HABITAT SUITABILITY AND DEMOGRAPHY OF MUSKRATS
INHABITING A HETEROGENEOUS LANDSCAPE

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Habitat Suitability and Demography of Muskrats
Inhabiting a Heterogeneous Landscape

Recent ecological theory predicts that change in population size is linked to the spatial and temporal variation in demographic performance of individuals. Adult survival and juvenile recruitment rate is often correlated with habitat suitability which may be related to food resources and/or predation risk. Spacing behaviour, which forces individuals to emigrate from prime to marginal habitats can regulate abundance in prime habitat, and influence local population size. However, few empirical studies have adequately tested all predictions of this spatially-dependent population model. I examined three hypotheses related to the spatial and temporal variation in demography of a local muskrat population inhabiting a landscape with unequal suitability among habitats.

Results confirmed that habitat selection in muskrats was density-dependent. Water level limited population size of muskrats by influencing adult and juvenile survival during the breeding (May-October) and non-breeding (October-May) period. Consequently, water level played a major role in determining the abundance and distribution of muskrats among habitats. Differences in habitat suitability were primarily related to the survival rate of juveniles during the breeding period, and all individuals overwinter. Since food resources could not be linked to habitat suitability, I hypothesize that spatial variation in predation risk is a key factor influencing habitat suitability for muskrats.

Overall, variation in demographic parameters indicated that
residents of island shorelines (prime habitat) were less affected by the density-independent effects of water level than individuals occupying emergent vegetation (more marginal habitats). In addition, spacing behaviour played an integral part in regulating the breeding density of muskrats in prime habitat. At the local level, population dynamics appeared to result from the interaction of spacing behaviour, predation, and water level.

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ABSTRACT

Recent ecological theory predicts that change in population size is linked to the spatial and temporal variation in demographic performance of individuals. In particular, directional dispersal of individuals from prime to marginal habitats can regulate abundance in prime habitat, and influence local population size. However, few empirical studies have adequately tested all predictions of this spatially-dependent population model. The focus of my research was to measure the spatial and temporal variation in demography of a local muskrat population inhabiting a landscape with unequal suitability among habitats.

First, I tested the hypothesis that water level limits population size and distribution of muskrats during the breeding period (May - October). The following predictions were supported: (1) population growth rate was affected negatively by extreme fluctuations in water level, (2) the relative distribution of dwellings among habitats was dependent on water-level conditions, and (3) adult survival and juvenile recruitment were lower under variable than constant water level, particularly in marginal habitats. I postulated that the nutritional condition of muskrats during the breeding period would be unaffected by water level regime due to continued access to food resources. However, individuals that experienced severe water fluctuations possessed an average of 5% less fat than individuals that
experienced constant water level, thus falsifying my prediction.

Next, I measured nine nutrient-dependent, phenotypic variables of muskrats and one index of forage quality during the ice-free period. Data were used to test the hypothesis that differences in food resources limits the demographic performance of muskrats in marginal versus prime habitats (food limitation hypothesis, FLH). None of the null predictions relating habitat suitability with reproductive parameters could be rejected statistically. Adult body mass and length were greater in prime habitats, but fat content did not differ, which suggested that the difference was associated with larger structural size of dominant animals in prime habitats. Growth rate of weaned juveniles was not different among habitats, which represented the strongest evidence for rejecting the FLH. Fecal crude protein content, which was used as an index of quality of food ingested, was marginally different between the two most suitable habitats, but the direction of the difference did not support our prediction. Overall, the temporal variation in fecal crude protein indicated that forage quality was more or less homogenous among habitats.

Lastly, I examined the spatial and temporal variation in demography among habitats during the breeding (May - October) and non-breeding (October - May) period. Specifically, I tested several predictions of the source-
sink model. Data showed that habitat selection in muskrats was density-dependent. Variation in population size and density was lower in the source habitat (island shorelines; HAB 1) than in the two postulated sink habitats located in emergent vegetation (HAB 2 and HAB 3). During the breeding period, survival rate of juveniles was significantly higher in HAB 1 than HAB 2 and 3 in two of three years, but no spatial difference in adult survival was found. The probability of a muskrat surviving the non-breeding period was greatest in HAB 1, especially when autumn water level was low. Emigration of adults from HAB 3 during the autumn and spring also suggested that expected fitness there was less than in the other habitats. Spatial variation in population growth, density, survival, and dispersal movements indicated that HAB 1 represented a source habitat for muskrats, while HAB 2 was marginal and HAB 3 was a sink habitat. Failure to detect directional emigration from source to marginal habitats in spring was likely due to declining population size overwinter. Nonetheless, dispersal among and within habitats provided support for the role of spacing behaviour in regulating breeding density of muskrats in prime habitats.

Water level strongly limits population size of muskrats by influencing adult and juvenile survival during the breeding and non-breeding period. Consequently, water level plays a major role in determining the abundance and
distribution of muskrats among habitats. Differences in habitat suitability were primarily related to the survival rate of juveniles during the breeding period, and all individuals overwinter. Variation in demographic parameters indicated that residents of island shorelines (prime habitat) were less affected by the density-independent effects of water level than individuals occupying emergent vegetation (more marginal habitats). Since food resources could not be linked to habitat suitability, I hypothesize that spatial variation in predation risk is a key factor influencing habitat suitability in muskrats. Spacing behaviour plays an integral part in regulating the breeding density of muskrats in prime habitat. At the local level, population dynamics appears to result from the interaction of spacing behaviour, predation, and water level.
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1. GENERAL INTRODUCTION

1.1 Population dynamics and habitat selection theory

The abundance and distribution of organisms varies over ecological space and time. Hypotheses concerning the factors responsible for the persistence and stability of populations have occupied the scientific literature since the turn of the century (see Cappuccino 1995). Andrewartha and Birch (1954) believed that regional persistence could be maintained through the temporal colonization and extinction events of several local or subpopulations. Ecologists that adopted this view were generally interested in how density-independent factors determine population abundance and distribution. Population persistence was believed to be a result of favourable and unfavourable conditions occurring randomly through space and time (Andrewartha and Birch 1954; Den Boer 1968; Reddingius 1971; Reddingius and Den Boer 1989).

