniles until a period of 14 days was covered. The 14 day period allows for individual differences in growth rate, as well as possible imprecisions in weight measurements. This procedure was repeated until no new group could be formed. We used Kruskal-Wallis analyses (Scherrer 1984) to compare corn and hay bordered ditches for: (1) the weight of adults when first captured (by sex and year, and by sex combining years), (2) dates of muskrat births (by year), (3) the number of litters per studied section (by year, and combining years), (4) the number of young per litter (by year, and combining years), (5) the average number of litters per adult female in studied sections (by year, and combining years), (6) the number of adult males per studied section (by year, and combining years), (7) the number of adult females per studied section (by year, and combining years), (8) the total number of adults per studied section (by year, and combining years), and (9) the number of juveniles per studied section (by year, and combining years). Because failure to reject H_o does not necessarily mean that H_o is true, particularly when studied variables express high variability and when sample size is small, we calculated the power of the tests on combined data from all years by using the package developed by Brown et al. (1993). Whenever possible, we also determined the size of the difference for the variable studied in hay and corn ditches, that was necessary to obtain a statistical power of 0.8. In order to identify this difference ,we determined the two group means, equally distant from the overall mean required to obtain a statistical power of 0.8, using the standard deviations and sample sizes observed. The statistical power of 0.8 has been cited as the minimal acceptable value for clinical trials, and represents a compromise between having a high probability of rejecting the null hypothesis when it is incorrect, and an affordable sample size (Brown et al. 1993). Power values are used as indicator values only, since the software allows only to calculate the power on normally distributed data. As we used non-parametric tests on non-normally distributed data, it is possible that the real statistical powers of the tests are higher than the values shown here.

The adult residents of a given ditch were defined as any adult detected at least twice during the summer and over a minimum period of ten days. The number of resident females was adjusted conservatively by assigning a minimum value of 1 to ditches where juveniles were captured, as juvenile muskrats tend to stay in the vicinity of their mother's territory until spring (Errington 1963, Le Boulengé and Le Boulengé-Nguyen 1981, Caley 1987).

We used the general association statistic (SAS 1988) between rows (crop type) and columns (population variables) in frequency tables, controlling for years, to compare between crops: (1) the sex-ratio of adults, (2) the sex-ratio of juveniles, and (3) the sex-ratio of all individuals. Using Chi-square tests, we compared the sex-ratios in adults and juveniles, separately and together, and combining data from all years, to the expected 50/50 ratio. Juvenile muskrat mortality in the summer was estimated by: (1) multiplying the number of litters by the mean number of 6.6 embryos/gravid female (as obtained by Stewart and Bider 1974), (2) subtracting the number of young captured, and then dividing the result of (2) by (1). The population turnover for a ditch was calculated as the proportion of the population in spring 1990 and 1991 that was not present the previous summer.

In order to evaluate the difference between corn and hay ditches for several population variables simultaneously, we performed a factorial correspondence analysis (SAS 1988) using the 18 ditch-year as objects and using all variables with non-missing values such as: the total number of individuals, the number of residents, the number of young, the number of litters, the number of young per litter, the number of burrows, and the annual population turnover. The first three dimensions are represented graphically.

BURROWS AS INDICATORS OF MUSKRAT POPULATION SIZE

After a training period, the author recorded the number of muskrat burrows in studied ditch sections in July 1990 by walking along the sections and probing both submerged banks with his feet. In the study area, muskrat burrows cannot be mistaken with burrows of other species, and can easily be detected by an experienced observer. After testing for the normality of the variables (SAS 1988), we used the linear regression (SAS 1988) to test the relationship between the natural logarithm of the number of burrows and (1) the number of summer adult residents, (2) the number of litters, and (3) the maximum number of individuals detected during the same week. The natural logarithm of the number of burrows was employed to cover the possibility that the relationship between the number of muskrats and the number of burrows be non-linear, and to reduce the variability in the number of burrows due to environmental factors that could either affect the detection level of burrows, or increase the persistence of unused burrows.

RESULTS

TRAPPING DATA

The ditches selected in this study were small water courses with low water velocity, and with vegetation generally covering more than 50% of the water and bank surface (Table 3.1). The absence of a ground cover in corn fields before mid-July was the main observed difference in habitat related to the type of crop cultivated in fields adjacent to ditches. As a result, an important accumulation of sediments due to erosion was observed in some ditches (#1, 8, 11) bordered by corn fields. We did not observe consumption of crop plants by muskrats along the selected ditches. While no evidence of pesticide use was observed in hay fields, insecticides were used on corn at seeding time. The herbicide Atrazine™ (triazine) was applied on one corn field at seeding time, and the herbicide Pardner™ (bromoxynil) was used to kill broad-leaved weeds on all corn fields when corn plants were about 12" high.

In 1989, 1990, and 1991, we caught 5, 15, and 23 adult males and 7, 6, and 16 adult females, respectively . The number of adult residents was low and similar in 1989 and 1990 (Table 3.2), although mudtracking detected a few residents in 1989, and was not used in 1990. The number of adult residents presented here may be an underestimate of true residents, since in 1990, no male residents were captured in ditches (2, 5, 10) where at least two juveniles were caught. In 1989, tracking data show that one of the ten residents, a male, was trapped only once but was detected during each of the subsequent tracking periods that extended over 55 days. On the other hand, capture data showed that even if some adults could have been trap-shy, most of them were captured at least twice and up to nine times.

Table 3.1 Biophysical characteristics of selected ditches in southern Quebec in mid-July 1990.

Variable	Mean ± SD
Water depth in main channel (cm)	20 ± 11
Width of waterway (m)	2.39 ± 1.15
Mean bank height from water level (m)	1.39 ± 0.42
Width of non-cultivated belt from water edge (m)	3.46 ± 1.82
Water velocity (m/min)	5.28 ± 5.99
Plant cover on banks and in channel (%)	70 ± 21

Table 3.2 Number of adult residents in 1989 and 1990, maximum number of co-occurring adults in a given trapping session, maximum number of muskrats per week and total number of muskrats in 1989, 1990 and 1991 in selected ditch sections of southwestern Quebec.

Corn ditch	No. of adult residents				Maximum no. of co-occurring adults			Maximum no. of muskrats per week		Total number of muskrats		
	1989		1990		1989	1990	1991	1989	1990	1989	1990	1991
	♂	♀	♂	♀								
1	1	1	1	2	2	2	5	2	6	3	11	5
2	1	1	0	1	1	1	2	9	2	10	3	2
8	0	1	1	1	1	1	3	5	2	8	5	3
10	-	-	0	1	-	1	3	-	7	-	13	3
11	-	-	1	1	-	2	3	-	6	-	6	3

Table 3.2 Cont. Number of adult residents in 1989 and 1990, maximum number of co-occurring adults in a given trapping session, maximum number of muskrats per week and total number of muskrats in 1989, 1990 and 1991 in selected ditch sections of southwestern Quebec.

Hay ditch	No. of adult residents				Maximum no. of co-occurring adults			Maximum no. of muskrats per week		Total number of muskrats		
	1989		1990		1989	1990	1991	1989	1990	1989	1990	1991
	♂	♀	♂	♀								
4	1	2	1	1	3	3	3	8	4	10	5	3
5	-	-	0	1	-	1	9	-	9	-	9	9
6	0	0	0	0	1	1	4	1	1	1	1	4
7	1	1	1	0	2	2	4	10	2	10	2	4
9	-	-	1	1	-	3	4	-	7	-	13	4
Total	4	6	6	9	10	17	40	35	46	42	68	40

In 1989, one male resident was detected per 382 m of ditch length and one female was caught per 255 m in hay or corn ditches. In 1990, these numbers declined to one male resident per 450 m of ditch, and to one female resident per 300 m of ditch. The numbers of residents were too low to perform statistical analyses, but the number of ditch-years with resident male was identical for corn and hay ditches, while female residents were present in all eight corn ditch-years but in only five of the eight hay ditch-years (Table 3.2).

The average maximum number of muskrats known to be alive in any given week in each ditch was slightly higher in 1989 (2.3 ± 1.5 per 100 m of ditch linear distance, or 85.8 ± 60.6 per ha of ditch surface covered with water) than in 1990 (1.7 ± 1.0 per 100 m or 71.3 ± 42.7 per ha of water). In 1989 and 1990, the average minimum number of different individuals alive, including juveniles, was 2.01 ± 1.45 individuals per week per 100 m of ditch in hay ditches, and 1.84 ± 1.01 individuals/week/100 m in corn ditches, with an overall mean of 1.93 ± 1.21 individuals/week/100 m. We did not detect a significant effect of crop on the number of adult males (Table 3.3), but the statistical power of the test combining data for all years was low, due mainly to the high variability of results (average adult males per section for hay was 1.6 ± 0.9, and for corn, 1.6 ± 1.0). A statistical power of 0.8 was obtained with a difference by a factor of two between the average number of males in hay and corn ditches. The results were similar for females (Table 3.3), although the higher variability between ditches required that, for the analysis combining all years, the number of females in the two types of ditches differ on average by a factor of 7.8 to obtain a statistical power of 0.8. Because of the high variability in 1991, a three-fold difference in the average number of females between hay and corn ditches was not significant. No difference was observed for adults altogether (Table 3.3) in any year or in the analysis combining all years. For the analysis on combined data from all years, a statistical power of 0.8 could be reached only with a difference in the number of adults in corn and hay ditches of an order of magnitude of 2.1:1.

Table 3.3 Results of statistical tests on muskrat population variables, comparing corn and hay bordered farm ditches in southern Quebec in 1989, 1990 and 1991.

Variable	Results of test	Mean ± SD in hay ditches	Mean ± SD in corn ditches	Power
Number of adult males	1989: N = 6, K-W. χ^2 = 1.000, 1 df, P = 0.317	1.0 ± 0.0	0.67 ±0.58	
	1990: N = 10, K-W. χ^2 = 0.013, 1 df, P = 0.910	1.4 ± 0.5	1.4 ± 1.1	
	1991: N = 10, K-W. χ^2 = 0.013, 1 df, P = 0.910	2.2 ± 1.1	2.4 ± 0.5	
	All years: N = 26, K-W. χ^2 = 0.012, 1 df, P = 0.913	1.6 ± 0.9	1.6 ± 1.0	0.025
Number of adult females	1989: N = 6, K-W. χ^2 = 0.222, 1 df, P = 0.637	1.0 ± 1.0	1.3 ± 0.6	
	1990: N = 10, K-W. χ^2 = 0.000, 1 df, P = 0.999	0.6 ± 0.9	0.6 ± 0.9	
	1991: N = 10, K-W. χ^2 = 2.028, 1 df, P = 0.154	2.6 ± 2.3	0.8 ± 1.3	
	All years: N = 26, K-W. χ^2 = 0.614, 1 df, P = 0.433	1.5 ± 1.8	0.8 ± 1.0	0.200

Table 3.3 Cont. Results of statistical tests on muskrat population variables, comparing corn and hay bordered farm ditches in southern Quebec in 1989, 1990 and 1991.

Variable	Results of test	Mean ± SD in hay ditches	Mean ± SD in corn ditches	Power
Total number of adults	1989: N = 6, K-W. $\chi^2 = 0.000$, 1 df, $\underline{P} = 0.999$	2.0 ± 1.0	2.0 ± 1.0	
	1990: N = 10, K-W. $\chi^2 = 0.108$, 1 df, $\underline{P} = 0.742$	2.0 ± 1.2	2.0 ± 1.9	
	1991: N = 10, K-W. $\chi^2 = 2.336$, 1 df, $\underline{P} = 0.126$	4.8 ± 2.4	3.2 ± 1.1	
	All years: N = 26, K-W. $\chi^2 = 0.332$, 1 df, $\underline{P} = 0.564$	3.1 ± 2.5	2.5 ± 1.4	0.117
Adult sex-ratio	G.A.=1.076, 1 df, $\underline{P} = 0.300$	66 ♂ : 34 ♀	52 ♂ : 48 ♀	0.202
Number of juveniles	1989: N = 6, K-W. $\chi^2 = 0.000$, 1 df, $\underline{P} = 0.999$	5.0 ± 4.4	5.0 ± 4.4	
	1990: N = 10, K-W. $\chi^2 = 0.894$, 1 df, $\underline{P} = 0.344$	3.6 ± 4.5	4.8 ± 4.2	
	All years: N = 16, K-W. $\chi^2 = 0.181$, 1 df, $\underline{P} = 0.671$	4.1 ± 4.2	4.9 ± 3.9	0.051
Juvenile sex-ratio	G.A.= 1.318, 1 df, $\underline{P} = 0.251$	53 ♂ : 47 ♀	69 ♂ : 31 ♀	0.256
All individuals sex-ratio	G.A.= 2.474, 1 df, $\underline{P} = 0.116$	53 ♂ : 47 ♀	67 ♂ : 33 ♀	0.394
Weight of adult males	All years: N = 43, K-W. $\chi^2 = 0.326$, 1 df, $\underline{P} = 0.568$	1317 ± 157	1271 ± 192	0.125

Table 3.3 Cont. Results of statistical tests on muskrat population variables, comparing corn and hay bordered farm ditches in southern Quebec in 1989, 1990 and 1991.

Variable	Results of test	Mean ± SD in hay ditches	Mean ± SD in corn ditches	Power
Weight of adult females	All years: N = 32, K-W. χ^2 = 1.232, 1 df, P = 0.267	1227 ± 140	1148 ± 146	0.288
Number of litters	1989: N = 6, K-W. χ^2 = 0.222, 1 df, P = 0.637	1.7 ± 1.5	2.0 ± 1.7	
	1990: N = 10, K-W. χ^2 = 0.410, 1 df, P = 0.522	1.8 ± 2.0	2.4 ± 1.1	
	All years: N = 16, K-W. χ^2 = 0.348, 1 df, P = 0.555	1.7 ± 1.7	2.2 ± 1.3	0.081
Number of litters/ resident adult female	1989: N = 6, K-W. χ^2 = 0.222, 1 df, P = 0.637	2.0 ± 1.7	2.0 ± 1.4	
	1990: N = 10, K-W. χ^2 = 0.410, 1 df, P = 0.522	2.0 ± 0.7	1.8 ± 2.0	
	All years: N = 16, K-W. χ^2 = 0.348, 1 df, P = 0.555	2.0 ± 1.1	1.8 ± 1.8	0.041
Number of young/litter	1989: N = 11, K-W. χ^2 = 0.079, 1 df, P = 0.778	2.5 ± 1.4	3.0 ± 2.3	
	1990: N = 21, K-W. χ^2 = 0.176, 1 df, P = 0.675	2.2 ± 1.3	1.9 ± 1.0	
	All years: N = 32, K-W. χ^2 = 0.078, 1 df, P = 0.779	2.3 ± 1.3	2.3 ± 1.6	0.025

Table 3.3 Cont. Results of statistical tests on muskrat population variables, comparing corn and hay bordered farm ditches in southern Quebec in 1989, 1990 and 1991.

Variable	Results of test	Mean ± SD in hay ditches	Mean ± SD in corn ditches	Power
Birth date of juveniles	1989: N = 30, K-W. χ^2 = 5.689, 1 df, P = 0.017	172 ± 24	142 ± 35	
	1990: N = 42, K-W. χ^2 = 0.013, 1 df, P = 0.909	139 ± 27	139 ± 28	
	All years: N = 72, K-W. χ^2 = 3.270, 1 df, P = 0.071	154 ± 30	140 ± 31	0.479
Annual population turnover	All years: N = 16, K-W. χ^2 = 0.008, 1 df, P = 0.927	97 ± 9	95 ± 14	0.045
Juvenile summer mortality rate	1989: N = 11, K-W. χ^2 = 0.079, 1 df, P = 0.778	62 ± 21	53 ± 39	
	1990: N = 21, K-W. χ^2 = 0.176, 1 df, P = 0.675	67 ± 20	72 ± 16	
	All years: N = 32, K-W. χ^2 = 0.078, 1 df, P = 0.779	66 ± 20	65 ± 26	0.03
Muskrat activity	Loglinear analysis, Pres/abs*Crop: 1 df, P = 0.0066, Pres/abs*Month: 2 df, P < 0.0001, Pres/abs*Crop* Month: 2 df, P = 0.2273			

The sex-ratio of adults was not found to be different between corn (21 ♂: 19 ♀) and hay ditches (21 ♂: 11 ♀; Table 3.3). The statistical power of 0.8 required a difference in proportion of the order of 1.7:1. The sex-ratio of adults in both types of ditches together was similar to the expected 50/50 ratio (General association = 1.154, 1 df, P = 0.283, Power = 0.360). If there was a difference, the proportion of males was not greater than 65% (Statistical Power of 0.8). When data from all years were combined, we obtained a proportion of 60.7% males (N = 135) that was not significantly different from the expected 50/50 ratio (χ^2 = 3.151, 1 df, P = 0.08 - with a Power of 0.8 at α = 0.04).

In 1989 and 1990, we caught 30 and 45 young of the year, respectively. In 1989, 15 young were recorded in both hay ditches and corn ditches, while in 1990, 19 young were recorded in hay ditches and 26 in corn ditches (Table 3.4). We did not detect a difference in the number of juveniles between corn and hay ditches (Table 3.4), but high standard deviations and small sample size resulted in low statistical power (Table 3.3). A statistical power of 0.8 required that the average number of juveniles between ditch type differ by a factor of 5.1:1.

We did not detect a difference in the sex-ratio of juveniles between corn ditches (24 ♂: 11 ♀) and hay ditches (17 ♂: 15 ♀). A difference in the proportion of males was not greater than by a factor of 1.7:1 (Statistical Power = 0.8). We did not detect any difference between the sex-ratio of juveniles altogether (41 ♂: 26♀) and the expected 50/50 ratio (χ^2 = 1.64, 1 df, P = 0.199, Power = 0.547, α = 0.043). If the proportion of males was greater than the proportion of females, it was not greater than 65% (Statistical Power = 0.8). The analysis of the sex-ratio for all individuals captured between crop type, controlling for years, showed a tendency for a higher proportion of males in corn ditches than in hay ditches (Table 3.3). The difference in the proportion of males was not greater than by a factor of 1.5:1 (Statistical Power = 0.8). When data on all individuals from all ditches in all years were pooled together, the sex ratio (60 ♂: 40♀) showed a tendency in favour of males when compared to the expected 50/50 ratio (χ^2 = 2.647, 1 df, P = 0.104- Power = 0.08 at α = 0.06).

Table 3.4 Total number of young captured, average (± SD) number of litters per adult female resident, and average (±SD) number of young per litter in 1989 and 1990 in selected ditch sections of southwestern Quebec.

Ditch	# of young	# of litters/ adult resident ♀	Young per litter	# of young	# of litters/ adult resident ♀	Young per litter
	1989			1990		
1	0	0	0	7	2	1.7±1.0
2	8	3	2.3±1.5	2	1	2.0±0.0
8	7	3	2.3±1.5	3	2	1.5±0.7
10	-	-	-	12	3	4.0±1.0
11	-	-	-	2	2	1.0±0.0
4	7	1	3.5±2.1	1	1	1.0±0.0
5	-	-	-	8	4	2.3±1.1
6	0	NA	0	0	0	0
7	8	3	2.7±2.9	0	0	0
9	-	-	-	10	4	2.2±1.0
Total	30			45		
Mean ± SD		2.0±1.4	2.7±1.8		1.9±1.4	2.1±1.1

The non-parametric analyses of variance performed to compare male and female adult weight per crop and year did not allow rejection of the null hypothesis for equality of weight for muskrats inhabiting corn or hay ditches (Table 3.3). H_o was not rejected either when testing the difference in weight of adult males between hay (1317 ± 157 g) and corn ditches (1271 ± 192) for all years altogether. A difference in male weight between crop ditches was not greater than 12% (Statistical Power = 0.8). Pooling data from all years, we did not detect a difference in weight of adult females between hay (1227 ± 140 g) and corn ditches (1148 ± 146 g - Table 3.3). A difference in the weight of adult females between crop ditches was not greater than 15% (Statistical Power = 0.8). When data on all adults from all years and all ditches were pooled, we found that the weight of adult males (1295 ± 174 g) was significantly greater than the weight of females (1197 ± 145 - Kruskal - Wallis $\chi^2 = 7.882$, 1 df, $\underline{P} = 0.005$).

Juveniles were captured in 2 of 3 ditches in 1989, both for corn and for hay ditches. In 1990, 2 of the 5 hay ditches had juveniles compared to 5 of the 5 corn ditches. The mean number of litters detected per 100 m was slightly higher and less variable in corn ditches (0.84 ± 0.49) than in hay ditches (0.67 ± 0.66). In 1989 and 1990, only 3 ditches accommodated more than 3 litters (Table 3.4). We did not detect any difference in the number of litters between corn ditches (2.2 ± 1.3) and hay ditches (1.7 ± 1.7), as determined by temporal relationships (Table 3.3). However, the statistical power of the test combining data from all years was low, largely due to high standard deviations.
A sample size of 142 ditches would have been necessary to obtain a power of 0.8 given the level of variation observed. The results for the number of litters per resident female were similar to the ones on the number of litters (Table 3.3). When combining data for 1989 and 1990, we did not detect a difference in the number of young per litter between hay ditches (2.3 ± 1.3) and corn ditches (2.3 ± 1.6). A power of 0.8, given the same standard deviations, required that the number of young per litter in corn and hay ditches differ by a factor of 2:1.

The number of samples used to estimate the mean weight gain per day of juveniles was low (n=10), due to the clumping of captures of the same individuals in a short period of time, precluding the possibility of defining individual weight gain, and the first capture of many young in the last trapping session. The estimated mean weight gain per day of juveniles was 6.13 ± 3.86 g/day .

The average growth rate seemed higher in hay ditches (7.57 g/day ± 4.51) than in corn ditches (5.16 g/day ± 3.45), but the small sample size precluded statistical verification. In 1989, muskrats were born earlier in corn ditches (142 ± 35, using Julian calendar days) than in hay ditches (172 ± 24 - Table 3.3). However, we did not detect a difference in the date of birth of young muskrats between hay ditches (139 ± 27) and corn ditches (139 ± 28) in 1990 (Table 3.3). Muskrats were born earlier in 1990 (139 ± 28) than in 1989 (157 ± 33) (Kruskal - Wallis $\chi^2 = 5.271$, 1 df, $\underline{P} = 0.022$).

The individual turnover was 100% in both hay and corn ditches between the summer of 1989 and the spring of 1990. Between the summer of 1990 and the spring of 1991, the individual turnover was 89.3% in hay ditches and 93.9% in corn ditches. When combining data from 1989 and 1990, we did not detect a difference in population turnover between corn ditches (97 ± 9%) and hay ditches (95 ± 14% - Table 3.3). Any difference was less than 18% (Power = 0.8). Only one hay ditch (#9) and one corn ditch (#1) did not show a 100% turnover. The three muskrats recaptured in 1991 were captured as juveniles in 1990. One female was recaptured in hay ditch #9 at the same location as in 1990. The two other juveniles, a male and a female, were recaptured in corn ditch #1, the male being captured at the same site as in 1990. Considering all years and data, juvenile annual turnover was 94.7% from the first capture to the following spring. We did not detect a significant difference in birth-to-capture juvenile mortality rate between corn and hay ditches (Table 3.3), and if there was a difference, it was not greater than 32% (Power = 0.8).

Figures 3.2, 3.3, and 3.4 present the first 3 dimensions of the factorial correspondence analysis on the 18 ditch-years and the following variables: the total number of individuals, the number of residents, the number of young, the number of litter, the number of young per litters, the number of burrows, and the annual population turnover. There is no clear separation of corn and hay ditch-years. Most ditch-years are in a cluster around the intersection of the two axis. Only three ditch-years show a different behaviour: corn ditch 2 (1990) is far apart from any other ditch-year on any combination of the first three dimensions, while corn ditch 1 (1990), and hay ditch 9 (1990) are also apart from the central cluster of ditch-years due to their coordinates on the second dimension. The observation of the positions of ditches 1, 2, 4, 6, 7, and 8 shows that the inter-annual variation is very important.

MUDTRACKING DATA

Tracks from 15 taxa were identified on the mudtracking boards. In decreasing order of importance (number of boards with tracks in parentheses) we had: raccoon (296), frog (283), muskrat (255), mink (103), turtle (57), bird (53), weasel (*Mustela frenata* or *Mustela erminea*) (13), meadow vole (*Microtus pennsylvanicus*) (12), jumping mouse (*Napeozapus* spp.) (6), Norway rat *(Rattus norvegicus*) (4), shrew (3), domestic cat (*Felis catus*)(3), red fox (*Vulpes velox*) (2), other canidae (2), and deer mouse (*Peromyscus maniculatus*) or white footed mouse (*Peromyscus leucopus*) (1).

In 1989, we had adult muskrat tracks in two hay ditches and in two corn ditches. The activity of muskrats varied with time and with crop type (Table 3.4). Muskrat activity was greater in August than in June or July, and within each month, was greater in hay ditches than in corn ditches (Figure 3.5). Although the number of resident males detected was similar in corn and hay ditches (Table 3.2), the average number of males detected was slightly higher in hay ditches than in corn ditches, but not statistically different (Table 3.3). Males travelled on the average longer distances (80 ± 9 m) than females (39 ± 19 m). No adult males were present in corn ditches after 4 May, while two adult males, that travelled a lot, were present in hay ditches. The mean of maximum movement in a given tracking session was 190.5 ± 43.5 m for males and 76.5 ± 70.5 m for females. The weekly activities of adult males and adult females within a given ditch, as detected by the mudtracking technique, overlapped in space by 68% ± 40%, while adult female weekly activities overlapped in space by 67% ± 52%. There were not enough pairs of co-occurring adult males to calculate their average overlap in spatial activity.

Figure 3.2 Graphical representation of the first two dimensions of the correspondence analysis using the 18 ditch-years and seven population variables: the total number of individuals (Nbind), the number of residents (Nbresid), the number of young (Nbyoung), the number of litter (Nblit), the number of young per litters (Litsize), the number of burrows (Nbbur), and the annual population turnover (Popturn). Ditch numbers with an asterisk represent 1989 data.

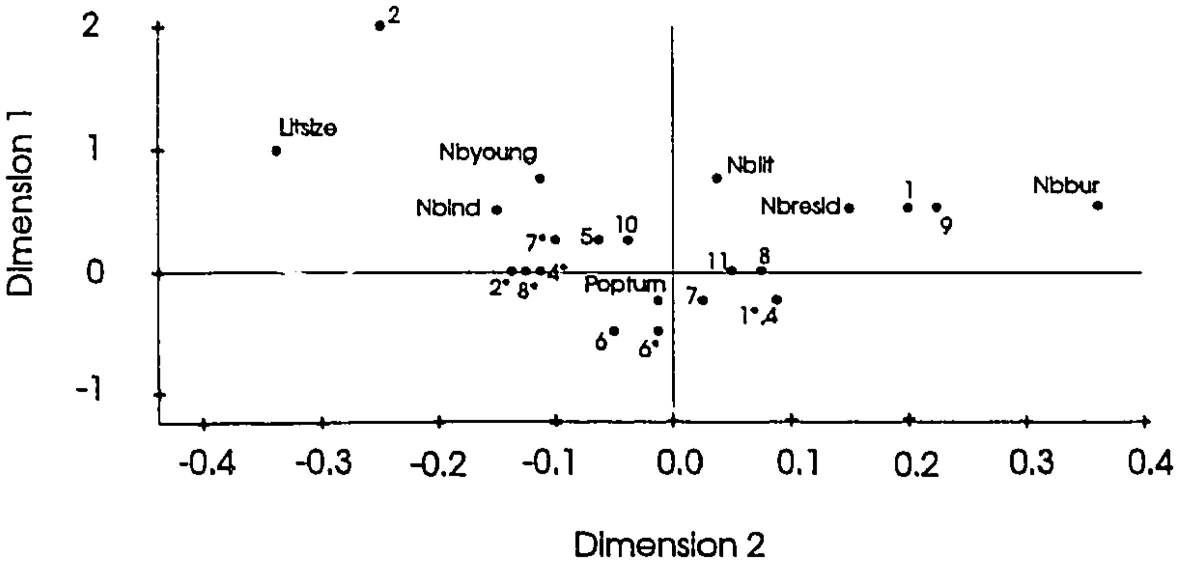

2
1
0
-1
Dimension 1
2
Litsize
Nbyoung
Nbind
Nblit
Nbresid
1
9
Nbbur
7*
5
10
11
8
2*
8*
4*
Poptum
7
1*
4
6
6*
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
Dimension 2

Figure 3.3 Graphical representation of the first and third dimensions of the correspondence analysis using the 18 ditch-years and seven population variables: the total number of individuals (Nbind), the number of residents (Nbresid), the number of young (Nbyoung), the number of litter (Nbiit), the number of young per litters (Litsize), the number of burrows (Nbbur), and the annual population turnover (Popturn). Ditch numbers with an asterisk represent 1989 data.

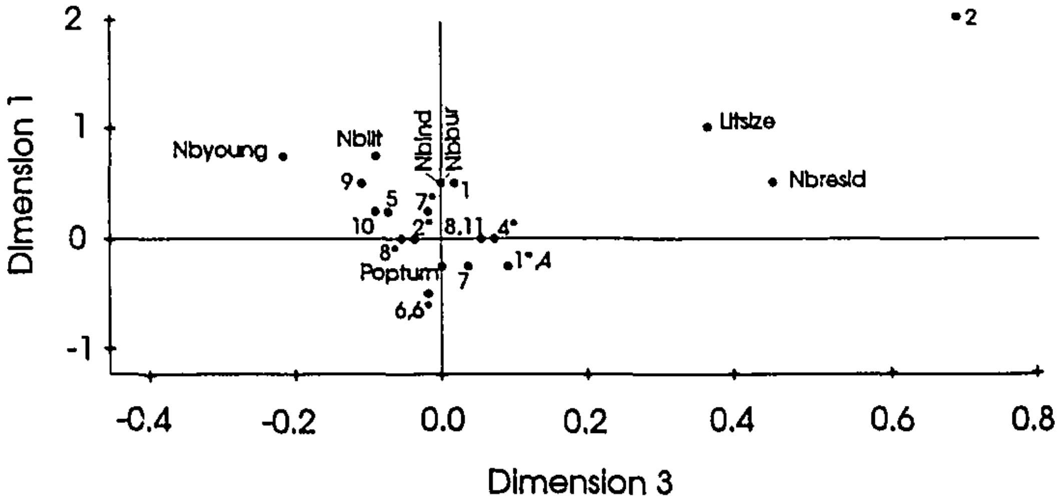
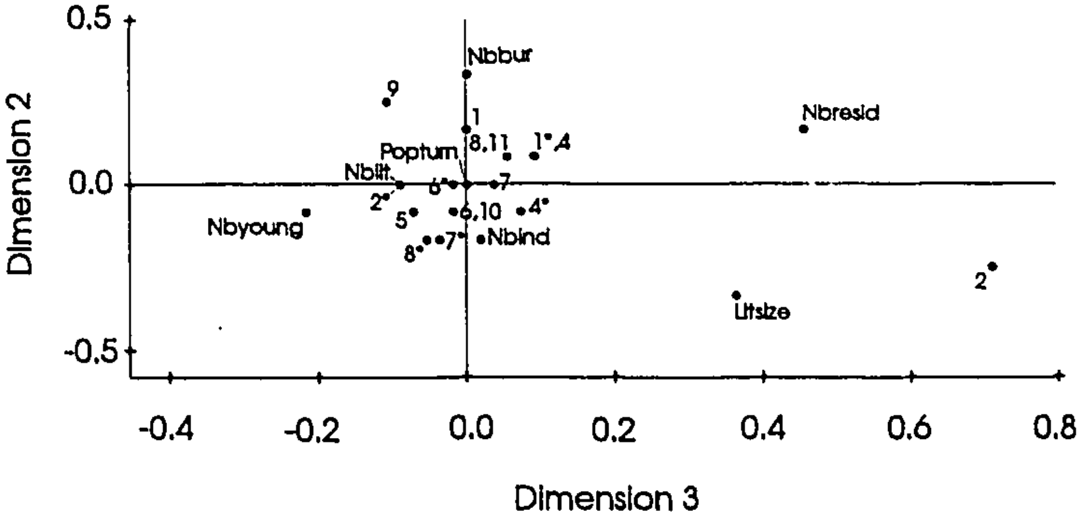

2
1
0
-1
Dimension 1
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
Dimension 3
Nbyoung
Nblit
Nbind
Nbbur
Litsize
Nbresid
2
9
5
1
7
10
2
8,11
4
8
1
A
Poptum
7
6,6

Figure 3.4 Graphical representation of the second and third dimensions of the correspondence analysis using the 18 ditch-years and seven population variables: the total number of individuals (Nbind), the number of residents (Nbresid), the number of young (Nbyoung), the number of litter (Nblit), the number of young per litters (Litsize), the number of burrows (Nbbur), and the annual population turnover (Popturn). Ditch numbers with an asterisk represent 1989 data.

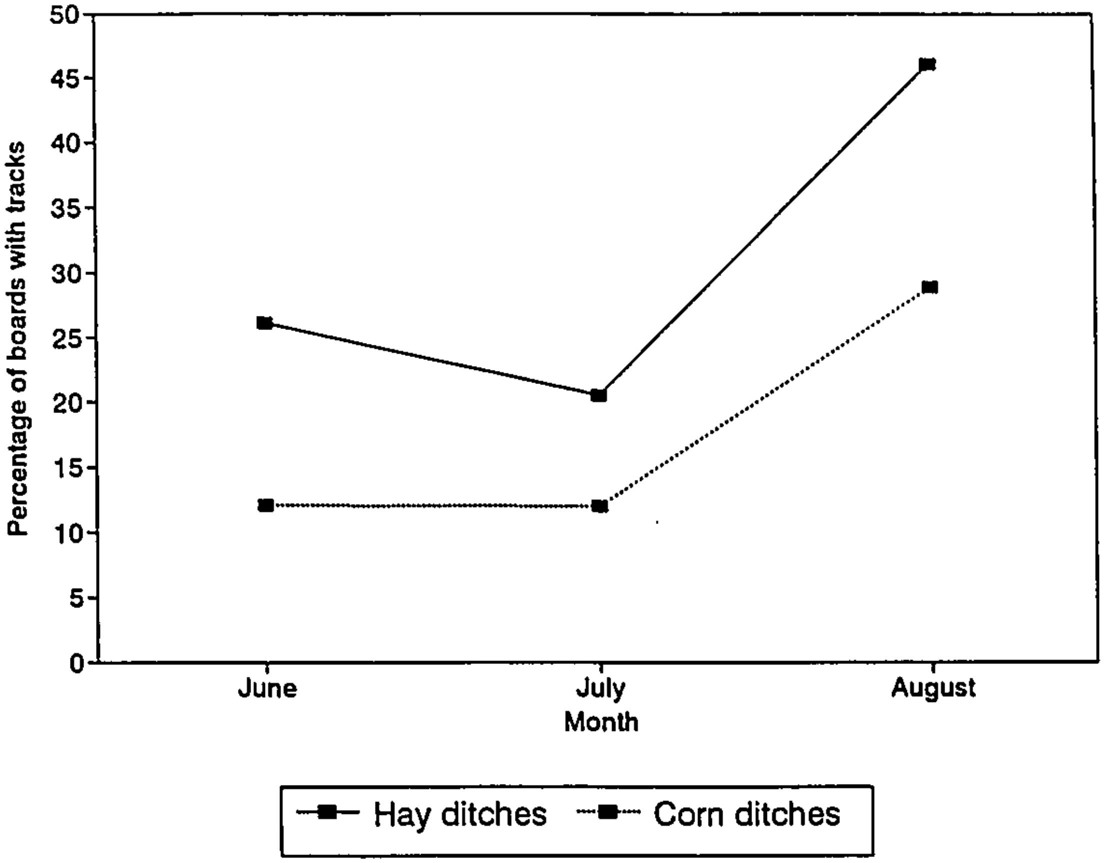

0.5
0.0
-0.5
Dimension 2
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
Dimension 3
Nbbur
9
1
8,11
1
A
Poptum
Nbresid
Nblit.
6
7
2
5
6,10
4
Nbyoung
7
Nbind
8
2
Litsize

Raccoon activity varied significantly from month to month, and higher activity was detected in corn ditches than hay ditches (Table 3.5), with this difference increasing throughout the summer (Figure 3.6). Mink activity was similar near both crop types, and increased throughout the summer (Table 3.5 and Figure 3.7). Turtle activity was not affected by crop type, and varied from month to month (Table 3.5), but instead of increasing steadily during the summer, it peaked during July, with June and August showing similar values (Figure 3.8). Only eastern painted turtles (*Chrysemys picta picta*) and snapping turtles (*Chelydra serpentina*) were captured in muskrat traps, and no other species of turtle was observed. Frogs were the only taxon whose activity did not change throughout the summer (Table 3.4), and frog activity was greater in hay ditches than in corn ditches (Table 3.4 and Figure 3.9). The only frog species observed in ditches in 1989 and 1990 were the leopard frog (*Rana pipiens*) and the green frog (*Rana clamitans*).

BURROWS AS INDICATORS OF MUSKRAT POPULATION

The natural logarithm of the number of muskrat burrows (lnburrow) was positively linked with the number (Nbresid) of resident muskrats (Nbresid = 0.73 (lnburrow); N = 16, 1 df, F=54.28, $R^2 = 0.78$, $\underline{P} = 0.0001$;), with the number (Nblit) of litters (Nblit = 1.02 (lnburrow); F=56.14, $R^2 = 0.79$, $\underline{P} = 0.0001$), and with the maximum number (Maxind) of individuals detected in the same week (Maxind = 2.44 (lnburrow); F=56.79, $R^2 = 0.79$, $\underline{P} = 0.0001$).

Figure 3.5 Percentage of mudtracking boards that showed muskrat tracks in 3 corn and 3 hay ditches of southwestern Quebec in June, July and August of 1989. Data were pooled for all corn ditch sections, and for all hay ditch sections.



50
45
40
35
30
25
20
15
10
5
0
Percentage of boards with tracks
June
July
August
Month
Hay ditches
Corn ditches

Table 3.5 Results of loglinear analyses on summer monthly activity of raccoon, mink, frogs, and turtles between three hay and three corn bordered ditches of southern Quebec in 1989.

Vertebrate activity	Results of loglinear analyses
Raccoon	Pres/abs[1]*Crop: 1 df, $\underline{P} < 0.0001$ Pres/abs*Month: 2 df, $\underline{P} < 0.0001$ Pres/abs*Crop*Month: 2 df, $\underline{P} = 0.0672$
Mink	Pres/abs*Crop: 1 df, $\underline{P} = 0.6929$ Pres/abs*Month: 2 df, $\underline{P} < 0.0001$ Pres/abs*Crop*Month: 2 df, $\underline{P} = 0.6668$
Frogs	Pres/abs*Crop: 1 df, $\underline{P} = 0.0066$ Pres/abs*Month: 2 df, $\underline{P} = 0.1558$ Pres/abs*Crop*Month: 2 df, $\underline{P} = 0.1074$
Turtles	Pres/abs*Crop: 1 df, $\underline{P} = 0.2412$ Pres/abs*Month: 2 df, $\underline{P} < 0.0001$ Pres/abs*Crop*Month: 2 df, $\underline{P} = 0.3205$

[1] Pres/abs: The number of mudtracking boards with presence of a given species tracks over the number of boards where the species tracks were absent. For species other than raccoon, boards without tracks had to be free of raccoon tracks.