Other researchers directed their attention toward factors that generate population stability or regulate population size around some dynamic equilibrium (Nicholson 1933; Hassel and May 1973; Fowler 1987; Royama 1992). Population regulation is the result of demographic parameters (e.g., mortality, natality) responding directly to changes in density. Intra- and interspecific competition
and predation are processes that can produce density-dependent responses in demographic parameters. In addition, strong density-dependent regulation can make populations more resistant to limiting factors characterized by stochastic variation (Sinclair and Pech 1996). Currently, it is generally accepted that both density-independent and density-dependent factors operate to determine fluctuations in population size (Sinclair 1989; Hanski 1990; Messier 1991; Murdoch 1994; Turchin 1995; Sinclair and Pech 1996).

At the local scale, Fretwell and Lucas (1970) incorporated density dependence in the ideal free distribution model to explain habitat selection in animals occupying habitats of unequal suitability. Habitat suitability, which influences demographic performance (i.e., survival, juvenile recruitment), has been linked to food quality and quantity, and predation risk (Boutin 1990; Desy et al. 1990; Doncaster 1994). Two key assumptions of the ideal free distribution model are: (1) the number of individuals in each habitat is proportional to the resources available, and (2) individual fitness is equivalent across all occupied habitats. In non-territorial species, differences in habitat suitability are offset by differences in competitor density, hence causing similar rates of survival and reproduction among habitats (Fretwell and Lucas 1970). Alternatively, in territorial species, the ideal despotic distribution predicts that some individuals may
attain greater fitness by defending some critical resource(s) (Fretwell and Lucas 1970). Spacing behaviour will therefore alter the spatial abundance and distribution of individuals compared to predictions of the ideal free model.

1.2 Spacing behaviour as a regulatory mechanism in animal populations

Spacing behaviour has been implicated as a proximate mechanism for regulating population size in birds and small mammals (see O’Connor 1985; Stenseth and Lidicker 1992). The hypothesis stating that forced emigration of individuals from prime (source) to marginal (sink) habitats could regulate the number of small mammals in prime habitats was proposed in the 1970’s (Lidicker 1975; Hansson 1977; Stenseth 1977; Łomnicki 1978). Later, the source-sink concept of population regulation was fully developed and mathematically formulated by Pulliam (1988). Spatial variation in habitat suitability generates differential population growth rate among habitats. In source habitats, reproduction exceeds mortality resulting in a surplus of animals relative to the number of available breeding sites. Conversely, in sink habitats, juvenile recruitment is less than mortality which results in vacant breeding sites. Surplus individuals from prime habitats then immigrate into marginal habitats which stabilizes population density in
source habitats (Pulliam 1988). Depending on the current immigration and intrinsic growth rate, sink habitats can exhibit wide temporal variations in population size (Pulliam 1988).

Support for predictions of the source-sink model has been found, and source-sink dynamics has been inferred from a number of demographic studies of birds and small mammals (Keith et al. 1993; Paradis 1995; Curnutt et al. 1996; Holmes et al. 1996). However, few studies have successfully demonstrated the relative importance of emigration and mortality to habitat-specific population dynamics (Ostfeld and Klosterman 1986; Gliwicz 1989; Keith et al. 1993). Determining the correct spatial scale on which to analyze and detect source-sink dynamics has been a problem in some studies (Diffendorfer et al. 1995; Brawn and Robinson 1996). If the distance between prime and marginal habitats is greater than the dispersal capability of individuals, a key aspect of source-sink dynamics (directional emigration) will not be detected. More research on the significance of emigration in regulating the density of small mammals in prime habitats is required.
1.3 The muskrat as a model for investigating demography among habitats

A critical aspect of this research programme on muskrat population dynamics was the ability to distinguish between dispersal and mortality among habitats. Such studies of avian and mammalian dispersal are extremely rare (Koenig et al. 1996; Wolff et al. 1996). By selecting muskrats as a model to examine source-sink dynamics I sacrificed true replication of experimental units for a large spatial scale approach (Hurlbert 1984; Hairston 1989; Brown 1995). Without replication, my power of induction or ability to place the findings of this research into a broader ecological paradigm was limited. However, I believe that the ability to monitor mortality and dispersal across an entire population, combined with prior knowledge of muskrat population dynamics helped to reduce the limiting effect of lack of replication.

Because water level influences the spatial distribution of emergent macrophytes in marsh environments (Kantrud et al. 1989; Kenkel 1993), muskrats should provide a useful model for studying demographic parameters among habitats. Muskrats are also vulnerable to a host of different predators while traversing upland habitat (Errington 1963). Therefore, populations separated by relatively large tracks of land should have little exchange of individuals and can be considered "closed" populations. This attribute is
critical when attempting to distinguish between emigration and mortality.