Figure 3.6 Percentage of mudtracking boards that showed raccoon tracks in 3 corn and 3 hay ditches of Southwestern Quebec in June, July and August of 1989. Data were pooled for all corn ditch sections in and for all hay ditch sections.

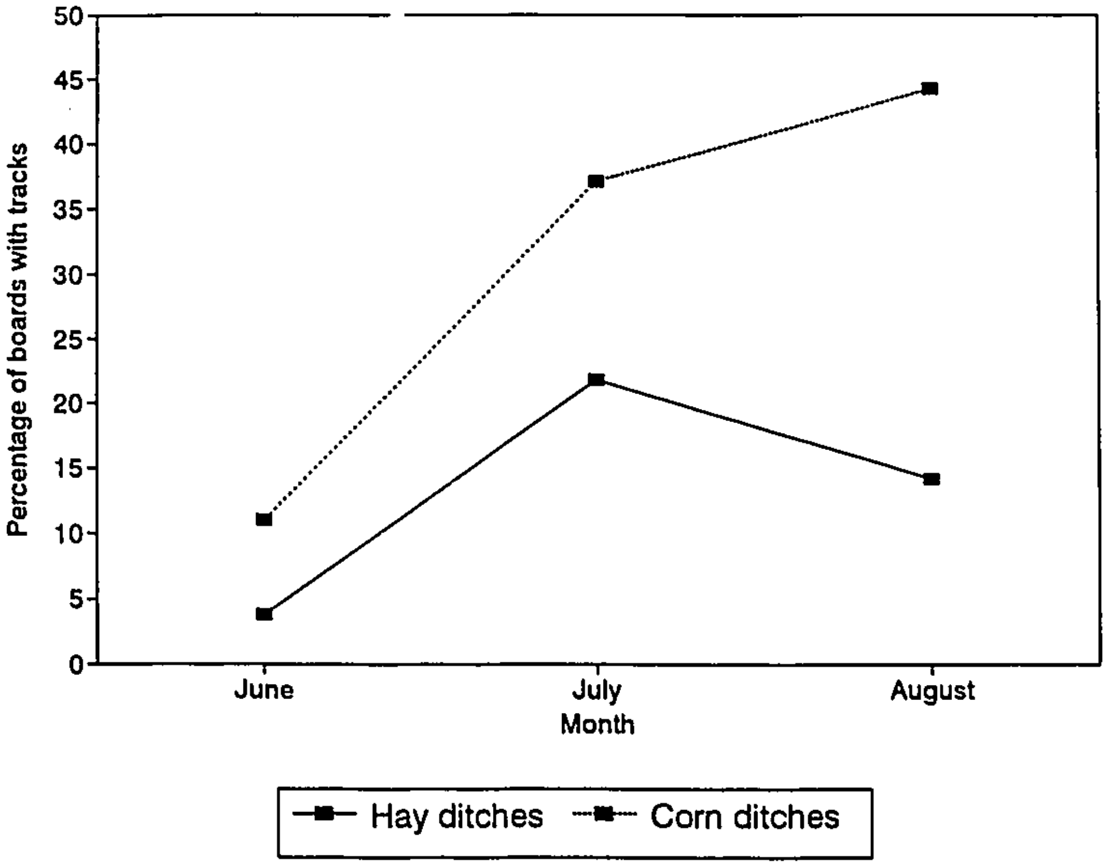
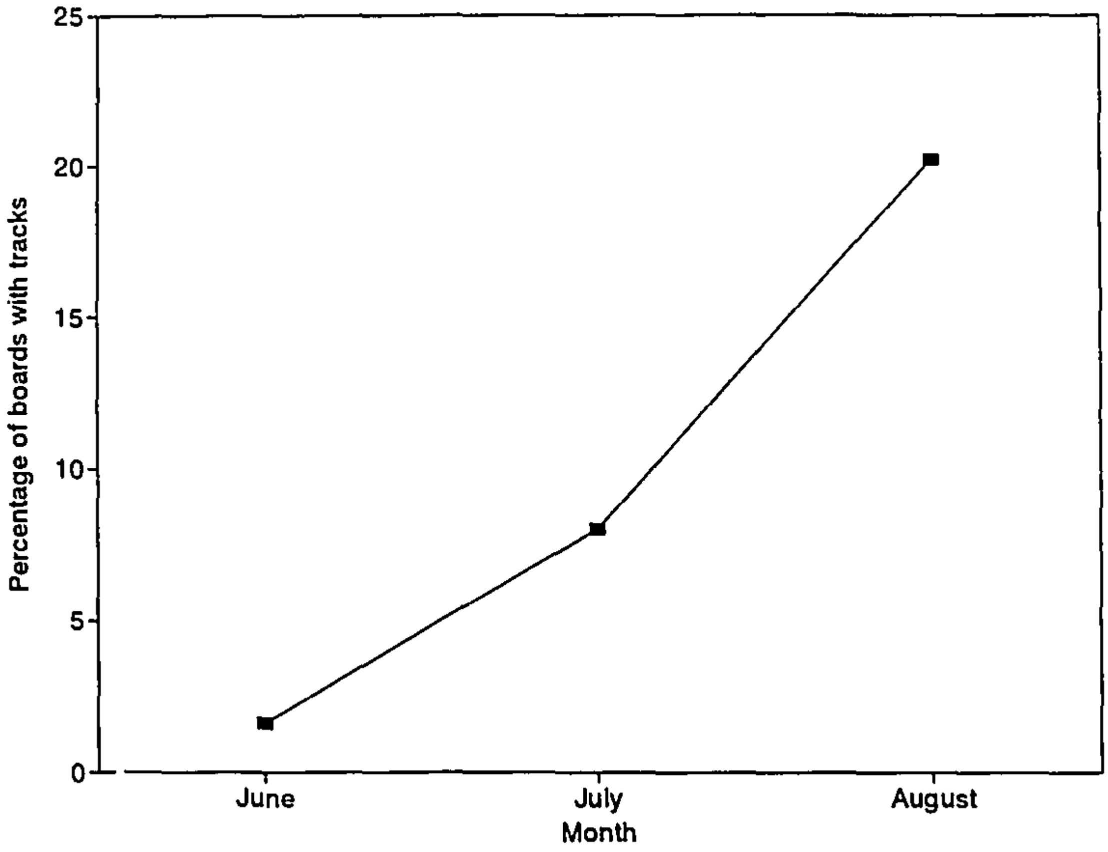
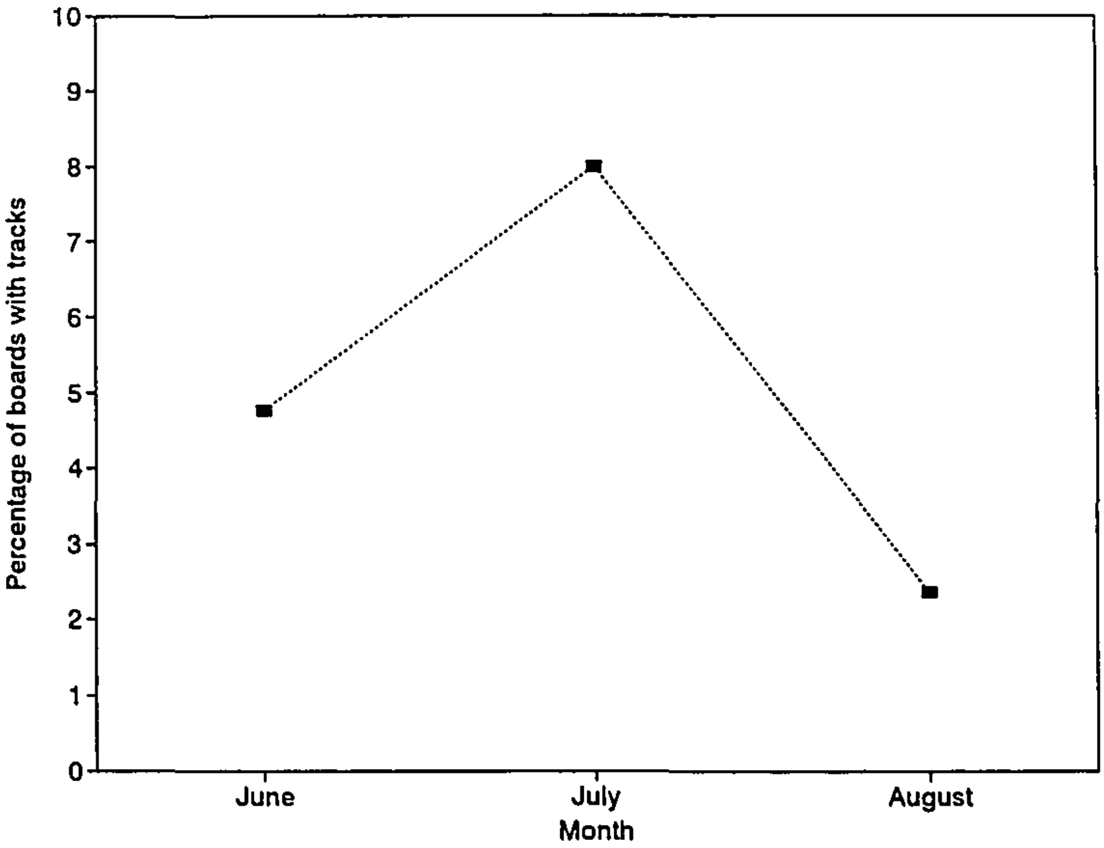

Percentage of boards with tracks
50
45
40
35
30
25
20
15
10
5
0
June
July
August
Month
Hay ditches
Corn ditches

Figure 3.7 Monthly activity of mink in six 240-m to 270-m ditches of southwestern Quebec in June, July and August of 1989, as measured by the percentage of mudtracking boards with tracks. Boards were considered free of mink tracks only when raccoon tracks were also absent. Data from hay and corn ditch sections were pooled because there was no difference in mink activity between hay and corn ditches.



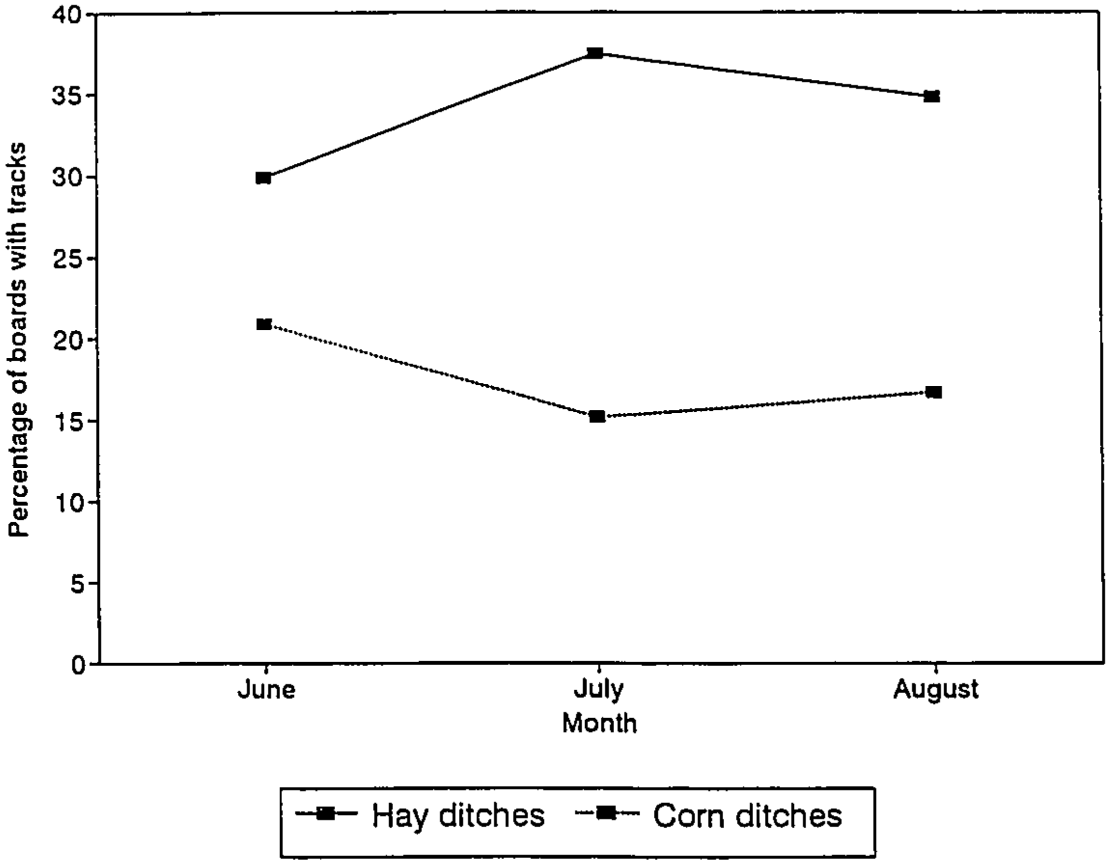
Percentage of boards with tracks
0
5
10
15
20
25
June
July
August
Month

Figure 3.8 Monthly activity of turtles in six 240-m to 270-m ditches of southwestern Quebec in June, July and August of 1989, as measured by the percentage of mudtracking boards with tracks. Boards were considered free of turtle tracks only when raccoon tracks were also absent. Data from corn and hay ditch sections were pooled because there was no difference between hay and corn ditches.



10
9
8
7
6
5
4
3
2
1
0
Percentage of boards with tracks
June
July
August
Month

Figure 3.9 Monthly activity of frogs in three corn and three hay ditches of southwestern Quebec in June, July and August of 1989, as measured by the percentage of mudtracking boards with tracks. Boards were considered free of frog tracks only when raccoon tracks were also absent.



Percentage of boards with tracks
40
35
30
25
20
15
10
5
0
June
July
August
Month
Hay ditches
Corn ditches

DISCUSSION

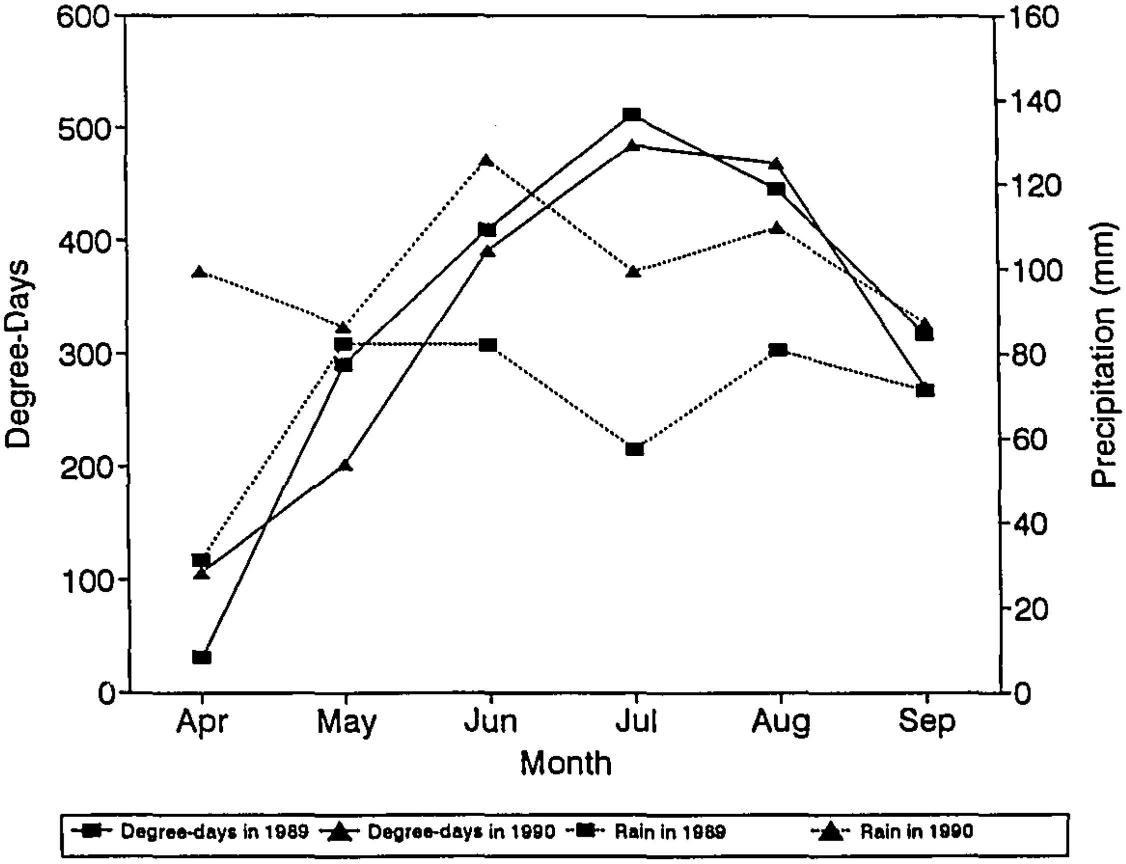
We did not detect a difference between corn and hay bordered ditches for thirteen muskrat population variables, namely the number of adult males, the number of adult females, the overall number of adults, the sex-ratio of adults, the number of juveniles, the sex ratio of juveniles, the weight of adult males, the weight of adult females, the number of litters, the number of litters per resident adult female, the number of young per litter, the annual population turnover, and juvenile summer mortality rate. Juvenile muskrats were born earlier in corn ditches in 1989, while muskrat activity was higher in hay ditches in 1989. We also detected a tendency for a higher proportion of males to occur in corn ditches. The same growth rate value was used in corn ditches and hay ditches to calculate birth dates. This value is greater than the value of 5.34 ± 0.10 g/day obtained by regressing data from Erickson (1963) (Linear regression, $R^2 = 0.9921$, 24 df, $\underline{P} = 0.0001$), but we chose to use the value of 6.13 g/day derived from our study area because following Erickson's growth curve, many of the juveniles captured should have been born in March. This is doubtful, as none of the 16 females killtrapped at the end of March 1991 was bearing embryos. The result of the test on birth dates of juveniles between corn and hay ditches suggest that, in fact, juvenile growth rate could have been higher in corn ditches than in hay ditches. The factorial correspondence analysis performed using the seven population variables without missing values did not produce a clear separation of corn and hay ditch-years. An examination of the average values obtained for the population variables studied (in each year, or for pooled data, Table 3.3) shows that the number of times it was in favour of corn ditches (10) was similar to the number of times it was in favour of hay ditches (11), while values were equal seven times in both types of ditches. The failure to detect significant effects for some population variables, such as the number of adult females between corn and hay ditches in 1991, may have been due to the low statistical power of the tests resulting from small sample size and high standard deviations. Many variables had standard deviations greater than 50% of the value of the mean. The correspondence analysis also showed that the position of several ditches varied from year to year, as different results were obtained for some of the population variables. For example, eight young were recorded in ditch 7 in 1989, while none were detected in 1990, and seven were produced in ditch 1 in 1990, while none were detected in 1989.

Juvenile mortality during the vegetation growing season has been shown to vary from 20% to 57.5% in various habitats (See Clough 1987; Proulx and Buckland 1986; Dauphiné 1965; Smith 1954) and annual survival of juveniles to vary from 8.5% to 20% (Boutin, Moses and Caley 1988; Clark 1987; Proulx and Gilbert 1983; Le Boulengé and Le Boulengé-Nguyen 1981; Stewart and Bider 1974). Annual survival of adult muskrats has also been shown to vary from 5.8% to 20% in riverine environments (Clark 1987; Clay and Clark 1985; Le Boulengé and Le Boulengé-Nguyen 1981). With normal water level conditions on the Delta Marsh, annual survival of muskrats of all ages was shown to be as low as 3.1% (Clark and Kroeker 1993). In the present study, the birth-to-first capture juvenile mortality rate was found to be 66% in hay ditches and 65% in corn ditches. These high values could have been due to predation. Predation rates were shown to be higher with low water levels (Proulx et al. 1987). In this study, the presence of mink and raccoon was shown to increase as water level declined throughout the summer. The high rate of muskrat annual population turnover in both types of ditches suggests that the availability of food in hay fields bordering ditches in winter did not provide higher chances of survival for muskrats. High turnover could also be due to the high risk that ditches freeze up in winter, and a rigorous winter could prevent the detection of a crop effect on muskrat annual population turnover. In December 1989, the temperature dropped to or under -15.0°C at night for 28 days (Environment Canada, Unpublished data), and there was little snow on the ground to prevent deep freezing of water bodies (J. Quenneville, pers. comm.). A study similar to the present one, but conducted at a lower latitude may have shown a difference between corn and hay ditches in muskrat annual population turnover. Muskrat survival in winter may be higher than what is suggested by the annual population turnover found in the present study, as a proportion of each muskrat population in each ditch section could have dispersed in the fall and survived elsewhere.

The maximum number of muskrats per surface unit of water in this study is the second highest value reported. A maximum of 86.5 individuals per ha was obtained by Errington (1940) in an Iowa marsh where cattail and bulrush were abundant (see review by Le Boulengé and Le Boulengé-Nguyen 1981). The high muskrat density but high annual turnover rate could be a sign that the studied ditches represent marginal habitats harbouring sink populations, or simply very good seasonal habitat. If muskrat distribution is best explained by a despotic model than by an ideal-free distribution model (Messier et al. 1990), then less competitive muskrats may be forced to occupy marginal habitats. Myllymaki (1977) suggested that overlap of home ranges was a function of density. The high overlap in adult muskrat activity obtained in our study is an indication of high density. It is expected that better habitats should yield lower rates of annual population turnover , higher production of juveniles and growth rate. No indication of consistent differences regarding annual population turnover and production of juveniles was detected between crops, suggesting that the presence of corn fields adjacent to ditches did not result in a better habitat than the presence of hay.

The growth rate of juveniles (6.13 ± 3.86 g/day) was greater than the value of 5.34 ± 0.1 g/day obtained by Erickson (1963) from captive muskrats, and greater than values of about 5 g/day obtained by Vincent and Quéré (1972) in drainage ditches and ponds of Belgium, and 4 g/day obtained by Simpson (1987) in lakes of northern Yukon. On the other hand, despite the abundance of food in the ditches of the present study, higher values were obtained in Ontario (7.1-8.84 g/day; Simpson 1987) and New Brunswick marshes (7.1-7.5 g/day; Parker and Maxwell 1984). The same arbitrary growth rate value was used in 1989 and 1990 to calculate birth dates. The resulting birth dates were earlier in 1990 than in 1989, suggesting that in fact, individual growth rate was higher in 1990 than in 1989, possibly due to the higher number of degree-days and precipitation in May, June and July 1990 (Figure 3.10). The higher amount of rain in 1990 could have favoured muskrat foraging activities (Stewart and Bider 1974) and provided better access to food supply. A higher number of degree-days could reduce energetic costs in the spring as muskrats would normally be out of their thermoneutral zone (10°C - 32°C, McEwan et al. 1974) for several nights. As pregnancy and lactation have been shown to double female rodent energy requirements (Kaczmarski 1966, Migula 1969, Randolph et al. 1977, Millar 1978), reduced female energetic costs due to favourable temperature could have contributed to increased juvenile growth rate.

Figure 3.10 Number of degree-days and amount of rain in 1989 and in 1990 for May, June and July measured at the intersection of La Guerre River and Lake St-Francis (Environment Canada, Unpublished data).


600
500
400
300
200
100
0
Degree-Days
160
140
120
100
80
60
40
20
0
Precipitation (mm)
Apr
May
Jun
Jul
Aug
Sep
Month
Degree-days in 1989
Degree-days in 1990
Rain in 1989
Rain in 1990

The greater weights of males, when compared to females, could be an adaptation to facilitate male dispersal and improve mating chances, while females, that have been shown to stay closer to their birth site (Sather 1958, Caley 1987), would rather put their energy into producing young. The average number of litters per resident adult female was similar to the average of 2 obtained for populations experiencing a cold winter season (See review by Clough 1987 and Dauphiné 1965). Muskrats occupying terrestrial habitats have a much lower average of 1.4 litter per adult female (Clough 1987).

As was the case for muskrats, raccoons were more active in August than in June-July, but unlike muskrats, they were more active in corn ditches. Raccoons may concentrate their activity in the ditches along corn fields because of the absence of cover and food in those fields in early to mid-summer, corn seeds being unavailable at this time. The higher level of raccoon activity in corn ditches may have impacted on the detection of muskrat activity, since muskrats could have been more secretive in corn ditches than in hay ditches because of the higher activity of a potential predator (Lacki et al. 1990).

Mink activity was not affected by crop type, although some of its preys, including muskrats and frogs, that have been shown to form up to 55% of its prey items (Hamilton 1959) showed higher activity in hay ditches than corn ditches. In the summer, mink can prey on a variety of other animals such as crayfish, fish, birds, voles and shrews (Hamilton 1959). An absence of crop effect on mink activity could mean that there was no overall significant crop effect on the guild of potential mink preys, including muskrat, or that if there was one, the availability of prey species did not represent a limiting factor for mink in summer. The greater frog activity in ditches bordered by hay fields could be an indication of higher population density. Animal activity measured by recording tracks was shown to be a good measure of population density for hare (*Lepus americanus*), squirrel (*Tamiasciurus hudsonicus*), and marten (*Martes americana*) (Thompson et al. 1989). The leopard frog is known to disperse in meadows and hay fields in the summer (Cook 1984). Corn fields may not be as suitable. Moreover, increased raccoon activity in corn ditches may have resulted in higher levels of predation on frogs, one of their favourite food items (Rivest and Bergeron 1981).

Turtle activity in ditches was not affected by adjacent crops. Since painted turtle nesting activities have been shown to peak in June in southern Quebec (Christens and Bider 1987), the detected July peak in turtle activity probably corresponded with the period of high basking activity. Floating objects, like our mudtracking platforms, would then be readily used.

The highly positive relationship between the natural logarithm of the number of burrows and the number of residents or the maximum number of muskrats showed the potential usefulness of using the number of burrows as a measure of population size. This finding is important because of the non-intrusiveness of such a tool, that could be used to assess muskrat abundance. Aerial surveys of lodges have already been used to assess muskrat abundance (Dozier et al. 1948, Proulx and Gilbert 1984). Although muskrat burrows could last longer in more cohesive soils, older burrows could have more openings than recent ones. The number of young per litter could vary with environmental conditions (Boyce 1977, Smith et al. 1981). The absolute ratio of muskrat per burrow could also change with density. However, the use of the logarithm of burrows should have diminished the effects of these factors on the relationship with the number of muskrats.

In this study, we did not find consistent differences between crop type for muskrat population variables, thereby showing no convincing evidence that corn-bordered ditches provided better habitat than hay-bordered ditches for muskrats. This is in contradiction with untested statements by previous authors (Errington 1963; Chulick 1979; R. Foley, pers. comm.) regarding the higher or lower habitat quality provided by corn fields bordering wetlands. These reports did not provide information on macrophyte cover, width of the non-cultivated belt from water edge to the adjacent crop, or water level, three variables that could affect muskrat presence (see Chapter 2, and Nadeau et al. 1995). Results obtained for muskrat activity were not predictive of results obtained for other vertebrate taxa.

MANAGEMENT IMPLICATIONS

Given that muskrat density in small farm ditches can be high, and that this type of wetland often dominates in the agricultural landscape, there is a high potential for managing habitat and muskrat populations. Actions that would reduce annual natural population turnover would increase the availability of muskrat during the spring trapping season. Maintaining a water level sufficient to avoid the complete water freeze-up could allow muskrat to survive harsh winters in small ditches. Another management option would be to allow trapping in small ditches in the fall, as most muskrats will have disappeared from their respective ditch the following spring anyway.

At this time, it would not be justified to act on the type of crops bordering ditches to favour muskrat populations. Management of habitat along farm ditches would also have to consider separately the effects on co-occurring species. In areas where muskrats are mainly burrow-dwellers, counting the number of burrows could permit an estimation of population size.

ACKNOWLEDGEMENTS

We are grateful to Kateri Lescop-Sinclair and Heather Cunningham for their significant contribution to the field work. We thank all landowners who allowed us to work on their land, and particularly to Gilles Queneville, Jacques Leblanc and M. St-Onge This work was financed by NSERC grants to J.R. Bider and a NSERC Doctoral fellowship to S. Nadeau.

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In Chapter 3, I found no convincing evidence that corn crop along ditches provided different habitat quality for muskrat than hay fields, as measured through population variables. The results of muskrat population dynamics in different habitat can be further analyzed by looking at population genetics. In the fourth chapter, we used DNA fingerprinting to test the differential effects of corn and hay fields on the genetic proximity between adult muskrats inhabiting a given ditch within the same year, and between adults of the same ditch in two successive years. If adjacent crops affect habitat quality for muskrats, it was expected that a lower quality habitat would cause a higher genetic diversity in muskrat populations, within and between years. This would either be due to the absence of philopatry in low quality habitat or to higher population turnover.

CHAPTER FOUR

Effect of habitat quality on genetic proximity among muskrats

ABSTRACT

Low philopatry or high population turnover, usually a consequence of low habitat quality, may result in greater genetic distance among adult muskrats inhabiting such habitats than among adults in high quality habitats. To test this hypothesis, we used DNA fingerprinting to compare farm ditches bordered with corn versus hay fields for Band Sharing Indices (BSI's) among adult muskrats within the same ditch in a given year, and among different adults of a given ditch but in two successive years. The BSI of adult female-female and male-female pairs in a given ditch within the same year was higher (♀♀: 0.361 ± 0.179; ♂♀: 0.361 ± 0.208) than the value obtained in different ditches (♀♀: 0.200 ± 0.143; ♂♀: 0.219 ± 0.159; ♀♀: N = 133, K-W. $\chi^2 = 21.099$, 1 df, P = 0.0001; ♂♀: N = 200, K-W. $\chi^2 = 23.248$, 1 df, P = 0.0001). No difference was found between male-male adult pairs from the same ditch and from different ditches (N = 66, K-W. $\chi^2 = 2.618$, 1 df, P = 0.1057), but the statistical power of the test was low. The DNA fingerprinting technique did not allow us to detect a significant effect of corn versus hay bordered ditches on the genetic proximity between adult pairs divided in sex groups (♂♂, ♀♀, ♂♀), within and among years, as measured by their Band Sharing Indices. The relatively small number of adults limited the statistical power of the analyses.

Although there are some limitations in using the DNA fingerprinting technique on animals exhibiting short-distance dispersal such as muskrat, we were able to confirm the usefulness of this technique to determine muskrat parental linkages. The analysis of band sharing indices also generally confirmed relatedness between individuals as determined by spatio-temporal association of livetrapped individuals. Analyses of BSI's also showed that livetrapping did not always permit the detection of all parents of livetrapped young muskrats.

Key words: *Ondatra zibethicus*, muskrat, habitat quality, population genetics, DNA fingerprinting.

INTRODUCTION

Various techniques have been used to determine kinship or pair-bond associations between individuals. The most commonly used measure is the association of individuals based on their spatial and temporal distribution. As outlined by Caley (1987), this technique is relatively inefficient for the detection of cuckoldry or for the identification of the true father in species exhibiting extra-pair mating. Spatio-temporal association of individuals also requires multiple captures, or detection of the same animal in space and time. Low trappability of some individuals is a constraint to this technique. The dusting ("shake'n bake") technique with fluorescent pigments could be used as an alternative, combined with the injection of radionuclides in pregnant females (Wolff et al. 1988), and followed by an allozyme analysis to identify father-offspring links. However, this technique is time-consuming and still faces limitations associated with the obligation to trap all adult males and females. A better technique for the identification of mother-offspring links would be the analysis of mitochondrial DNA profiles generated by several restriction endonucleases (Avise et al. 1989). This technique has the advantage of permitting the identification of lower order relatives, but fathers cannot be identified, nor is information about the extent of nuclear gene flow or variability provided by mitochondrial DNA analyses (Gilbert et al. 1990). Genomic DNA multilocus fingerprinting has been used to test spatio-temporal associations or mating behaviour in birds (Wetton et al. 1987, Burke and Bruford 1987, Gyllenstein et al. 1990, Westneat 1990, Lifjeld et al. 1991), mammals (Reeve et al. 1990, Hoagland et al. 1991, Ribble 1991) and fish (Rico et al. 1991). The DNA fingerprinting technique has the advantage of being applicable to both male and female lineage analyses. With this technique, kinship and parentship can be determined without the requirement of having to trap all individuals and without having to use several endonucleases or to analyze several allozyme patterns.

In this study, we used DNA fingerprinting to test for difference between corn and hay bordered ditches of the Band Sharing Indices (BSI's) among adult muskrats inhabiting a given ditch within a year, and among different adults in the same ditch in two successive years. If adjacent crops affect habitat quality for muskrat, it is expected that a low quality habitat will cause a higher genetic diversity in muskrat populations, within and between years than a high quality habitat. This would either be due to a lower rate of philopatry in low quality habitat or to lower population turnover in high quality habitat. Young muskrats born in good habitats are likely to remain closely associated with their birth site the first year (Errington 1937). The analyses were done using adults only, as they can leave a low quality patch to find a better one, and are not dependent on other individuals, as juvenile muskrats are.

The usefulness of the spatio-temporal technique to determine potential littermates (see Chapter 3), as well as parentage relationships, was investigated by testing BSI's among juveniles and between juveniles and putative parents in a given ditch.

METHODS

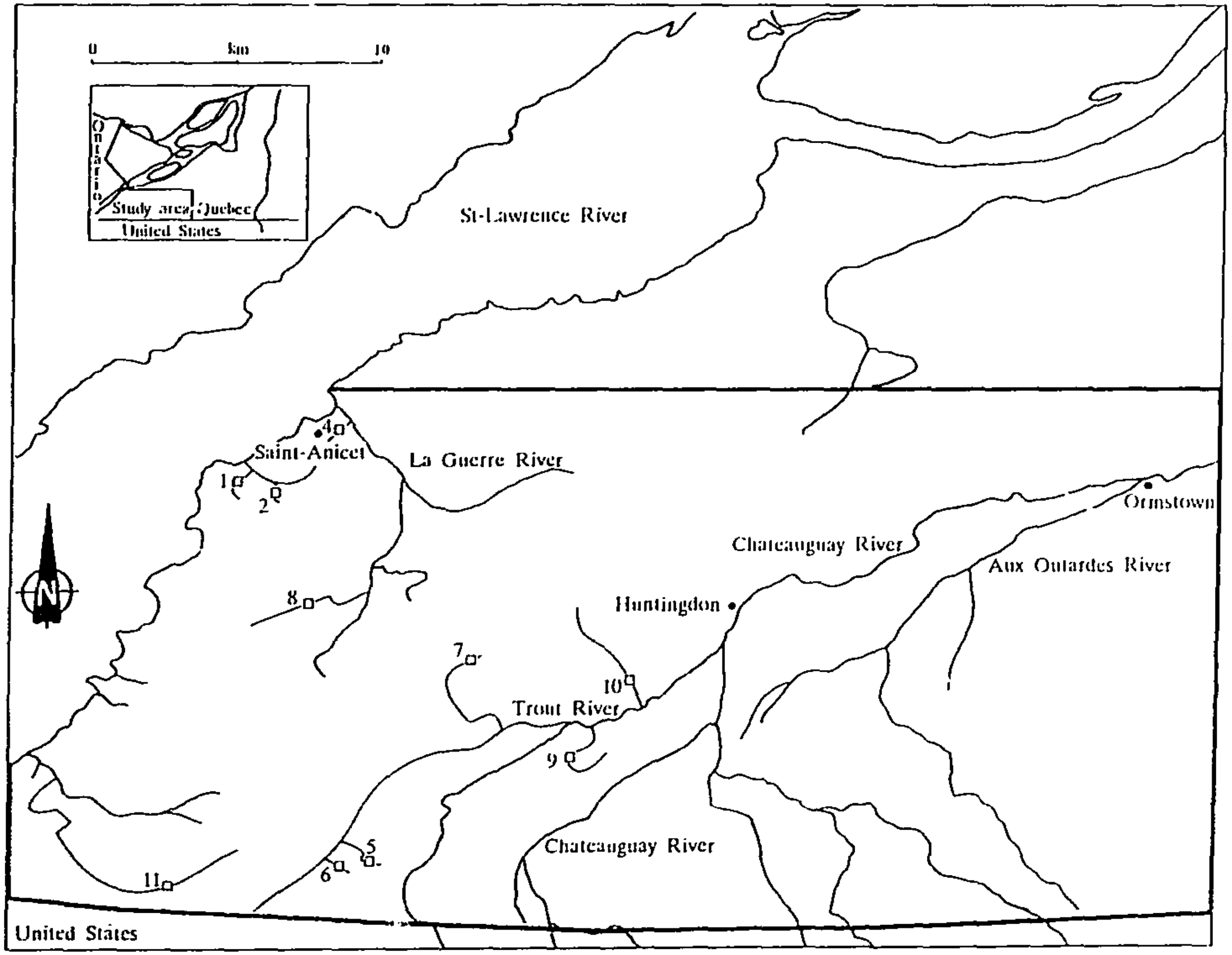
STUDY AREA

The study area was located in southwestern Quebec, between the Saint-Lawrence River and the New-York State border (Figure 4.1). Three sections of ditches bordered by corn fields (ditches 1, 2, 8) and three sections bordered by hay fields (ditches 4, 6, 7) were selected in 1989. Paired sections varied in length from 240 m to 270 m. In 1990 and 1991, the number of ditches was raised to five in corn-bordered ditches (ditches 1, 2, 8, 10, 11) and hay-bordered ditches (ditches 4, 5, 6, 7, 9).

TRAPPING

Muskrats were livetrapped in 1989 and 1990, and killtrapped in 1991, as described in Chapter 3. In each trapping period, livetraps were also set up along an additional distance of 75m outside of the sections studied in Chapter 3, in order to capture more adults for the test comparing band sharing index between adults within and among ditches. In 1989 and 1990, all animals were marked by toe-clipping, and the phalanx was preserved for DNA extraction. Phalanges were kept on ice or dry ice, frozen at -20°C less than 3 hours after being cut and stored at -70°C within 7 days for subsequent DNA fingerprinting analyses. In 1991, a forepaw of each killtrapped animal was preserved for DNA extraction. Forepaw samples were kept on ice or dry ice for five to six hours before being frozen at -70°C.

Figure 4.1 Study area in southwestern Quebec. Animals were either livetrapped (1989 and 1990) or killtrapped (1991) along ditch sections bordered either by corn fields (1, 2, 8, 10, 11) or hay fields (4, 5, 6, 7, 9).