Several studies have demonstrated the influence of water level on muskrat population size (Errington 1963; Donohoe 1966; Proulx and Gilbert 1983; Messier and Virgl 1992; Clark and Kroeker 1993). The depth and stability of water level indirectly affects habitat suitability, which is reflected in the demographic parameters of muskrats. For example, high and stable water level leads to high adult survival and juvenile recruitment, while declining water level results in increased mortality and negative population growth (Clark and Kroeker 1993; Clark 1994). Increased predation risk and nutritional stress during periods of decreasing water level are two mortality agents that could limit population size of muskrats, particularly during the winter (Messier et al. 1990; Clark and Kroeker 1993). The ability to manipulate the limiting effect of such an important environmental variable was critical in this study.

1.4 Objectives

My general objective was to determine the demographic processes that explain the abundance and distribution of a local population of muskrats inhabiting a heterogeneous landscape. I employed an intensive mark-recapture programme to estimate population size, survival, reproduction, and dispersal movements among three contiguous habitats at Indi
lake, Saskatchewan. Several nutrient-dependent, phenotypic characteristics were also measured to determine if habitat suitability was related to food resources. Trapping data was collected during the ice-free period (May - October) in 1988, and from May 1992 through May 1995. Specific objectives for each chapter are presented below.

In Chapter 2, I describe the study area, and temporal variation in population size and water level from 1987 to 1995. In Chapter 3, I test the hypothesis that water level limits the population size and distribution of muskrats during the ice-free period. During the breeding season (May - August), water level was manipulated to simulate moderate drought conditions in 1988 and relatively high and stable water level in 1992. Population growth, distribution, adult survival rate, juvenile recruitment rate, and nutritional condition are contrasted between years at the population and/or habitat-specific level.

In Chapter 4, using data from May 1992 through October 1994, I test the hypothesis that food resources significantly affect habitat suitability in muskrats (i.e., food limitation hypothesis). Statistical differences in habitat suitability are first established by analysis of litter survival rate. Nine nutrient-dependent, phenotypic attributes and one independent index of forage quality are used to determine if food limits demographic performance of muskrats among habitats.
In Chapter 5, using data from May 1992 through May 1995, I first examine factors that limit population size and determine habitat selection in muskrats. Subsequently, estimates of density, survival rate, recruitment rate, emigration and immigration rate among habitats are analyzed to test predictions of the source-sink model. The results are used to discuss the potential for detecting source-sink dynamics in populations inhabiting spatially structured environments with temporary changes in habitat availability.
2. STUDY AREA AND POPULATION

The study area was a 293-ha marsh (Indi lake; Fig. 2.1) located 50 km south of Saskatoon, Saskatchewan (51°41’N, 106°31’W). One important aspect of the marsh was its isolation from other bodies of water by a landmass of at least 1 km. I therefore assumed the muskrat population at Indi lake to be "closed" as exchanges of individuals with neighbouring populations would be extremely rare. The presence of an irrigation canal and control valve also permitted manipulation of water level in the marsh. Commercial trapping was prohibited to avoid potential confounding effects. Mink (Mustela vison), coyote (Canis latrans), striped skunk (Mephitis mephitis), raccoon (Procyon lotor), and northern harriers (Circus cyaneus) were common in the area.

I categorized the marsh into three contiguous habitats based on emergent vegetation and water depth. Thirty small islands, with perimeters ranging from 112 to 244 m, provided muskrats the opportunity to excavate burrow systems (Fig. 2.1). These island shorelines, which were surrounded by open water and submergent vegetation, constituted the first habitat. The average distance between island shorelines and emergent vegetation was approximately 75 m. The second and third habitats were located in emergent vegetation comprised of common bulrush (Scirpus validus), broadleaf cattail
Fig. 2.1. Spatial configuration of habitat types at Indi lake, Saskatchewan. HAB 1 = island shorelines, HAB 2 = common bulrush and cattail, HAB 3 = prairie bulrush.
(Typha latifolia), prairie bulrush (Scirpus paludosus), and spangletop (Sclochloa festucacea). Common bulrush and cattail formed dense stands that predominated in water levels between 30 and 50 cm deep, while stands of prairie bulrush (interspersed with patches of spangletop) were located in areas with less than 25 cm of water.

My study was part of a long-term research programme on muskrat population dynamics that began in May 1987 and terminated in October 1995. During this period, systematic surveys of the entire marsh were conducted approximately every two weeks throughout the ice-free period to check the occupancy of existing and newly constructed dwellings. Water level was also recorded from a permanent gauge. A summary of spring (May) and autumn (October) surveys for each year illustrates the large temporal variation in population size (Fig. 2.2).

From 1987 through 1995, the mean (±1 SD) number of muskrat dwellings at Indi lake was 146 ± 156. Water level was relatively less variable and averaged 94 ± 11 cm. In general, population size increased between spring and autumn, then decreased during winter. Spring population size increased from 1987 to 1988. In 1988, however, water level was allowed to decline from 85 to 40 cm during the breeding period which resulted in low adult survival and juvenile recruitment, and negative population growth (see Chapter 3). Subsequent overwinter mortality resulted in the lowest
number of dwellings in spring 1989. From October 1989 through October 1992, water level was maintained above 90 cm and spring population size steadily increased until May 1993 (Fig. 2.2). Low water level prior to freezing in autumn 1993 was associated with a decline in spring density in 1994. Overall, spring-to-spring change in population size appeared to be a result of the interaction between water level and muskrat density during autumn.
Fig. 2.2. Number of muskrat dwellings and water level during May (M) and October (O) from 1987 through 1995 at Indi Lake, Saskatchewan.
3. POPULATION STRUCTURE, DISTRIBUTION, AND DEMOGRAPHY OF MUSKRATS DURING THE ICE-FREE PERIOD UNDER CONTRASTING WATER FLUCTUATIONS

3.1 Introduction

Identifying factors that affect the rate-of-increase of populations (i.e., limiting factors) is critical for predicting population abundance (Berryman et al. 1987; Sinclair 1989; Messier 1991). In addition, determining the amount of variation in population growth rate explained by density-dependent (regulatory) versus density-independent factors provides an indication of how much these two processes influence the dynamics of a population. Investigating the spatial and temporal scales under which limiting and regulating factors operate is also fundamental to a fuller understanding of the demography of a population (Berryman et al. 1987; May 1989; Pulliam & Danielson 1991; Ostfeld 1992).

The muskrat (Ondatra zibethicus) is likely the most important herbivore species in freshwater marsh systems. Because marshes are well structured spatially, muskrats can be used as a model for studying population dynamics among habitats. Muskrats are extremely vulnerable to predators

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while travelling across upland habitat (Errington 1963). Therefore, populations separated by relatively large tracks of land should have little exchange of individuals and can be considered closed populations. This attribute provides a unique opportunity to investigate demographic parameters both among habitats, and at the population level.

Previous studies have suggested that water level affects the recruitment and survival of muskrats, and thus, limits muskrat populations (Errington 1939, 1963; Donohoe 1966; Proulx & Gilbert 1983). In general, the stability and depth of water level is directly related to habitat suitability and also influences the distribution of muskrats. Declining water levels during the ice-over (winter) season are associated with higher winter mortality, probably due to a combination of increased predation risk and nutritional stress caused by inaccessible forage (Proulx et al. 1987; Messier et al. 1990; Clark & Kroeker 1993). However, during the ice-free season, access to forage is generally not limiting, and therefore, water level should not affect the nutritional condition of muskrats. For example, muskrat populations can persist in upland habitat with minimum water and no predators (Clough 1987).

The presence of predators may limit population size of muskrats in marginal habitats (i.e., low water level; Errington 1956). If predation risk is habitat-specific, then survival and recruitment of muskrats in marginal habitats
should be lower compared to individuals in prime habitats. Although survival and recruitment may be high enough to promote an increase of muskrat numbers in prime habitats, low survival and recruitment in marginal habitats may cause a negative growth rate at the population level. In such systems, population parameters in both source and sink habitats must be investigated to assess the full limiting effect of a mortality agent (Pulliam & Danielson 1991). Such studies are, however, rare in the mammalian literature.

The objective of this study was to test experimentally the hypothesis that water level during the ice-free season represents a major limiting factor of muskrat population size. The number and distribution of muskrat dwellings, demography, and nutritional condition of individuals were contrasted under two different water level regimes: (1) a decline during early summer (i.e., moderate drought conditions) followed by reflooding in late summer, and (2) relatively high and stable water level throughout the ice-free season. I tested the predictions that (1) the population experiencing variable water level will exhibit a negative growth rate, while the population experiencing stable water level will have a positive growth rate, (2) differences in water level will cause a shift in the relative distribution of dwellings among habitats, (3) survival and recruitment will be lower under variable water than stable water level, particularly in marginal habitats,
and (4) nutritional condition of muskrats will be unaffected by water level due to continued access to food resources.

3.2 Methods

3.2.1 Water level and habitat availability

From mid-June through early August of 1988 the inflow of water was stopped, which resulted in a 40-cm drop (≈40%) in water level in the marsh. In contrast, during the summer of 1992, water level was maintained at 90-100 cm to simulate a more constant water regime.

The distribution of emergent vegetation in marsh ecosystems is largely dependent on long-term water level (Kantrud et al. 1989). In order to document the change in distribution of emergent hydrophytes, I estimated the surface area of HAB 2 and HAB 3 in December 1987 and 1992 by systematic point sampling. Fifty seven line transects were spaced 100 m apart in a east-west direction. Water depth and vegetation type were recorded every 25 m (n = 1160) along these transects.

I also considered the effect of water level on the fraction of habitat that is operationally available to muskrats (i.e., operational habitat availability, OHA). OHA was defined as the habitat area located in water ≥10 cm deep. This appears to be the minimum depth suitable for lodge construction (Clark 1994). OHA applies only to HAB 2
and HAB 3 as the availability of island shores (HAB 1) is not affected by changes in water level (i.e., depth of burrow entrances can be adjusted to changes in water level). The area of HAB 1 was calculated by summing the area bordering island shoreline. The area of HAB 1 for each island shoreline was calculated by multiplying the perimeter of the island by 100 m (i.e., the typical diameter of an adult muskrat’s home range; Marinelli and Messier 1993).

3.2.2 Dwelling numbers and distribution

Beginning on May 15, 1988, systematic surveys of existing and new muskrat dwellings were conducted at two-week intervals until September 1, 1988. Two additional surveys were carried out at the end of September and October when permanent ice formed. A total area of 126 ha was surveyed, of which open water accounted for 51 ha, HAB 1 for 29 ha, HAB 2 for 11 ha, and HAB 3 for 35 ha.

During 1992, surveys for active burrows and lodges began on May 1 and continued at two-week intervals until October 20 when permanent ice formed. Surveys were carried out over a 152 ha area. Open water accounted for 88 ha, HAB 1 for 21 ha, HAB 2 for 23 ha, and HAB 3 for 20 ha. In both years, water level was recorded from a permanent water gauge during each survey.
3.2.3 Capture-recapture

Three primary trapping periods were conducted during June, July, and August of 1988 and 1992 in the surveyed areas. Each primary trapping period consisted of 3 trapping nights per muskrat dwelling carried out over a 3-week period. Three to four modified Tomahawk traps were set near each burrow system or lodge. Traps contained dry vegetation for bedding, were baited with a piece of carrot, and covered with vegetation or a wood box. Lodges were also opened with minimum disturbance and checked for young (Caley & Boutin 1985). All young >40 g were marked with 2 monel 1 ear-tags (National Band & Tag Co., Newport, Kentucky).