0
km
10
Ontario
Study area
Quebec
United States
St-Lawrence River
4
Saint-Anicet
La Guerre River
1
2
Ormstown
Chateauguay River
Aux Outardes River
N
8
Huntingdon
7
10
Trout River
9
5
6
11
Chateauguay River
United States

DNA FINGERPRINTING

Genomic DNA was extracted following the method described by Müllenbach et al. (1989). The protocol was slightly modified by adding betamercaptoethanol at the digestion step to a final concentration of 2%. After being precipitated in isopropanol, the DNA pellet was put in ethanol for an hour. Five micrograms of DNA from each individual were digested with the restriction enzyme Alu I at 37°C for a minimum of 4 hours. Electrophoresis was carried out in 1% agarose in a TPE buffer (0.089M Tris, 0.128% phosphoric acid, 0.02M EDTA, pH 8.0) at 1.5 Volts/cm for 17 hours. After electrophoresis, the gel was successively soaked in a solution of 5 mg/l ethedium bromide for 15 min., in 0.25M HCl for 25 min., in an alkaline solution (1.2M NaCl, 0.4M NaOH) for 30 min., and in a transfer solution (1M ammonium acetate, 0.02M NaOH) for 30 min. The gel was then capillary-blotted overnight in the transfer solution on a nitrocellulose membrane (Schleicher & Schuell) after the Southern (1975) method. The membrane was then baked for 2 hours at 80°C, and prehybridized for at least 5 hours at 60°C in a Corex tube containing 7% SDS, 0.263 Na phosphate, 1 mM EDTA and 1% bovine serum albumin (fraction V). The probe pYNZ132 (Nakamura et al. 1987) was produced by DNA purification in a low melting point agarose gel from cultures of *E. Coli* HB101 containing the plasmid clone pYNZ132 (American Type Culture Collection). [α-^{32}P]dtcp labelling was carried out with an oligo-prime labelling kit (Pharmacia) or a quick-prime kit (Bohringer). The number of isotope degradations per minute was between 3.22×10^8 and 9.64×10^8 per μg of DNA. Fifty nanograms of probe were used per filter. The probe mix was added to the prehybridized filters, and let to hybridize from 17 to 48 hours at 60°C in a "rotisserie" style hybridization oven. Then the filter was washed according to the protocol described for M13 by Westneat et al. (1988). Autoradiographs of varying exposure times and intensities were obtained by exposing filters to X-ray films from half a day to 14 days. As washed and rehybridized filters proved to give better autoradiographs, most of the filters were "strip-washed" in a solution of 0.1 X SSC with 0.1% SDS at 95°C for 20 min. This was repeated a second time, after which the filter was rinsed with water and placed again in the prehybridization mix. All manipulations were done by the author.

STATISTICAL ANALYSES

The Band Sharing Index (BSI) between adult pairs was calculated using the equation BSI = $2(N_{AB})/N_A+N_B$, where N_{AB} represents the number of bands shared by two individuals and N_A+N_B the total number of bands of the two individuals (Wetton et al. 1987). Band Sharing Indices were calculated for each possible combination of adult pairs captured in the same ditch and for adults captured in different ditches in 1989, 1990 and 1991. Band Sharing Indices were also calculated between pairs formed of one adult captured in a given ditch in a given year and another adult captured in the same ditch the following year. For each type of sexual pair (♂♂, ♀♀, ♂♀), we used independent Kruskal-Wallis non-parametric analyses of variance (NPAR1WAY procedure, SAS 1988) to compare BSI's between adult pairs within the same ditch and in two different ditches. Kruskal-Wallis analyses were used to compare ditches bordered by hay or corn ditches, for the BSI's between pairs of adults by sex group (♂♂, ♀♀, ♂♀) within a given ditch the same year. Kruskal-Wallis analyses were also used to compare, by sex group (♂♂, ♀♀, ♂♀),ditches bordered by hay or corn ditches for BSI's between pairs formed of one adult captured in a given year and another adult captured the following year in the same ditch. For both analyses, years 1989, 1990, and 1991 were combined due to the insufficient availability of samples in any given year. Individuals with less than five bands were excluded. Two bands were considered to be identical when the migratory difference of their centres was less than 0.5 mm. Because failure to detect a significant difference does not necessarily mean that there is no difference, especially when studied variables express high variability and when sample size is small, we calculated the statistical power of the tests that showed no significant difference, using the software package developed by Brown et al. (1993). The statistical power of 0.8 has been cited as the minimal acceptable value for clinical trials, and represents a compromise between having a high probability of rejecting the null hypothesis when it is incorrect, and an affordable sample size (Brown et al. 1993). Power values are used as indicator values since the software calculates the power for normally distributed data. As we used non-parametric tests on non-normally distributed data, it is possible that the real statistical powers of the tests are higher than the values shown here. We also determined the size of the difference for the variable studied in hay and corn ditches necessary to obtain a statistical power of 0.8. In order to identify this difference, we determined the two group means, equally distant from the overall mean, and using the standard deviations and sample sizes observed, required to obtain a statistical power of 0.8. However, this was not possible for the ♂♂ pairs for the analysis of BSI's between different adults inhabiting a given ditch in successive years. For this analysis, we would have had to lower the mean BSI among ♂♂ pairs in hay ditches under the observed average BSI among adults from different ditches ($x = 0.2144$). As it is unlikely that males inhabiting the same ditch in two successive years should be less related than individuals from different ditches, we used the value of 0.2144 for ♂♂ pairs in hay ditches, and determined the mean BSI value in corn ditches, to obtain a statistical power of 0.8.

We used the method of Birkhead et al. (1990) for parentage statistical tests. We used the Goodness-of-fit test with the Williams correction to test whether each pair of individuals represented first order relatives (brother-brother, parent-offspring) or not. We used the average BSI among adults of the same ditch captured the same year ($x = 0.3487$, $N = 131$) to calculate the expected proportions of shared bands between parents and offspring (P_{pj}), using the equation $P_{pj} = (1+q-q^2)/2-q = 0.6395$, where q is the mean allele frequency in the population and is a function of the mean probability (x) of band sharing between adults trapped in the same ditch in 1989 and 1990: $q = 1-(1-x)^{1/2} = 0.1929$. For example, if the BSI between an adult and a juvenile is 4/16, using $P_{pj} = 0.6395$, these two individuals are expected to share 10.232 bands, while 5.768 bands would not be shared. The Goodness of fit value is calculated using the following equation: $G = 2\,(4 \ln (4/10.232) + 12 \ln (12/5.768)) = 10.07$. The Williams correction is calculated using the following formula: $W = 1 + (r^2 - 1)/6n(r - 1) = 1.03125$, where r = number of rows (here $r = 2$) and n = the total number of bands (here $n = 16$). Thus the corrected Goodness of fit is: $G/W = G_c = 9.76$. This value is then compared to the Chi-square value ($\chi^2 = 3.84$) ,at $df = 1$ and at the significant threshold of 0.05. Since G_c was superior to χ^2, this pair of individuals would not be formed of a parent and its offspring.

The following equation was used to calculate the expected proportions of shared bands between potential littermates [$P_{jj} = 1 - (1 - ((1 + x)/2(2 - q)))(1 - q)$] = 0.4941. To test whether a pair of adults were coming from the same ditch or different ditches, we used the same equation, but we used the average BSI between adults coming from different ditches ($x = 0.2144$) to calculate the mean allele frequency q in the population, where $q = 1-(1-x)^{1/2}$

= 0.1136. We calculated the expected proportions of shared bands (P_{pr}) between unrelated adults using the equation [$P_{pr} = 1 - (1 - ((1 + x)/2(2 - q)))(1 - q)$] = 0.3989. We assumed equal frequency of all alleles and independent inheritance of bands.

The scoring of bands and determination of shared bands among individuals were all done by the author.

RESULTS

DNA FINGERPRINTING

The DNA extraction from clipped phalanges of 120 animals yielded an average of 33.939 ± 17.352 μg (Mean ± SD) of DNA per phalanx. Some samples did not yield any DNA, while others never produced a clear banding pattern, despite several attempts. The combination of Alu I digestion and hybridization with the probe pYNZ132 on muskrat DNA gave an average of 7.6 ± 3.2 clear bands (Mean ± SD) . Individuals showing less than five bands were discarded because of the possibility that their DNA was degraded, thus not showing the high molecular weight bands.

GENETIC TURNOVER

Comparisons within and among ditches

To compare BSIs among adults inhabiting the same ditch and among adults inhabiting different ditches in 1989, 1990 and 1991, we used data from 71 individuals, 10 ditches, and 9 different gels. A gel with samples from corn ditches #10 and #1, used to generate 24 BSI values is presented (Figure 4.2). Fifty distinct resolvable fragments are apparent on this gel. Other gels showed that resolvable fragments were, on average, 2.3 to 24 kb long. Kruskal-Wallis analyses of variance showed that ♀♀ pairs and ♂♀ pairs had significantly higher BSI's when individuals came from the same ditch than when they came from different ditches. Pairs of males (♂♂) showed a similar but not significant tendency, but the statistical power of the test was low (Table 4.1).

Figure 4.2 Autoradiograph showing banding patterns for adults captured in 1990 (10 letter code) and in 1991 (4-5 letter code) along corn-bordered (D1 and D10) ditches of southwestern Quebec.

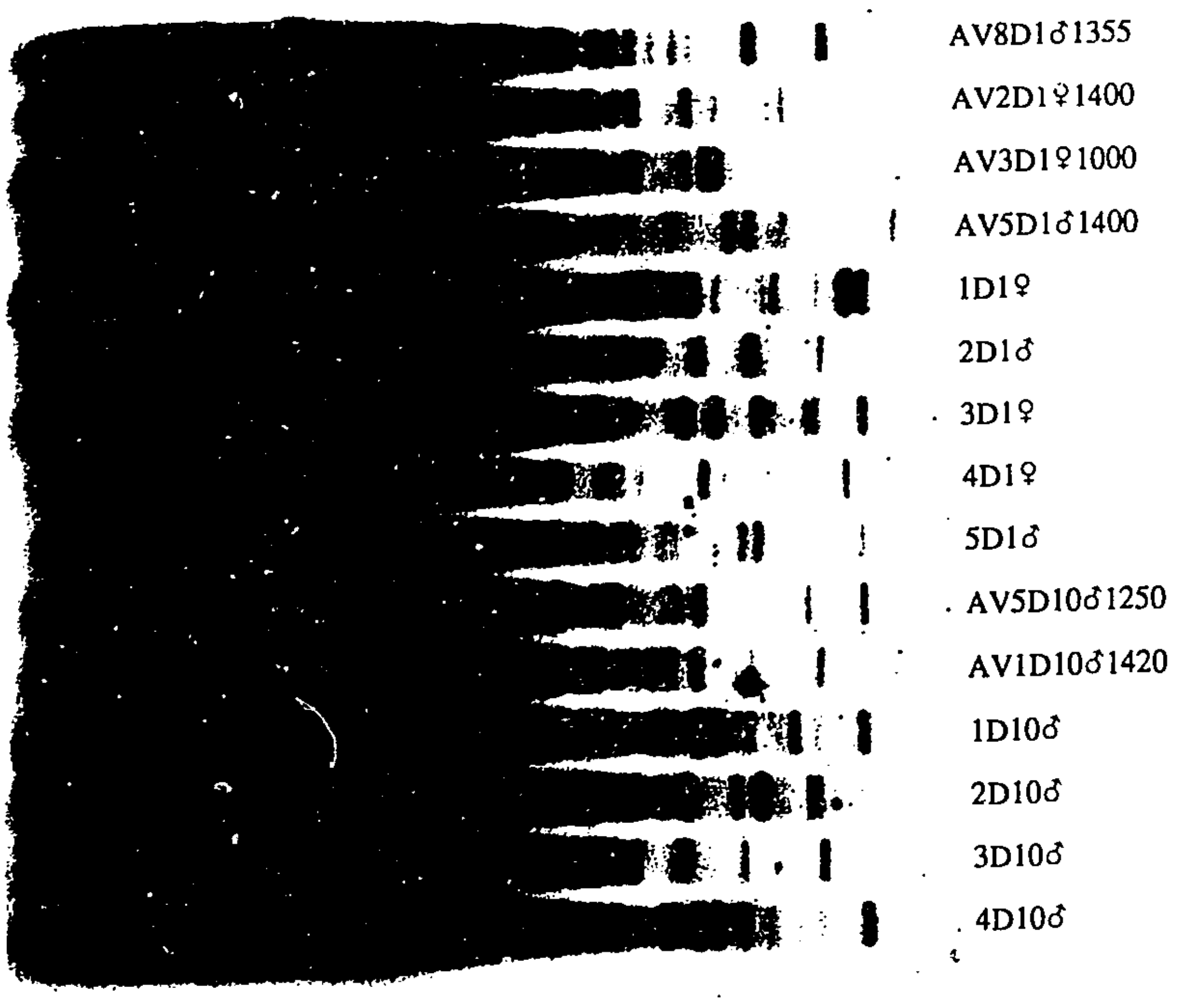

AV8D1♂1355
AV2D1♀1400
AV3D1♀1000
AV5D1♂1400
1D1♀
2D1♂
3D1♀
4D1♀
5D1♂
AV5D10♂1250
AV1D10♂1420
1D10♂
2D10♂
3D10♂
4D10♂

Table 4.1 Kruskal-Wallis non-parametric analyses of variance on the band sharing index (BSI) among adult pairs coming from the same ditch, and pairs coming from different ditches in southern Quebec farm ditches in 1989, 1990 and 1991.

Sex group	Results of tests	Same ditch	Different ditch	Power
♂♂	N = 66, K-W. χ^2 = 2.618, 1 df, P = 0.1057	0.296 ± 0.176	0.235 ± 0.170	0.269
♀♀	N = 133, K-W. χ^2 = 21.099, 1 df, P = 0.0001	0.361 ± 0.179	0.200 ± 0.143	
♂♀	N = 200, K-W. χ^2 = 23.248, 1 df, P = 0.0001	0.361 ± 0.208	0.219 ± 0.159	

Comparison, between corn and hay bordered ditches, of the band sharing index (BSI) among pairs formed of one adult captured in a given year and another adult captured the following year in the same ditch

The analysis was performed on data from five hay ditches and three corn ditches, using seven gels. Two examples of gels used are presented on Figures 4.3 and 4.4. The autoradiograph on Figure 4.3 shows 36 different resolvable fragments, while 40 were detected in the autoradiograph appearing on Figure 4.4. Banding patterns of individuals AV6D7♂1060 and 2D6♀ were not used for comparisons because their respective number of bands was less than five. We did not detect significant differences in the analyses performed on each sex group between corn and hay ditches (Table 4.2). This result is consistent with the similar population turnover among years detected in corn and hay ditches from trapping data (see Chapter 3). The statistical powers of the tests were low (Table 4.2), and differences in BSI's by a factor of 1.9 (♂♂), 2.5 (♂♀), and 1.6 (♀♀) were required in the different sex groups to obtain a statistical power of 0.8.

Effect of crops bordering ditches on the BSI of muskrats within the same ditch in a given year

No effect of crop on the BSI between muskrats within the same ditch in a given year was detected in any sex group (Table 4.3). The statistical powers of the tests were low, and differences in BSI's by a factor of 1.6 (♂♂), 2.0 (♂♀), and 1.4 (♀♀) were required in the different sex groups to obtain a statistical power of 0.8.

Figure 4.3 Autoradiograph showing banding patterns for adults captured in 1990 (10 letter code) and in 1991 (4 letter code) along hay-bordered (D6 and D7) and corn-bordered (D8) ditches of southwestern Quebec.

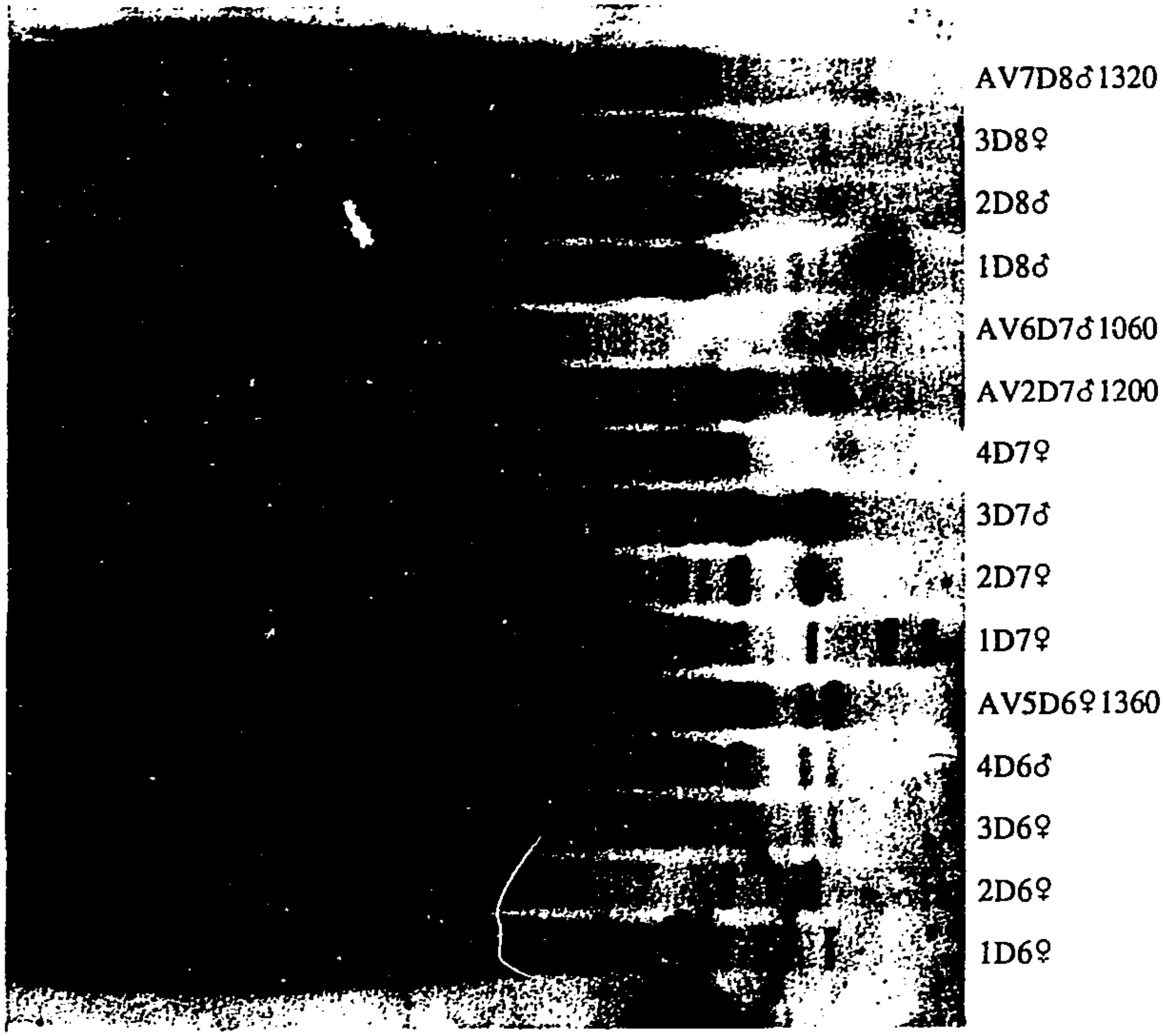
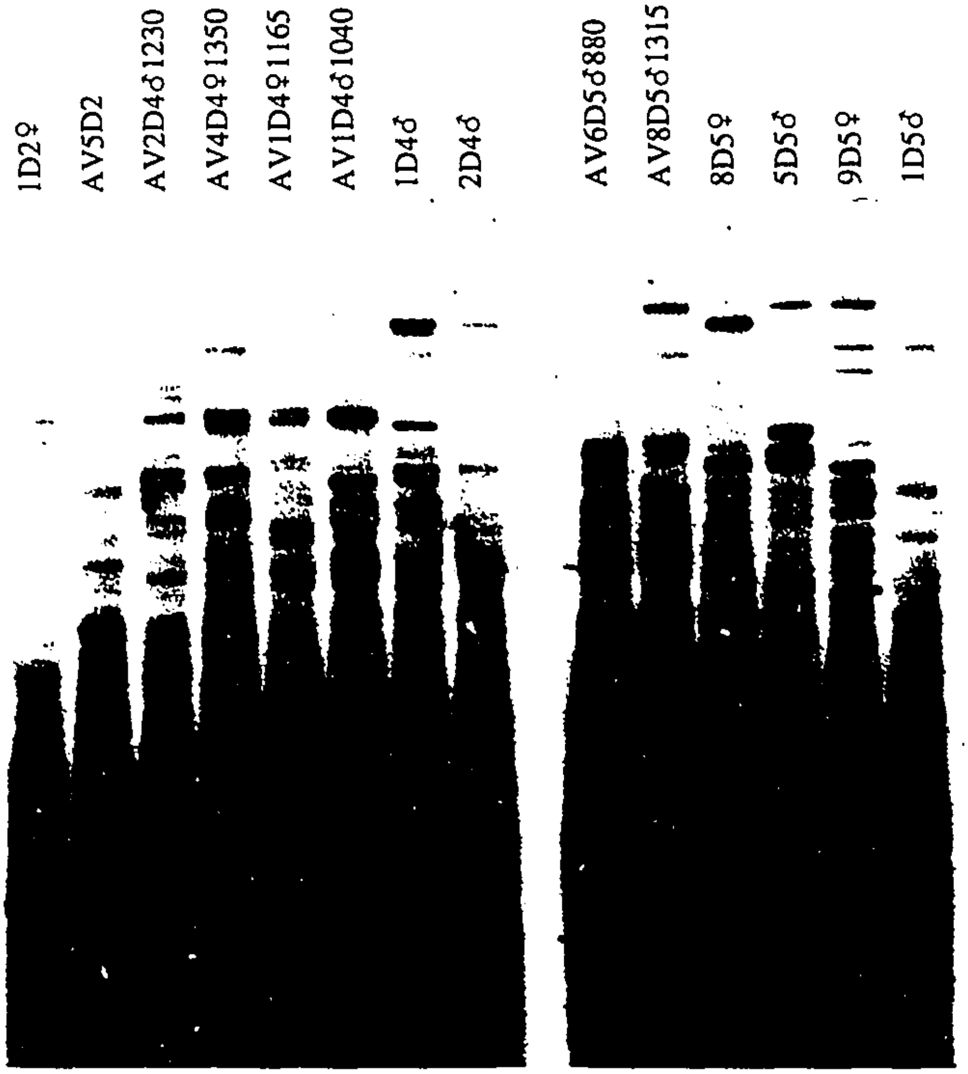