Upon capture, muskrats were checked for ear-tags, sex, and reproductive condition (i.e., males: scrotal or not scrotal, females: pregnant or not pregnant). Body mass was recorded to the nearest 1 g. Total body length, tail length, and hind foot length were recorded to the nearest 1 mm. Unmarked animals were marked with two ear-tags. Muskrats were then released near the capture site.

I made two assumptions regarding the categorization of individuals which were recaptured in different habitat types. First, an individual captured a minimum of two consecutive times (either between primary sampling periods or within a primary sampling period) in a different habitat than that of initial capture was deemed to have changed habitats. Data from dispersing and exploratory (short
excursions followed by a return to original dwelling) individuals suggested that this assumption was valid. Second, if the dwelling originally occupied by a marked individual was no longer active, then a single capture of this muskrat at a new dwelling in a different habitat was indicative of a habitat change.

The frequencies of mink captures in muskrat traps, although opportunistic, was interpreted as an index of predator abundance. I formulated a habitat-specific predator abundance index based on the number of mink captured per 100 trap night per habitat during the primary trapping periods of June, July, and August.

### 3.2.4 Demography

Population size of adult muskrats was estimated at both the population and habitat-specific level using the minimum number known alive (MNA) method (Krebs 1966). Using MNA estimates, I determined the relative distribution and habitat-specific density of adult muskrats. Relative distribution of muskrats was calculated by dividing the population size per habitat by the total population size. Absolute density was determined by dividing habitat-specific population size by the area of operational habitat.

Adult survival rate was also calculated at both the population and habitat-specific level. Survival rate at the population level ($\Phi_p$) was calculated as:
\[ \Phi_p = \frac{\text{MNA}_{i+1}}{\text{MNA}_i} \quad (3.1) \]

where \( i \) represents the primary sampling period. Habitat-specific survival rate was calculated using the same formula, but the MNA estimates were adjusted for the number of immigrants and emigrants. Immigrants were not included in the survival estimates until the next sampling period (i.e., \( i+1 \) to \( i+2 \)). Conversely, emigrants were included in the analysis from time \( i \) to \( i+1 \). The assumption was that individuals that emigrated from a particular habitat between primary sampling periods survived in the previous habitat. This assumption was necessary because it was impossible to determine the exact time of emigration or immigration.

Habitat-specific immigration and emigration rates (from \( i \) to \( i+1 \)) for adult muskrats were calculated by dividing the number of immigrants or emigrants by the number known to be alive in that habitat at time \( i+1 \). Population growth rate was calculated as:

\[ \lambda_p = \frac{\text{MNA}_{i+1}}{\text{MNA}_i} \quad (3.2) \]

where \( \lambda_p \) is the finite rate of increase, and MNA estimates represent the total number of adults and juveniles (i.e., <6 months of age) known to be alive during each primary sampling period. Habitat-specific juvenile recruitment rate was estimated as the ratio of juveniles to adults for each primary sampling period. Both numerator and denominator were determined from MNA estimates. Survival, immigration and emigration rate, and finite rate of increase were
standardized as rates per 30-day interval.

3.2.5 Nutritional condition

As part of a study on the seasonal changes in body composition of adult muskrats, animals were also collected from the southern part of Indi lake (i.e., outside the study area) during the spring and summer of 1988 (Virgl & Messier 1992a). Fat content was determined from chemical analysis of carcass composition for muskrats with a fresh mass (hereafter referred to as body mass) >550 g collected during each primary sampling period. Although some of these individuals represent juveniles, I have previously demonstrated that juveniles with a body mass >550 g exhibit similar tissue dynamics as adults (Virgl & Messier 1992b). Fat content was then expressed as a proportion of body mass.

During 1992 the isotopic dilution method was used to determine the amount of body water possessed by adults (excluding pregnant females) during each primary sampling period. Tritiated water (1 mCi/mL) was injected interperitonealy and allowed 70-90 minutes to equilibrate with body water. A 1 mL blood sample was collected by cardiac puncture, placed in a 1.5 mL micro-cap, and stored in a cooler. Samples were then placed in a micro-centrifuge, and the serum was collected and stored at -20 °C.

The activity of tritium in the serum was determined by mixing 0.050 mL of serum with 5 mL of scintillation cocktail
in a glass vial and placing the vial in a liquid scintillation counter (Packard TRI-CARB 2000CA). Quench curves were constructed in order to correct for the decline in liquid scintillation counting efficiency due to chemical/colour quenching. Since isotopic dilution space overestimates body water concentration (percent body water) by 7-15% (Sheng and Huggins 1979), I decreased estimates of body water concentration by 5%. Fat concentration was then estimated using the predictive equation:

\[ Y = 71.88 - 1.03X \] (3.3)

where \( Y \) is percent body fat and \( X \) is percent body water of ingesta-free body mass \( (r^2 = 0.93, P < 0.01) \) as previously determined by Virgil & Messier (1993).

### 3.2.6 Statistical analyses

Log-likelihood ratios were used to analyze the effect of year on the distribution of dwellings among the three habitats during spring (15 May), summer (15 August), and autumn (1 November 1988; 20 October 1992). Spring and summer sampling points corresponded with maximum and minimum water levels, respectively. Autumn analysis corresponded with the time of freezing when muskrats no longer construct new dwellings.

I used the change in the number of dwellings between consecutive surveys as an index of population change (Danell 1978; Kroll & Meeks 1985; Thurber et al. 1991). Dwelling
numbers were log transformed and regressed on date of census. The slope of the curve provides an estimate of population growth rate ($r$). Using survey date as a covariable, analysis of covariance was then performed to test for the effect of year on population growth rate.

Log-likelihood ratios were used to test if the relative distribution of adult muskrats among habitats changed significantly during the summer months of 1988 and 1992. The $Z$-test for two independent proportions was used to test if the survival rate of adults in the population and in each habitat was significantly lower in 1988 compared to 1992 (i.e., one-tailed tests). I also determined if the survival rate of adults between sampling periods was statistically different within year and habitat. Two-way analysis of variance (ANOVA) was performed to test the effect of month and year on fat concentration (after arcsine transformation; Zar 1984). Previous work has indicated that female and male muskrats do not differ significantly in fat content during the summer (Virgl & Messier 1992a). Thus, I did not partition the data further (and reduce statistical power) by analyzing the effect of sex on fat content. All statistical analyses were performed using two-tailed probability levels (except where indicated) and the SAS statistical package for microcomputers. $P$-values $>0.05$ were considered not significant.
3.3 Results

Water level during the ice-free season differed markedly between 1988 and 1992, both in depth and variability (Fig. 3.1). The average bi-weekly water depth was 67.6 ± 13.5 cm (±1 SD) in 1988 compared to 101.5 ± 7.7 cm in 1992. The decline in water level during the summer of 1988 caused the OHA in HAB 2 to decrease from 95% of the area in May to 3% in August, while the OHA in HAB 3 decreased from 70% to 0% during the same period. Subsequently, the increase in water level during autumn resulted in the return of normal OHA for both habitat 2 and 3. Conversely, stable water levels in 1992 were associated with minimum changes in OHA in habitats 2 and 3. The only change was recorded in August when OHA in HAB 2 and HAB 3 declined 5%, but returned to maximum conditions in autumn. Overall, through control of water inflow in the marsh, moderate "drought" conditions were simulated in 1988, while more constant water level was created in 1992.

3.3.1 Dwelling numbers and distribution

During the period of drought conditions in 1988, the number of muskrat dwellings declined from 105 to 40 (Fig. 3.1). In contrast, there was a four-fold increase in the number of dwellings during 1992 when water level was more stable.
Fig. 3.1. Bi-weekly changes in the number of muskrat dwellings under different water level regimes during the ice-free season at Indi lake. In 1988 water level was experimentally reduced during the breeding period, and then increased during autumn (shaded area). In contrast, water level in 1992 was kept within normal conditions throughout the ice-free season. The number of dwellings was used as an index of population size.
Regressing dwelling numbers on date of census generated significant relationships for 1988 ($F_{1,8} = 15.25$, $P < 0.01$, $r^2 = 0.66$) and 1992 ($F_{1,10} = 184.30$, $P < 0.01$, $r^2 = 0.95$). Estimates of population rate of change ($r \pm 1 \text{ SE}$) from these regressions were $-0.082 \pm 0.021$ and $0.125 \pm 0.009$ for 1988 and 1992, respectively. Analysis of covariance indicated that the population rate of change was significantly different for these two periods ($F_{1,18} = 93.71$, $P < 0.01$).

The relative distribution of dwellings among the three habitats during the spring was not significantly different between 1988 and 1992 ($G = 2.38$, $df = 2$, $P > 0.20$). On average, 40% of occupied dwellings were located in each of HAB 1 and 2, and 20% were distributed in HAB 3 (Fig. 3.2). With declining water level in 1988, the proportion of dwellings located in habitats 2 and 3 decreased, which caused an increase in the proportion of dwellings in island shorelines. At the time when the lowest water level was recorded (August), there were no occupied muskrat lodges in HAB 3 and the 50 remaining dwellings were distributed evenly between habitats 1 and 2. During the summer of 1992, the increase in dwellings was associated with a decrease in the proportion of dwellings in HAB 1, an increase in HAB 2, and minimal change in HAB 3 (Fig. 3.2). Statistical analysis at the time of lowest water level (August) indicated that the relative distribution of dwellings among habitats in 1988 was significantly different than that observed in 1992.
Fig. 3.2. Bi-weekly changes in the relative distribution of muskrat dwellings among habitats during the ice-free season in 1988 and 1992. The shaded area represents the period when water level was manipulated.
\( G = 25.0, \text{ df} = 2, P < 0.01 \).

During autumn 1988, the distribution of dwellings among habitats changed little from the distribution during summer, despite an increase in water level. Of the 55 dwellings occupied at time of freeze-over, 25 (45\%) were located in HAB 1, 26 (46\%) in HAB 2, and 4 (8\%) in HAB 3. In contrast, of the 193 dwellings occupied at time of freeze-over in 1992, 35 (18\%) were located in HAB 1, 112 (58\%) in HAB 2, and 46 (24\%) in HAB 3. The distribution of dwellings among habitats at time of freeze-over was significantly different between years \( G = 19.54, \text{ df} = 2, P < 0.01 \).

### 3.3.2 Demography

Minimum number alive and relative distribution of adult muskrats inhabiting the study area during early summer of 1988 and 1992 were similar (Table 3.1). With declining water level in 1988, the distribution of adults among habitats changed significantly during the summer months \( G = 10.38, \text{ df} = 4, P = 0.03 \). Concurrent with the decrease in adult abundance there was a decrease in the occupancy of HAB 2 and 3, and an increase in HAB 1 (Table 3.1). In contrast, the distribution of adults among habitats in 1992 did not vary significantly from June through August \( G = 1.30, \text{ df} = 4, P > 0.50 \).
Table 3.1. Total minimum number alive (MNA) and relative distribution of adult muskrats during the summer months of 1988 and 1992 at Indi lake, Saskatchewan. Relative distribution is given as the proportion of individuals occupying each habitat.