AV7D8♂1320
3D8♀
2D8♂
1D8♂
AV6D7♂1060
AV2D7♂1200
4D7♀
3D7♂
2D7♀
1D7♀
AV5D6♀1360
4D6♂
3D6♀
2D6♀
1D6♀

Figure 4.4 Autoradiograph showing banding patterns for adults captured in 1990 (5-9-10 letter code) and in 1991 (4 letter code) along corn-bordered (D2) and hay-bordered (D4 and D5) ditches of southwestern Quebec.


1D2♀
AV5D2
AV2D4♂1230
AV4D4♀1350
AV1D4♀1165
AV1D4♂1040
1D4♂
2D4♂
AV6D5♂880
AV8D5♂1315
8D5♀
5D5♂
9D5♀
1D5♂

DETERMINATION OF PARENTAGE

The BSI generated from within-ditch adult male-female comparisons in a given year averaged 0.3606 ± 0.2084 (N = 70). The four BSI values among four pairs of putative parents detected in three ditches in 1990 (#1, #9, #11, Table 4.4) were 10/18 (G_c = 1.74), 4/17 (G_c = 1.98), 8/19 (G_c = 0.04), and 2/16 (G_c = 5.69). The first three values are not statistically different from the expected value among adults coming from different ditches (P_{pp} = 0.3989; $G_c < \chi^2$), and the last one shows two individuals even less related than expected between adults coming from different ditches. Similarly, of the three heterosexual pairs trapped in the same burrow in 1991, two (4/14 - G_c = 0.75, 6/22 - G_c = 1.50) presented values not statistically different from expected values between adults coming from different ditches. On the other hand, the other pair was formed by a brother and sister (BSI = 10/13 - G_c = 7.12) captured in 1990. The detection of an adult pair formed of related individuals forced us to use the average BSI among adults of the same ditch captured the same year (x = 0.3487, N = 131) to calculate the expected proportions of shared bands between parents and offspring and among offspring. The testing of the technique using spatio-temporal criteria to associate young within a given litter (see Chapter 3) was done using BSI's between potential littermates. The analysis for 1989 and 1990 was possible only on gels representing eight different ditch-years out of a possible of 16. Figure 4.5 is an example of gels used to generate BSI values for pairs of littermates and non-littermates. Overall, of the 38 BSI's generated for littermates (0.62 ± 0.14), as determined by spatio-temporal associations, none reflected statistically unrelated individuals. Among the BSI values generated for non-littermates (N = 47, 0.55 ± 0.16), only one was significantly lower than expected between littermates (#9-1990: BSI = 0/10, Table 4.4). By comparing banding patterns of all potential pairs of parents with each of the two young forming the pair of littermates, we found that the two young had been produced by one identified pair (AV1♂1330 and AV8♀1200), where all bands in one offspring were present in parents. The other young (AV8♀505) was not statistically related to AV1♂1030, and it had at least two bands that were not present in any combination of the 4 adults showed on the gel.

Table 4.2 Kruskal-Wallis analyses of variance on the effect of hay versus corn fields bordering southern Quebec farm ditches on the band sharing index (BSI) between adult pairs formed of different individuals captured in a given ditch in two successive years in 1989, 1990 and 1991.

Sex group	Results of tests	Adult average BSI in hay ditches	Adult average BSI in corn ditches	Power
♂♂	N = 23, K-W. χ^2 = 2.919, 1 df, P = 0.0876	0.248 ± 0.174	0.358 ± 0.134	0.359
♀♀	N = 14, K-W. χ^2 = 0.206, 1 df, P = 0.6496	0.408 ± 0.218	0.397 ± 0.205	0.030
♂♀	N = 33, K-W. χ^2 = 0.675, 1 df, P = 0.411	0.350 ± 0.204	0.403 ± 0.129	0.132

Table 4.3 Kruskal-Wallis analyses of variance on the effect of hay versus corn fields bordering ditches on the band sharing index (BSI) between adult pairs formed of individuals captured in a given ditch the same year in southern Quebec farm ditches in 1989, 1990 and 1991.

Sex group	Results of tests	Adult average BSI in hay ditches	Adult average BSI in corn ditches	Power
♂♂	N = 37, K-W. $\chi^2 = 2.317$, 1 df, $\underline{P} = 0.1280$	0.328 ± 0.174	0.405 ± 0.182	0.233
♀♀	N = 24, K-W. $\chi^2 = 1.247$, 1 df, $\underline{P} = 0.2641$	0.358 ± 0.143	0.270 ± 0.186	0.195
♂♀	N = 70, K-W. $\chi^2 = 0.159$, 1 df, $\underline{P} = 0.900$	0.344 ± 0.144	0.372 ± 0.243	0.084

We were not able to generate a BSI between AV8♀505 and an adult female (AV6♀1300) that had been captured nearby on June 7. AV6♀1300 had a distended vagina, a sign that she had recently given birth. Moreover, the date of birth of AV8♀505 was estimated to be May 23, two weeks before the capture date of AV6♀1300. In 1989, the five young trapped in ditch #4 for which we obtained good banding patterns were linked to AV2♀1025 (all mean BSI's ≥ 0.61) while AV1♀1100 had five of the five BSI values with young statistically lower than expected between parents and offspring (Table 4.4). All five young may have been descendants of the same father since all bands not present in the mother were present in at least two young. This could be an indication of the absence of promiscuity between non-paired adults. The results for ditch #2 in 1989 were similar to ditch #4. The four young with good banding patterns had BSI values with the only adult female detected (AV6♀1195) not statistically different from the expected value between mother and offspring (Table 4.4). All the bands that were not displayed in the mother were shared by three of the four young, suggesting a common father. Only one adult male (no banding pattern available) had been captured in ditch #2 in 1989. BSI values within and among litters showed that the four young were likely brothers and sisters (Table 4.4).

In ditch #10 in 1990, one adult male (AV1♂1420) was captured, and no adult female. Another adult male (AV5♂1250) was captured at a distance of 30 m from the studied section. Six of the eleven BSI values between the distant male and juveniles were statistically lower than expected for father-offspring relationships, while none of the four BSI values between the closer male and juveniles were different from the expected value between father and offspring (Table 4.4). Also, all young from the three litters were likely brothers and sisters. For this ditch, these data support the use of the spatio-temporal technique to determine parentage relationships. In ditch #11 in 1990, the only adult female captured (AV2♀1200) only once was probably not the mother of the two juveniles because one BSI value (with AV5♂700) was statistically lower (6/16; $G_c = 4.46$) than expected between first order relatives (Table 4.4). Also, one band in AV5♂700 was not present in either the putative father AV5♂1350 or in the putative mother AV2♀1200.

Table 4.4 Results of parentage tests between individual muskrats captured in the same ditch in a given year in southern Quebec, in 1989 and 1990.

Ditch #	BSI among young	BSI among putative parents and young	BSI among adults
1 (1990)	Within litter: 8/14, 10/15, 14/17*, 8/16, 12/18, 6/15, 12/19, 6/16, 10/17, 10/17 Among litters:8/15, 8/15, 10/16, 8/17, 10/18,	AV3♀1000: 6/18*, 10/17, 8/15, 8/15, 10/16, 10/16 AV8♂1365:8/16, 10/17, 12/18, 10/18, 8/16, 16/19* AV2♀1400: 14/19*, 8/16, 8/16, 6/17, 10/17, 10/18 AV5♂1400: 4/16*, 8/16, 10/17, 10/17, 10/18, 10/19	AV3♀1000 + AV8♂1365: 4/17 AV2♀1400 + AV8♂1365: 10/18 AV2♀1400 + AV3♀1000: 10/17 AV2♀1400 + AV5♂1400: 6/18 AV3♀1000 + AV5♂1400: 6/17
2 (1989)	Within litter: 12/17, 4/13 Among litters: 10/16, 6/15, 8/15, 10/14	AV6♀1195: 16/21, 12/20, 10/19, 10/18	
4 (1989)	Within litter: 12/21, 14/21, 16/25, 14/18*, 14/22, 12/22 Among litters:16/24, 12/21, 12/21, 16/25	AV2♀1025: 18/23, 16/20, 14/23, 14/20, 18/24 AV1♀1100: 4/16*, 6/19*, 6/16*, 2/20*, 6/19*	AV2♀1025 + AV1♀1100: 4/18

Table 4.4 (Cont.). Results of parentage tests between individual muskrats captured in the same ditch in a given year, in southern Quebec, in 1989 and 1990.

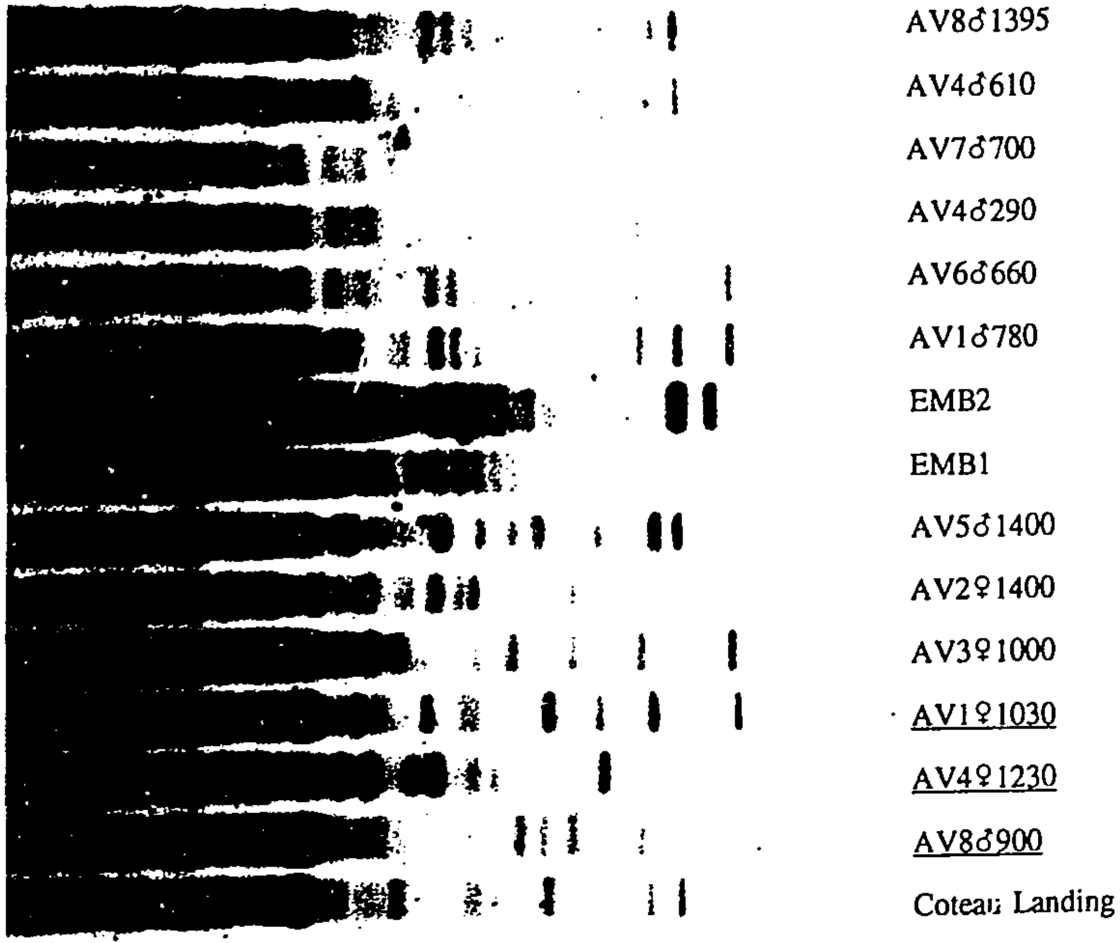
Ditch #	BSI among young	BSI among putative parents and young	BSI among adults
5 (1990)	Within litter: 6/11, 6/12, 10/14, 10/13, 8/11, 8/10, 12/13, 12/13, 8/12, 8/11 Among litters:8/12, 12/14*, 14/15, 8/11, 8/11	AV8♂1315: 2/16*	
9 (1990)	Within litter: 8/11, Among litters: 0/10*	AV1♂1330: 8/16, 2/16* AV8♀1200: 4/10, 4/11, 4/10 AV4♂1500: 2/12*, 4/12* AV6♀1300: 6/14, 2/14*	AV1♂1330 + AV8♀1200: 2/16* Other ♂-♀ combinations: 2/12, 8/20, 4/16 AV8♀1200 + AV6♀1300: 6/14 AV1♂1330 + AV4♂1500: 2/18*
10 (1990)	Within litter: 8/15, 10/15, 10/14, 8/13, 6/15, 8/14, 10/18, 6/16, 10/16 Among litters: 6/12, 6/15, 4/14, 8/16, 6/17, 10/17, 8/14, 4/13, 12/16*, 6/14, 4/13, 8/17, 8/15, 10/16, 6/15, 10/15, 8/13, 6/15, 8/16, 8/14, 8/14, 10/15, 12/15*, 10/17, 10/16, 10/16, 6/14	AV5♂1250: 2/14*, 2/13*, 2/15*, 4/16*, 0/14*, 4/14*, 6/15, 8/14, 6/14, 12/16, 6/12 AV1♂1420: 8/18, 8/11, 12/17, 8/15	AV5♂1250 + AV1♂1420: 4/17

Table 4.4 (Cont.). Results of parentage tests between individual muskrats captured in the same ditch in a given year, in southern Quebec, in 1989 and 1990.

Ditch #	BSI among young	BSI among putative parents and young	BSI among adults
11 (1990)	Among litters: 8/15	AV2♀1200: 6/16*, 8/17	AV2♀1200 + AV5♂1350: 8/19
		AV5♂1350: 10/17, 14/18	Other ♂♀: 2/16*, 6/17
		AV*♂930: 10/15, 8/16	AV5♂1350 + AV4♂1010:
		AV4♂1010: 6/14, 8/15	AV5♂1350 + AV8♂930:
			AV4♂1010 + AV8♂930:

* BSI statistically different from expected BSI between individuals of their respective category (young-young, parent-young, adult-adult).

Figure 4.5 Autoradiograph showing banding patterns for juveniles (first 8 lanes from the right, excluding the first one) and adults (all the other bands, excluding the last one) captured in ditch #1 in 1989 (underlined) and in 1990. The last individual was captured on the north side of Lake St-Francis, in Coteau-Landing (QC), during a preliminary study.


AV8♂1395
AV4♂610
AV7♂700
AV4♂290
AV6♂660
AV1♂780
EMB2
EMB1
AV5♂1400
AV2♀1400
AV3♀1000
AV1♀1030
AV4♀1230
AV8♂900
Coteau Landing

The other young captured (AV1♀550) could have been the offspring of AV2♀1200 (BSI = 8/17) and AV5♂1350 (BSI = 14/18; G_c = 1.57, Table 4.4), but two bands were absent in both putative parents. The putative father was present at least 44 days in the ditch. This ditch is an example where results of spatio-temporal associations would be misleading in determining kinship, as was the case for ditch #1 in 1990. The Goodness of fit analyses on BSI's between individuals in ditch #1 in 1990 suggested that the two adult females were more related to each other than expected between individuals coming from different ditches. Adult female AV3♀1000 was not the mother of one young (BSI = 6/18), but AV2♀1400 had a high BSI with that young (BSI = 14/19). However, the analysis of band segregation showed that all other young were more likely offsprings of AV8♂1365 and AV3♀1000 because all bands present in parents were also present in offspring, which was not the case for other combinations of potential parents (Figure 4.5). Adult male AV8♂1365 was detected by livetrapping over a minimum period of 97 days, and adult female AV2♀1400 over a period of 70 days, while AV3♀1000 was captured only once. The putative pair of parents AV2♀1400 and AV8♂1365 had a BSI higher than expected between unrelated individuals.

In ditch #5 in 1990, the only BSI value between potential parent and offspring was lower than expected between first order relatives (Table 4.4).

DISCUSSION

The average BSI obtained for unrelated muskrats was comparable to values obtained in good fingerprinting systems used on species that experience annual movements and mixing (Westneat 1990, Lifjeld et al. 1991, Rico et al. 1991). The combination of Alu I and probe pYNZ132 used here proved useful in resolving paternity cases in stickleback (Rico et al. 1991). As stated by Westneat (1990), fingerprints of species in which relatives settle near each other are much more difficult to interpret. However, the almost complete population turnover from year to year detected in chapter 3 contributed to increase the mixing rate in the population and improved the usefulness of the fingerprinting technique.