<table>
<thead>
<tr>
<th>Month</th>
<th>Total</th>
<th>%HAB 1</th>
<th>%HAB 2</th>
<th>%HAB 3</th>
<th>Total</th>
<th>%HAB 1</th>
<th>%HAB 2</th>
<th>%HAB 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>151</td>
<td>38</td>
<td>52</td>
<td>10</td>
<td>142</td>
<td>37</td>
<td>41</td>
<td>22</td>
</tr>
<tr>
<td>July</td>
<td>109</td>
<td>39</td>
<td>54</td>
<td>7</td>
<td>107</td>
<td>37</td>
<td>46</td>
<td>17</td>
</tr>
<tr>
<td>Aug</td>
<td>64</td>
<td>56</td>
<td>42</td>
<td>2</td>
<td>89</td>
<td>37</td>
<td>45</td>
<td>18</td>
</tr>
</tbody>
</table>
In summer 1988, the absolute density (individuals / ha ±1 SD) of adult muskrats occupying HAB 1 during the summer averaged 1.6 ± 0.4. In contrast, the absolute density of adult muskrats in habitats 2 and 3 actually increased during the summer due to loss of habitat. For example, the density in habitats 2 and 3 increased by a factor of 1.4 between June and July (HAB 2: 8.6 - 11.7; HAB 3: 0.6 - 0.9 adults / ha). Subsequently, there was an 8 fold increase in density in HAB 2 between July and August (11.7 - 90.0 adults / ha). This implies that the rate of decline in operational habitat exceeded the rate of loss of muskrats from these two habitats. Although 1 individual occupied HAB 3 in August, no estimate of absolute density could be calculated because there was no operational habitat available.

In 1992, the absolute density (±1 SD) of adult muskrats in habitats 1, 2, and 3 were 2.0 ± 0.5, 2.3 ± 0.4, and 1.8 ± 0.7, respectively. Between July and August, the slight decline in water level and subsequent decrease in OHA coincided with a slight decrease in adult density in HAB 2 and 3. Thus, contrary to the response to conditions in 1988, the rate of loss of individuals from habitats 2 and 3 was equal to or greater than the rate of decrease in OHA.

During the summer of 1988, there was no significant change, at the population level, in survival rate (Z = 1.16, P = 0.24) of adult muskrats between June - July (interval 1) and July - August (interval 2). While the survival rate of
individuals in HAB 2 decreased significantly between the two intervals ($Z = 2.51, P = 0.01$), the increase in survival rate of adults in HAB 1 and decrease in HAB 3 were not significant ($Z < 1.12, P > 0.20; \text{Table 3.2}$). During the summer of 1992, there was no change in adult survival rate between the two intervals at the population level or within habitats ($Z < 0.93, P > 0.30$). Results do suggest, however, that through the summer individuals occupying HAB 3 suffer greater mortality than residents in HAB 1 and 2 (Table 3.2). The survival rate of the adult population from June - August, 1988 was significantly lower than the population during the same interval in 1992 ($Z = 2.81, P < 0.01$). Importantly, survival rate of adults in HAB 1 was not statistically different between years ($Z = 0.25, P = 0.40$), but adults in HAB 2 and 3 suffered significantly greater mortality in 1988 compared to 1992 ($Z > 2.32, P < 0.01$).

Dispersal movements of adult muskrats among habitats was greater during the summer of 1988 compared to 1992 (Table 3.3). In 1988, I recorded an immigration rate of 8% in July and 9% in August for HAB 1. No movement of muskrats into habitats 2 or 3 were recorded during this time. Although there was no emigration from HAB 1 during the summer of 1988, several muskrats moved out of HAB 2 and 3 (Table 3.3). For example, the emigration rate of adults from HAB 3 was 19% in July, and 51% in August. In 1992, immigration was observed only in HAB 1 and 2 during July. No
emigration from HAB 1 occurred during July and August although some dispersal movements out of habitats 2 and 3 were recorded in July (Table 3.3).

In 1988, the population finite rate of increase ($\lambda_p$) was 0.83 during June - July, and 0.64 during July - August. This decrease in population growth was not due only to the decline in adult survival rate in HAB 2 and 3, but was also attributable to low juvenile recruitment rates among all habitats (Table 3.4). During the 1988 breeding season, the juvenile:adult ratio did not exceed 1.00 in any habitat. In contrast, $\lambda_p$ was 1.25 during June - July, and 1.74 during July - August of 1992. The positive growth rate of the population was the result of high juvenile recruitment rates in all habitats (Table 3.4). Pregnancy rate did not appear to be a contributing factor to the low number of juveniles recruited into the population in 1988 as the proportion of females sampled and visibly pregnant in 1988 was 29% ($\pi = 69$), compared to 32% ($\pi = 65$) in 1992.

3.3.3 Mink abundance

Abundance of mink increased in each habitat from June through August during 1988 (Table 3.5). Since there were no active dwellings in HAB 3 during August, and no traps were set, the mink abundance index could not be calculated. Considering that the risk of predation is equal to the number of predators / number of prey, and the number of
Table 3.2. Population ($\Phi_p$) and habitat-specific survival rates (30 d intervals) for adult muskrats during the summer months of 1988 and 1992. Survival rates for both levels are based on MNA estimates. Habitat-specific rates were corrected for immigration and emigration of muskrats among habitats.