The analysis of BSI's among adults within a year and among years did not allow us to find evidence that corn and hay crops affect muskrat rate of philopatry and population turnover differently . The comparison of average BSI values between muskrats inhabiting the same corn or hay ditch the same year showed similar relationships within sex groups to the ones observed between adults in successive years. There was a tendency for ♂♂ pairs occupying the same ditch in two successive years to have higher BSI's in corn ditches than in hay ditches. If young male muskrats disperse independently of population density or habitat quality, as it was shown to be the case in young male white-footed mice (*Peromyscus leucopus*) (Wolff et al. 1988), then we would not expect a change in male BSI's following a change in habitat quality.

Pairs of ♀♀ showed higher, but not significant, average BSI values in hay ditches than in corn ditches. Adult ♂♀ pairs showed higher, but not significant, average BSI values in corn ditches than in hay ditches. Young rodent females are known to show a higher level of philopatry (Bondrup-Nielsen 1985), and to disperse shorter distances than young males (Caley 1987). If ditches bordered by corn fields and those bordered by hay fields represented different habitat quality, this difference could then cause a change in the rate of philopatry or in the rate of mother-daughter territory retention between ditch type. However, such a difference was not found. These results are consistent with the almost complete population turnover from year to year detected from trapping data in both types of ditches (see Chapter 3), which would prevent the maintenance of burrows within families observed by Caley (1987).

The analyses used to test the significance of the type of crop bordering ditches on BSI's between adult muskrats may have been biased by the use of comparisons involving the same individual more than once. This would have increased the chances of finding differences where there are none. For the testing of the effect of crops bordering ditches on BSI's, it should not be a problem as no consistent effect was detected within the same ditch the same year, or in two successive years. Conversely, the statistical powers of the analyses were low, which could have prevented the detection of true limited differences.

The significantly higher average BSI among adults inhabiting the same ditch the same year, than among adults of different ditches the same year does corroborate Caley's (1987) suggestion that the rate of gene flow would decrease with distance through the breeding of muskrats within a few home range diameters of their natal site because of the costs associated with outbreeding, such as aggression from conspecifics, predation and costs of meiosis and breaking of coadapted gene complexes. Kin recognition by muskrats would allow discrimination between close relatives and others when forming pairs (Caley and Boutin 1987) . Two of the three pairs of confirmed parents had BSI values not statistically different from the expected value among adults coming from different ditches, and thus being not related to each other, and the third pair was even formed of individuals more unrelated than expected between individuals coming from different ditches. The use of data on multiple comparisons involving the same individuals could have influenced the test that showed higher BSI's between adults of a given ditch than adults from different ditches.

Inbreeding avoidance, i.e. the formation of pairs of unrelated individuals, has been shown to be important in rodents. Caley (1987) has shown that inbreeding avoidance between muskrat siblings is potentially responsible for dispersal of young. Barnard and Fitzsimmons (1989) showed that in the house mouse (Mus musculus), litter size of less related parents was larger at birth and post weaning. Haigh (1983) showed negative effects of inbreeding in Peromyscus. The high turnover observed in 1989-90 and 1990-91 (see chapter three) could have reduced the chance of inbreeding, but it is possible that kin migrate to the same area, thus there is a need to be able to recognize kin to avoid inbreeding.

In the present study, we observed more adult males than adult females in 1991, and we detected one instance of extra-pair mating (ditch #1 - 1990). Several authors have shown an unbalanced sex ratio in favour of males in young muskrats (Erickson 1963, Neal 1968, Parker and Maxwell 1980). If adult males were more numerous than adult females in spring (this was observed only in 1991), males should be the dispersing sex due to competition for mates, even if the species was completely monogamous. Greenwood (1980) stated that the mating system had a direct consequence on which sex would show greater dispersal. In mammals, females are generally philopatric, and males defend females instead of defending resources. Polygyny is the most common mating system in mammals (Kleiman 1977), but when the density of females is low, and the sex-ratio close to 50/50, the mating system will be monogamy because of the impossibility to defend more than one female. Sather (1958) and Erickson (1963) found evidence that muskrats are monogamous. As is the case for space use (Messier et al. 1990), competition for females may result in despotic behaviour, i.e. where a few males have access to a greater proportion of mating opportunities than others. A male-biased sex-ratio, however acts in favour of monogamy, as competition for females increases. However, in at least one instance Marinelli and Messier (1993) detected polygyny in a female biased low density population where space use suggested that each adult male territory overlapped two female territories.

Although the four identified pairs of parents had BSI values not statistically different from the average value for adults coming from different ditches, we did not use the mean BSI among unrelated individuals to calculate goodness of fit tests on potential relatives. The possibility that parental pairs can be formed of closely related individuals, as shown by a detected pair of brother and sister in 1991, led us to use the mean BSI for all possible combinations of adults in a given ditch. If, as shown by Caley (1987), muskrats have developed mechanisms to avoid inbreeding, the mean BSI value used to calculate Goodness of fit tests should be the mean BSI between members of known pairs, which would further improve the capacity of the DNA fingerprinting technique to analyze relationships between individuals. Although the frequency of inbreeding events may be low, a conservative approach in parentship tests needed to be used.

This study demonstrated some of the limitations associated with the livetrapping technique. For example, in one case, an adult female muskrat was detected only once while another adult female was detected for a longer period, and still, the first contributed more offspring to the productivity of the ditch section, as shown by BSI values. This could indicate that all females were not equally susceptible to be trapped. It is also possible that the survival of young of females that were trapped was reduced. Some of the parents of detected young were never captured, although other adults were captured in the same section. This may be due either to emigration of young from neighbouring territories or to the low trappability or death of some adults. Despite these exceptions, spatio-temporal associations (see Chapter 3) generally reflected kinship. The method, detailed in Chapter 3, to define litters by associating, within a ditch section, the two young with the closest birth dates and adding other young until a period of 14 days was covered, was proven relatively efficient. Ninety-eight percent of goodness of fit tests confirmed kinship between individuals of the identified litters.

On the other hand, the present study also shows the limitations of the DNA fingerprinting technique when used in the context of animals migrating short distances and which can breed with relatives. Although some young were apparently related to their putative parents, they had bands present in neither of the putative parents. The ability of muskrat to recognize kin would lower the risk of inbreeding and reduce the necessity to migrate long distance to avoid it (Caley 1987), but it creates a difficulty in determining the expected BSI between relatives, because not all combinations of adults would have the same probability of being formed.

MANAGEMENT IMPLICATIONS

The analysis of the genetic proximity between adult muskrats did not provide evidence that corn-bordered ditches represented different habitat quality than hay-bordered ditches for muskrat. Managing crops for muskrat would then not be warranted at this time. The DNA fingerprinting technique can generally be used to identify kinship in muskrats, but in some instances, banding patterns from both parents are required to confirm maternal or paternal linkages. The higher BSI values between muskrats within the same ditch, as compared to muskrats from different ditches (♂♀, ♀♀), supports the evidence that the extent of female migrations is limited, and thus that local environmental conditions may be more important than regional ones in affecting population dynamics. The results of this study generally support the use of trapping data to infer relatedness between juvenile muskrats and between juvenile and adult muskrats. We must however be careful, since spatio-temporal proximity does not always correlate with relatedness, and true parents are not always detected by trapping.

ACKNOWLEDGEMENTS

We are grateful to Kateri Lescop-Sinclair and Heather Cunningham for their significant contribution to the field work. We are indebted to both Magdalena Volkov and Ciro Rico who provided valuable advice during lab experiments. This work was finance by NSERC grants to J.R. Bider and U. Kuhnlein, and a NSERC Doctoral fellowship to S. Nadeau.

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Habitat use models in chapter two were used to test the relative influence of crops on muskrats. In order to test the effect of crop type, ditch sections were chosen where bank height and soil type, two variables known for their importance to muskrats, were optimum for muskrat habitat. These two variables were then not considered by the models. The effectiveness of habitat use models based on signs of presence in southern Quebec led to the testing of the methodology in other areas and wider environmental conditions. The next chapter of this manuscript presents a model of muskrat habitat use based on the observation of signs of presence recorded along a great number of wetlands of southeastern James Bay. Habitat use models are used here to determine a minimum set of habitat variables predictive of muskrat presence. If successful, the methodology presented here could be an alternative to the traditional aerial survey of lodges to describe the potential of an area for burrow-dwelling muskrats.

CHAPTER FIVE

Nonlinear modelling of muskrat use of habitat

ABSTRACT

Where muskrats (*Ondatra zibethicus*) are burrow dwellers, traditional aerial surveys of lodges to characterize the potential of different areas to sustain the species is not adequate. We present an alternative consisting of the identification of critical habitat variables on the basis of muskrat presence indices. We used stepwise logistic regression to create a habitat model based on the presence of muskrat in early fall along various wetlands of the James Bay boreal forest. We built two models, one based on presence of burrows only and one using the presence of muskrat feeding sign and droppings. Collecting the latter data required less field time than looking for burrows. The burrow model showed a classification rate of 88% and 92% for 60-m shore sections of wetland used to build the model and other sections of streams and rivers respectively. The classification rates for the feeding sign and droppings model were slightly lower (79% and 71% respectively). The logistic regression analysis on presence/absence of burrow ($\underline{P} < 0.001$) selected variables bank slope, percentages of floating and submerged plant cover, presence of clay-loam soil, and width of shore herbaceous belt. The number of muskrat burrows in the study area averaged (Mean ± SD) 2.1 ± 5.5/km of shoreline, and lodges were not found. Rivers with slow water velocity represented the best habitats. The methodology presented here may be used to determine variables significantly related to the presence of muskrat in riverine sections of wetlands. These habitat variables may be used to assign values reflecting the potential of each riparian section of a given wetland to harbour burrow-dwelling muskrats.

Key words: habitat, James Bay, *Ondatra zibethicus*, logistic regression, muskrat, Quebec.

INTRODUCTION

Muskrats occupy most types of wetlands (Boutin and Birkenholtz 1987, Kinler et al. 1990, Lacki et al. 1990, Messier et al. 1990). Aerial surveys of lodges are often used to evaluate the potential of marshes to sustain muskrats (Dozier 1948, Proulx and Gilbert 1984). However, aerial surveys are useless where muskrats inhabit bank burrows. Developing a habitat use model on the basis of presence/absence data collected along shore sections of wetlands scattered over a wide area could be the first step of an alternative methodology to determine the potential of wetlands to harbour muskrats. The model could then be validated with data collected elsewhere. If it is found valid, the model could be used to characterize a wetland for its ability to sustain muskrats, by attributing probability of muskrat presence to each of its shore sections.

Burrow location is thought to represent site selection (Brooks and Dodge 1981, 1986). Feeding signs and droppings are found close to the burrow site as muskrat movements around their burrows are generally restricted to a radius of 100 to 150 m (Ching and Chih-Tang 1962, Erickson 1963, Errington 1963, Neal 1968, Brooks 1980). However, because feeding sign and droppings data can be gathered faster than burrow data in the field, it would be more cost-effective to concentrate efforts on these signs of presence if they are linked to the same habitat variables than burrows. In previous studies, models used to describe links between muskrat populations and habitat variables focused on river ecosystems of the northern United States (Brooks and Dodge 1981, 1986). These linear models used variables measured on geological topographic maps and failed to predict accurately the number of muskrat burrows. We present nonlinear logistic regression models of muskrat use of habitat built from presence/absence of burrows and feeding sign and droppings in various wetlands in the northeastern boreal forest. We tested classification rate of the model using independent data.

METHODS

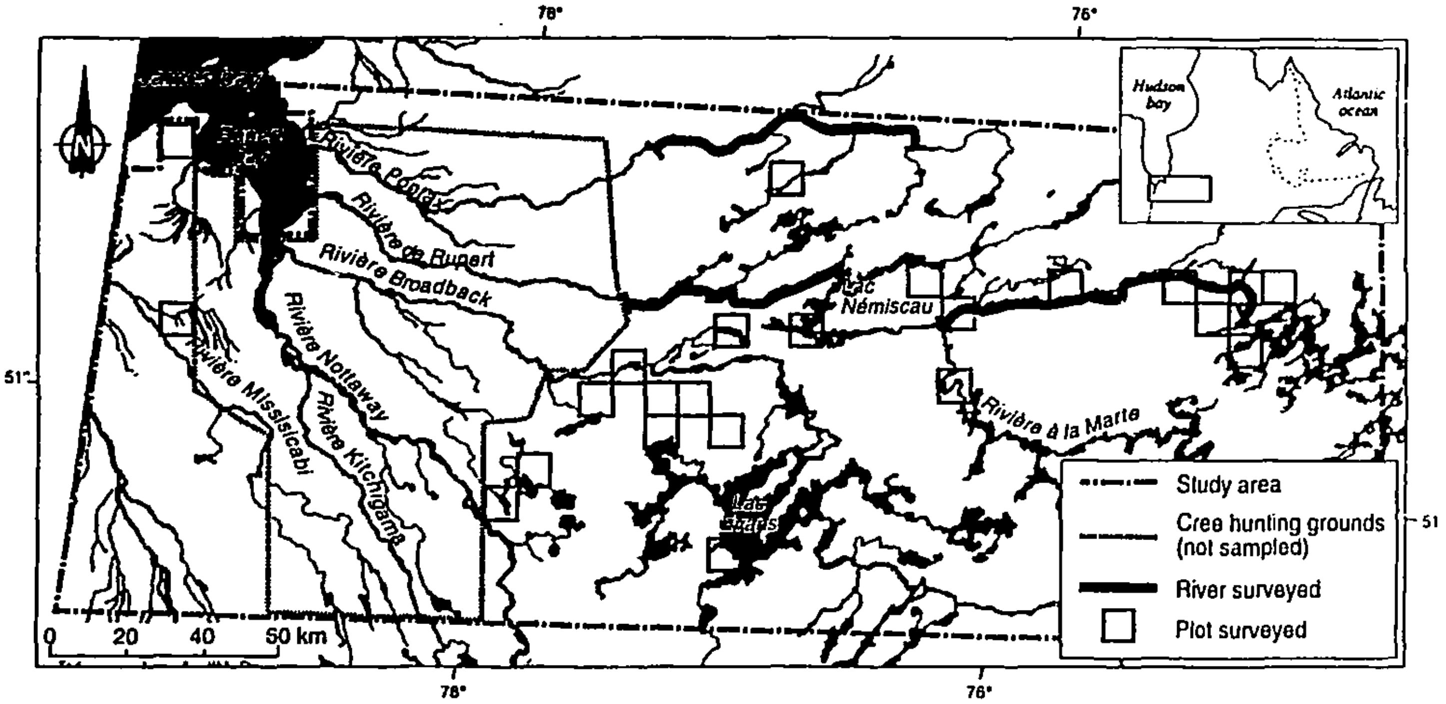
STUDY AREA

The study area extended from James Bay, Quebec (79°25'W) to 300 km east (75°00'), and from the drainage system of Pontax River (51°51'N) to 10 km south of the southernmost point of Broadback River (50°40')(Figure 5.1). The area covered 43 360 km^2 and was drained by 7 major rivers and smaller tributaries. Other wetlands in the area included a few large lakes, many mid- and small-sized lakes, with comparatively fewer bogs, fens, and beaver (*Castor canadensis*) ponds. Forest stands bordering these wetlands varied from postfire shrub stands of speckled alder (*Alnus rugosa*) and pin cherry (*Prunus pennsylvanica*) to conifer stands of variable age and density, dominated by black spruce (*Picea mariana*) or jack pine (*Pinus banksiana*) (Dutilly and Lepage, 1945a, 1945b, 1946, 1947). The microclimate prevailing in the low-lying area located south of James Bay, and the presence of clay-loam soil from the west end of the study area to 77°00'N favoured tamarack (*Larix laricina*) and other shrub taxa such as willow (*Salix* spp.). Clay-loam soil extended east along the Pontax River, while peat soil predominated where drainage was poor. Sandy and gravel soils dominated the rest of the study area.

SAMPLING

Field sampling extended from 15 September to 10 October, 1990. In different wetlands, we surveyed 235 60-m sections in 23 10-km x 10-km plots (Figure 5.1). In each plot, we surveyed, on foot, 10 60-m sections of riparian habitat distributed along lakes, bogs/fens, rivers, streams, and beaver ponds. Rivers were defined as any watercourse ≥5 m in width, while streams were any watercourse <5 m wide. When <2 wetlands of a given category were found in a plot, we sampled additional sections of other types of wetlands to achieve 10 sampled sections per plot. The uneven number of sections per wetland reflects the abundance of each wetland type.

Figure 5.1. The study area in James Bay, Quebec.


78°
76°
51°
51
James bay
Rupert bay
Rivière Pontax
Rivière de Rupert
Rivière Broadback
Rivière Nottaway
Rivière Kitchigama
Rivière Missisicabi
Lac Némiscau
Rivière à la Marte
Lac Evans
Hudson bay
Atlantic ocean
Study area
Cree hunting grounds (not sampled)
River surveyed
Plot surveyed
0
20
40
60 km
N

We intentionally selected sections to ensure variation in biophysical conditions to build a model that would apply to all wetland types. Sections were widely dispersed, to minimize spatial autocorrelation (Legendre and Legendre 1983). We systematically sampled supplementary sections on 3 segments of the Pontax and Rupert river watersheds. On the Pontax River, we sampled 1 section of the first stream encountered and thereafter alternated streams encountered on opposite sides of the river until the whole watershed was covered. We sampled 35 streams and 17 river sections along a 78.2-km river segment. We sampled river sections along the shoreline after every second stream was sampled. On the Rupert River, we followed the same methodology, but sampled only the second of every 2 streams encountered. We sampled 41 streams and 41 river sections along 2 river segments that totalled 160.6 km.

We confirmed muskrat presence in a 60-m shore section by presence of burrows, feeding sign, and droppings. We determined burrow presence by probing the submerged bank with our feet. Along streams, we probed both banks. A two-day training period at the beginning of the sampling period allowed familiarization of the new observer with muskrat and other vertebrate signs of presence. The principal investigator regularly checked the validity of the signs observed by the other observer.

Habitat variables were measured by the principal investigator at the central point of each 60-m section. Abiotic variables included wetland type, water velocity (≤10 and >10 m/min), protection of the site from wind (protected or unprotected, based on wetland size, emergent vegetational cover, and orientation of section with regards to prevailing winds), bank slope (>45 and ≤45°), distance (m) separating the shoreline from the nearest 50-cm elevation, distance (m) between shoreline and water depth of 50 cm, water depth (cm) at 2 m from shore, and the dominant substrate of the bank. The principal investigator sampled vegetation using: (1) the estimated percent covers by, respectively, emergent, floating, and submerged plants in a maximum square surface of 60 x 60 m bordering the shoreline, (2) the total area covered by aquatic plants (in m^2 and %) in the 60- x 60-m plot, (3) the distance (m) between the aquatic plant community and the shoreline, and (4) a visual estimation of the mean width of the shore herbaceous belt (0, ≤5, and >5 m).

STATISTICAL ANALYSES

To generate muskrat habitat models, we used data gathered in the 23 plots and in 8 fast-flowing stream sections sampled during the systematic sample along the Pontax and Rupert rivers (4 in each watershed). We added these sections because of the relatively low representation of fast-flowing streams in the 23 plots.

The following methodology, used to apply logistic regression to use of habitat, is similar to that of Brennan et al. (1986). To avoid aberrant results, due to excessive variables, we ran all quantitative habitat variables through univariate Wilcoxon 2-sample tests, using presence/absence of muskrat burrow as the dependent variable. We used Chi-square tests to test the relationship between presence/absence of muskrat burrow and (1) wetland type in 6 categories (lake, bog/fen, beaver pond, slow-flowing river, slow-flowing stream, and fast-flowing river and stream), and (2) the estimated mean width of the shore herbaceous belt. We used Fisher's exact tests on all other binary variables, including the variable soil type that was decomposed in a subset of binary variables (clay-loam, sand-gravel, peat), to test their relationships with the presence/absence of muskrat burrows. Only variables at $\underline{P} < 0.15$ were retained for further investigations. We then calculated Kendall correlations between the remaining variables. Two variables were considered redundant when they showed a Kendall correlation $\tau_b > 0.40$ ($\underline{P} < 0.05$). For ulterior model building, we retained only the 1 variable that showed the lowest probability in univariate tests. A stepwise logistic regression model using burrow data ($\underline{P} = 0.05$ for entry in and for exclusion from the model) was produced with retained habitat variables. We deleted data showing sign of presence but not burrows from this first analysis, because burrows may have been present outside the 60-m section. We used the Wald Chi-square, which was calculated as the square of the parameter estimate divided by its standard error, to evaluate variables selected in the regression (SAS 1990).

We used the index of rank correlation C (SAS 1990) to assess correlations between observed responses and predicted probabilities of the presence/absence of muskrat burrows. We also calculated the percentage of presence/absence of muskrat burrows correctly classified by the model.

We tested the model using independent data by calculating the percentage of sections of the Pontax and Rupert river watersheds correctly classified by the model as to the presence or absence of burrows. A $\underline{P} > 0.5$ was considered as predicted presence of muskrat burrows. Finally, we repeated all the above steps, using the presence or absence of muskrat feeding sign or droppings as the dependent variable.

RESULTS

Slow-flowing rivers and streams and beaver ponds exhibited the highest proportion of muskrat signs (42%) and burrows (24%), while none were detected in bogs/fens and fast-flowing rivers (Table 5.1). Muskrat burrows were found in greater proportion in sections of slow-flowing rivers than in lakes, beaver ponds, and slow-flowing and fast-flowing streams (Table 5.1). The mean number of burrows was 2.1 ± 5.5/km of shore for all habitats, and lodges were not observed. Water depth at 2 m from shore, the distance from shore to a water depth of 50 cm, emergent plant cover, and protection of the site from prevailing winds were not related to the presence or absence of muskrat burrows, feeding sign or droppings (Table 5.2) and thus were not considered for regressions. For identical reasons, the percentage of floating plant cover in the aquatic plant community and water velocity were not considered for building the logistic regression on presence or absence of feeding sign and droppings (Table 5.2). The area covered by the aquatic plant community and the mean aquatic plant cover were related to each other (Kendall correlation, $N = 235$, $\tau_b = 0.83$, $\underline{P} < 0.001$), and the former was used for building regressions because of its higher significance in univariate tests (Table 5.2).

Presence/absence of clay-loam soil was related to presence/absence of sand-gravel (Kendall correlation, $N = 235$, $\tau_b = -0.75$, $\underline{P} < 0.001$) and was used for model building because of higher significance in univariate tests (Table 5.2). Bank slope was correlated with the distance from shore to a 50-cm elevation (Kendall correlation, $N = 235$, $\tau_b = -0.69$, $\underline{P} < 0.001$). We used bank slope as a regressor in the logistic regressions because of a slightly higher significance in the univariate test of burrows (Table 5.2) and for comparison with results of published articles where this variable was important in use of muskrat habitat (Brooks and Dodge 1981, Jelinski 1984, Brooks 1985). The stepwiselogistic-regression analysis produced a model to predict the probability of burrow presence that is significant (Logistic regression, -2 log likelihood = 169.408, $\chi^2 = 41.786$, 5 df, $\underline{P} < 0.001$; Table 3). Peat soil, mean cover by aquatic plant, distance to hydrophyte community and water velocity did not enter the model ($\underline{P} > 0.05$). The model correctly classified 88% of the data used to build the model (Index or rank correlation = 0.815) and 92% ($\underline{n} = 102$) in test sections sampled in streams and rivers of the Pontax and Rupert river watersheds but not used to build the model.

The logistic regression on the presence/absence of muskrat feeding sign and droppings included 4 habitat variables (Logistic regression, -2 Log likelihood = 210.894, χ^2 = 40.002, 4 df, $\underline{P} < 0.001$; Table 3). Peat soil, mean cover by aquatic plant and distance to hydrophyte community did not enter the model ($\underline{P} > 0.05$). The model correctly classified 79% of the data used to build the model (Index of rank correlation = 0.777), and 71% of the 126 river and stream test sections not used for model building.

Table 5.1 Numbers and percentages of surveyed 60-m shore sections of wetlands with muskrat feeding sign/droppings and burrows and comparison of occurrence of burrows in slow-flowing rivers with other wetland types (P) in James Bay, Quebec, 1990.

Wetland	Surveyed	Muskrat feeding sign/droppings		Burrows		P[a]
	(n)	(n)	(%)	(n)	(%)	
Lake	64	8	12.5	4	6.2	<0.001
Bog/fen	37	0	0.0	0	0.0	<0.001
Beaver pond	43	13	30.2	6	13.9	0.006
Fast-flowing river (≥10m/min)	3	0	0.0	0	0.0	
Slow-flowing river (≤10m/min)	34	12	35.3	15	44.1	
Fast-flowing stream (≥10m/min)	16	2	12.5	0	0.0	0.001
Slow-flowing stream (≤10m/min)	46	19	41.3	9	19.6	0.030
Total	243	54	22.2	34	14.0	

[a] Fisher's exact test.

Table 5.2 Results of univariate tests on habitat variables measured along 60-m shore sections of various wetlands in James Bay, Quebec, and their significance (P) as to the presence/absence of muskrat burrows and feeding sign and droppings.

Variables	Burrows			Feeding sign/droppings		
	n	Statistic test^a	P	n	Statistic test^a	P
Water depth 2 m from shore^1	200	Z = -0.35	0.723	234	Z = -0.25	0.804
Distance to 50-cm water depth^1	199	Z = 0.67	0.503	233	Z = -0.57	0.566
Distance to a 50-cm elevation^1	200	Z = -2.42	0.015 –^{b}	234	Z = -2.17	0.030 –
% Submerged plant cover^2	200	Z = 2.55	0.010 +	235	Z = 3.53	<0.001 +
% Floating plant cover^2	203	Z = 2.11	0.035 +	235	Z = 1.25	0.212
% Emergent plant cover^2	200	Z = -0.56	0.558	235	Z = 0.11	0.911
% cover of hydrophytes^2	203	Z = 2.64	0.008 +	235	Z = 2.89	0.004 +
Surface covered by hydrophytes^2	202	Z = 2.97	0.003 +	235	Z = 3.04	0.002 +
Distance to hydrophyte community^1	200	Z = 2.41	0.016 +	235	Z = 2.42	0.015 +
Water velocity^1	200	Fisher	0.137 –	235	Fisher	0.258
Protection from wind^{1,3}	200	Fisher	0.322	233	Fisher	0.157
Bank slope^{1,4}	200	Fisher	0.013 +	235	Fisher	0.078 +
Width of shore herbaceous belt^{5,6}	200	χ^2 = 7.58	0.023 +	235	χ^2 = 10.88	0.004 +
Dominance of clay-loam soil^{3,7}	200	Fisher	0.003 +	235	Fisher	<0.001 +
Dominance of sand-gravel soil^{3,7}	200	Fisher	0.062 –	235	Fisher	0.034 –
Dominance of peat soil^{3,7}	200	Fisher	0.137 –	235	Fisher	0.130 –
Wetland type3,8	200	χ^2 = 32.81	<0.001	235	χ^2 = 32.10	<0.001

[a] Univariate tests used were Wilcoxon 2-sample, Chi-square, or Fisher's exact.

Table 5.2 Cont. Results of univariate tests on habitat variables measured along 60-m shore sections of various wetlands in James Bay, Quebec, and their significance (P) as to the presence/absence of muskrat burrows and feeding sign and droppings.

[b] The + or − sign indicates the direction of the relationship with the response variable.

[1] Variable measured at the central point of the 60-m shore section.

[2] Estimated in a maximum square surface of 60 x 60 m bordering the shoreline.

[3] Protection from wind was a binomial variable (protected, unprotected) based on wetland size, emergent vegetation cover and orientation of section in regards of prevailing winds.

[4] Bank slope was binomial: >45°, ≤45°

[5] Determined for the 60-m shore section.

[6] Width of herbaceous belt had 3 levels: 0, ≤5, >5 m.

[7] Measured as dominant or not dominant.

[8] Six types were compared: lake, bog/fen, beaver pond, slow-flowing river, slow-flowing stream, and fast-flowing river and stream.

Table 5.3 Results of the Wald Chi-square (P) for each habitat variable included in the logistic regression models on the presence/absence of muskrat feeding signs/droppings and burrows in various wetlands of James Bay, Quebec, 1990.

Variable	Feeding signs/droppings			Burrows		
	Coefficient	χ^2	P	Coefficient	χ^2	P
Intercept	3.1676	3.155	0.076	4.4569	2.717	0.099
% submerged plant cover[1]	0.0249	11.901	<0.001	0.0293	12.251	<0.001
Dominance of Clay-loam soil[2,3]	1.0637	8.045	<0.001	1.0328	4.000	0.045
Width of shore herbaceous belt[2,4]	0.7958	8.756	0.003	0.8387	5.916	0.015
Bank slope[5,6]	1.0461	7.381	0.007	1.5889	9.941	0.002
% floating plant cover[1]				0.0150	7.727	0.005

[1] Estimated in a maximum square surface of 60 x 60 m bordering the shoreline.

[2] Determined for the 60-m shore section.

[3] Measured as dominant or not dominant.

[4] Width of herbaceous belt had 3 levels: 0, ≤5, >5 m.

[5] Variable measured at the central point of the 60-m shore section.

[6] Bank slope was binomial: >45°, ≤45°

DISCUSSION

The use of presence and absence of muskrat sign to build muskrat habitat use models was done with the assumption that signs of presence were equally observable in different habitats and that detection of these signs was not dependent upon sign abundance. Because habitat selection may be density dependent it can affect the predictive power of a habitat use model. Messier et al. (1990) showed that the distribution of dwellings was best explained by a despotic model. If the distribution of critical habitat variables is uneven across the studied area, local densities of muskrat may be high where habitat is favourable, forcing less fit individuals to occupy less suitable habitats. The extent to which this situation was present in the study area is not known; however, the fact that the observed burrows/km was relatively low (Chulick 1979, Jelinski 1984, Brooks 1985, Blanchette 1985, Messier et al. 1990) indicates that such a situation was less likely to occur. The absence of muskrat from an apparently suitable habitat, however, may be due to the isolation of the site from potential colonizing muskrat populations.

In the burrow model, three variables (the floating and submerged plant covers and width of the shore herbaceous belt) represented potential sources of food. Shore herbaceous vegetation is important for muskrat in summer (Jelinski 1984) and this variable has been included in the Habitat Suitability Index model for estuarine habitats (Allen and Hoffman 1984). Access to this resource may, however, be constrained during winter due to ice build-up. The importance of accessibility to submerged hydrophytes has been shown to increase as summer progresses into winter (Jelinski 1984). The low density of muskrat burrows found in the study area could be attributed, in part, to the limited presence of well-developed hydrophyte communities (average cover of hydrophytes = 24.8%). The absence of lodges in the 23 plots surveyed was due to the absence of suitable emergent plant communities and to muskrat preference for burrows over lodges when the population level is low (Messier et al. 1990).

The probability of finding muskrat burrows in a given section was greater when clay-loam soils dominated the shore. The lower number of muskrat burrows or signs of presence on lakes can be explained, in part, by the absence of lakes with clay-loam bottom in the sample. In clay-loam soil, burrows are relatively permanent (Earhart 1969). Danell (1978) also observed more burrows/km on shores composed of finer grade sediments than on shores composed of coarser grade substrate. Burrows in peaty soil were rare due to the association of this type of soil with bog or fen, which are often isolated from the rest of the hydrographic system, and where banks in which to dig burrows are scarce to absent. The presence of peat also was negatively correlated with the surface covered by hydrophytes and the width of the shore herbaceous belt, while the presence of clay-loam soil was positively correlated with this last vegetation variable. The type of soil is directly related to muskrat presence possibly because of its cohesive properties and indirectly through its effects on plant distribution.

Bank slope was negatively related to the surface covered by hydrophytes and width of the shore herbaceous belt and positively correlated with water velocity. However, it also was positively correlated with burrow presence. Muskrat was shown to be associated with steeper bank slope in winter than in summer (Jelinski 1984). Steeper slopes would allow muskrats to put their burrows above the high water mark zone, while greater accumulation of snow on these slopes would provide a good insulation against the cold (Jelinski 1984). Brooks and Dodge (1981) reported that suitable habitat for a burrow-dwelling muskrat has a bank slope of ≥ 10°. However, in Massachusetts and Pennsylvania, bank slope at burrow sites varied between 57° and 77° (Brooks 1985). Here the use of a binomial variable was sufficient to demonstrate importance of bank slope. In a more southern environment, Brooks (1980) found that 60% of burrows were located where water velocity was <9.6 m/min. Errington (1963) also reported muskrat preference for lentic water bodies. In our study area, no burrows were found in sections of rivers or streams with a water velocity > 10 m/min. While water velocity was significant in the first step of the burrow logistic regression, it was not selected in the final model, probably because of its correlation with bank slope and presence/absence of clay-loam soil variables .

Water depth was not related to muskrat presence/absence probably because the average depth of 48 cm at 2 m from the shore was sufficient in early fall. The absence of muskrat in bogs or fens with deep (Mean ± SD: 101 ± 71 cm) water at 2 m from the shore, contributed to the nonsignificance of the water depth variable.

The burrow model included floating plant cover as the only variable not included in the feeding sign and droppings model. The inclusion of the other 4 same variables (% submerged plant cover, dominance of clay-loam soil, width of herbaceous belt, bank slope) in both models is not surprising because muskrat movements are generally restricted to the vicinity of their burrows (100-150 m: Ching and Chih-Tang 1962, Erickson 1963, Errington 1963, Neal 1968, Brooks 1980), and habitat is not likely to vary substantially over such a short distance. The deletion of data when sign of feeding or droppings were recorded but not burrows, to generate the burrow model, may have improved the classification power of this model. Deletion was biologically justified because muskrat producing feeding signs and droppings in early fall were likely to inhabit burrows just outside the sampled section. Attributing a muskrat absence to such a section would have lowered the classification rate of the burrow model.

Validation of both models using data not used to generate them is not a test of model performance in unsampled watersheds, as 11 of the 23 plots were located in these 2 watersheds. However, the considerable distance between sampled sections ensures independence between both data sets. Although the burrow model yielded a slightly better classification rate than feeding sign or droppings model, its use is costly because it requires more field time to gather burrow data. Depending upon question asked, the small improvement in classification power provided by the use of the burrow model may not be worth the extra cost.

MANAGEMENT IMPLICATIONS

A muskrat habitat model based on sign of presence may not provide information on actual muskrat densities associated with different habitats, but it has the advantage of being developed through a nonintrusive methodology and at lower cost than models based on trapping data. Sign of presence data can be acquired rapidly over a wide area. The habitat variables included in the both models could easily be recorded from a helicopter by experienced observers. Because characterization of the potential of define areas to sustain a species is often a requirement of environmental assessments, the methodology presented here could replace traditional survey of lodges in areas where muskrats are burrow dwellers.

ACKNOWLEDGEMENTS

This study was part of the Nottaway-Broadback-Rupert hydroelectric project feasibility studies conducted by Hydro-Québec (Montreal). J.-G. Ladouceur contributed to field work. We thank M. J. Lacki, G. J. Doucet, M. R. Julien, and S. Novak for their critical review of the manuscript.

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GENERAL CONCLUSION

In southern Canada, ditch and riverine wetlands are extremely frequent and could be affected by agricultural practices. In order to understand the importance of the type of crop bordering ditches and associated farming practices, studies of muskrat population dynamics, habitat use, and activity of co-occurring vertebrate species were undertaken.

In selected ditches with optimal soil type, bank slope and water flow, we did not detect important differences between ditches bordered by corn fields and ditches bordered by hay fields, for the following variables: the number of adult males, the number of adult females, the overall number of adults, the number of juveniles, the sex ratio of adults and juveniles, the number of litters, the number of litters per resident adult female, the number of young per litter, weight of adult males, weight of adult females, juvenile birth-to-capture mortality rate, and the annual population turnover. Muskrat activity in 1989 was higher in hay ditches than in corn ditches, but it was not predictive of raccoon, mink, turtle, or frog activity. The average date of birth of young muskrats was earlier in corn ditches than in hay ditches in 1989. Overall, it was not possible to say that one kind of crop provided better habitat quality than the other as measured with muskrat life history variables. Altogether the studied ditches showed a high muskrat population density and an almost complete summer-to-spring population turnover. The high population turnover in small farm ditches suggested that opening a fall trapping season for these wetlands should not affect muskrat population the following spring.

Our results suggest that it would not be justified to control the type of crop bordering ditches to influence muskrat populations. The highly positive relationship between the natural logarithm of the number of burrows and the number of muskrats showed the potential usefulness of using the number of burrows as an index of population size.

The analysis of the genetic proximity between individuals, confirmed by higher BSI's between pairs of adults within a year and from year to year, comparing ditches bordered by corn fields and ditches bordered by hay fields, through the use of the

DNA fingerprinting technique, supported the results of the study of population variables based on signs of presence and trapping data. The possibility of observing differences in genetic proximity between pairs of adult muskrats (for ♀♀ and ♂♀ pairs), confirmed by the difference obtained within and among ditches, would have permitted detection of important effects due to habitat quality on the rate of territory retention within families (Caley 1987) if such a difference in habitat quality existed between ditches bordered by corn fields and those bordered by hay fields. The absence of a corn/hay effect on genetic proximity between adult muskrats, within a year and from year to year, does not support a differential effect of corn versus hay fields bordering ditches on muskrat habitat quality. The study of the kinship between juveniles and between juveniles and co-occurring adults generally supported the use of trapping data to infer relatedness between juvenile muskrats and between juvenile and adult muskrats. However, caution must be exercised as we showed that spatio-temporal proximity did not always mean kinship, and that true parents were not always detected by trapping.

These same ditches were used for a study of muskrat habitat use by recording signs of presence. This study showed that the type of crops bordering ditches on muskrat habitat use was not important to explain muskrat presence or absence. The proportion of ditch sections with signs of muskrat grazing on crops was not different between three different types of row crops (alfalfa, grain, corn). We showed that, within a range of low water velocities, muskrat presence was positively related to current speed. This could support the idea that muskrat grazing contributes to maintain stream flow, or that muskrats select sections of ditches where the current would be high enough to reduce ice thickness in winter, without impairing their movements. A study of the effect of muskrat grazing on ditch vegetation, through the use of exclosures, would allow to investigate further the relationship with current speed.

The usefulness of muskrat signs of presence to test the effect of one environmental factor in southern Quebec led to the use of the same technique to build habitat use models in various habitats and environmental conditions of the James Bay area.

The study showed that rivers with slow current represented the best type of wetland, while muskrat was absent from bogs. The habitat use models identified a few key habitat variables, and yielded good classification rates for unused data. It is suggested that the collection of data on muskrat sign and habitat, followed by the development of a habitat use model to identify the most significant variables to muskrat presence can be part of a process to assess the relative potential of different areas to sustain muskrat populations.