<table>
<thead>
<tr>
<th>Interval</th>
<th>1988</th>
<th>1992</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\Phi_p$</td>
<td>HAB 1</td>
</tr>
<tr>
<td>June - July</td>
<td>0.67</td>
<td>0.70</td>
</tr>
<tr>
<td>July - Aug</td>
<td>0.60</td>
<td>0.80</td>
</tr>
<tr>
<td>June - Aug</td>
<td>0.63</td>
<td>0.75</td>
</tr>
</tbody>
</table>
Table 3.3. Habitat-specific immigration and emigration rates (number / MNA estimate; rate per 30 d interval) for adult muskrats during summer months of 1988 and 1992. The number of immigrants or emigrants are designated by parentheses.

<table>
<thead>
<tr>
<th></th>
<th>1988</th>
<th></th>
<th></th>
<th>1992</th>
<th></th>
<th></th>
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<tbody>
<tr>
<td></td>
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<td>HAB 3</td>
<td>HAB 1</td>
<td>HAB 2</td>
<td>HAB 3</td>
</tr>
<tr>
<td><strong>Month</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Immigration</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>rate</td>
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</tr>
<tr>
<td>June - July</td>
<td>0.08</td>
<td>0.00</td>
<td>0.00</td>
<td>0.03</td>
<td>0.05</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>(5)</td>
<td></td>
<td></td>
<td>(1)</td>
<td>(2)</td>
<td></td>
</tr>
<tr>
<td>July - Aug</td>
<td>0.09</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
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<td>(3)</td>
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<tr>
<td>rate</td>
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</tr>
<tr>
<td>June - July</td>
<td>0.00</td>
<td>0.03</td>
<td>0.19</td>
<td>0.00</td>
<td>0.03</td>
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</tr>
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<td>(3)</td>
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<td>(2)</td>
<td></td>
</tr>
<tr>
<td>July - Aug</td>
<td>0.00</td>
<td>0.08</td>
<td>0.51</td>
<td>0.00</td>
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</tr>
<tr>
<td></td>
<td>(2)</td>
<td>(1)</td>
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</tr>
</tbody>
</table>
Table 3.4. Population finite rate of increase ($\lambda_p$; total MNA$_{i+1}$ / MNA$_i$, rate per 30 d interval) and habitat-specific juvenile recruitment rates during the summer months of 1988 and 1992. Habitat-specific juvenile recruitment rates were calculated as the minimum number of juveniles divided by the minimum number of adults known to be alive.

<table>
<thead>
<tr>
<th>Month</th>
<th>$\lambda_p$</th>
<th>HAB 1</th>
<th>HAB 2</th>
<th>HAB 3</th>
<th>$\lambda_f$</th>
<th>HAB 1</th>
<th>HAB 2</th>
<th>HAB 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>---</td>
<td>0.02</td>
<td>0.05</td>
<td>0.00</td>
<td>---</td>
<td>0.00</td>
<td>0.10</td>
<td>0.03</td>
</tr>
<tr>
<td>July</td>
<td>0.83</td>
<td>0.17</td>
<td>0.25</td>
<td>0.33</td>
<td>1.25</td>
<td>0.63</td>
<td>1.00</td>
<td>0.56</td>
</tr>
<tr>
<td>Aug</td>
<td>0.64</td>
<td>0.25</td>
<td>0.37</td>
<td>1.00</td>
<td>1.74</td>
<td>1.73</td>
<td>2.55</td>
<td>2.75</td>
</tr>
</tbody>
</table>
muskrats in habitats 2 and 3 declined during the summer of 1988, I can assume that predation risk substantially increased in these habitats (Table 3.5). During the summer months of 1992, no mink were captured in habitats 2 and 3. In addition no mink were captured in HAB 1 until August.

3.3.4 Nutritional condition

A two-way ANOVA for the effects of month and year on percent fat content (concentration) in adult muskrats generated no significant interaction ($F_{3,111} = 1.99, P = 0.14$). Also fat concentration did not vary significantly among the summer months ($F_{3,111} = 0.13, P > 0.20$). However, there was a significant difference in fat concentration between years ($F_{1,111} = 42.02, P < 0.01$). The mean fat content ($\pm 1$ SE) of adult muskrats during the summer of 1988 was 1.4 $\pm$ 0.2% ($n = 63$), while those captured during the summer of 1992 had a mean fat content of 6.0 $\pm$ 0.7% ($n = 54$).
Table 3.5. Habitat-specific mink abundance index during the summer months of 1988 and 1992. The index represents the number of mink captured per 100 trap nights per habitat; n.d. = no data due to discontinued trapping effort. N represents the number of mink captured per month.

<table>
<thead>
<tr>
<th>Month</th>
<th>1988</th>
<th>1992</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>HAB 1</td>
</tr>
<tr>
<td>June</td>
<td>1</td>
<td>0.28</td>
</tr>
<tr>
<td>July</td>
<td>3</td>
<td>0.26</td>
</tr>
<tr>
<td>Aug</td>
<td>6</td>
<td>0.43</td>
</tr>
</tbody>
</table>
3.4 Discussion

In this chapter I have demonstrated that water level is an important limiting factor of population size and distribution of muskrats among habitats during the ice-free season. Unstable water level from spring through autumn in 1988 generated negative population growth, while more-or-less stable water level during the same period in 1992 coincided with a positive growth rate. Although the population size of adults, and relative distribution of dwellings and adult muskrats among habitats were similar during the spring in both years, different water level regimes during the remaining ice-free season resulted in significant differences in these demographic parameters between years. During 1988 the relative distribution of dwellings and adult muskrats increased in the island shoreline habitat (HAB 1), but decreased in the emergent vegetation (habitats 2 and 3). In contrast, during 1992 the relative distribution of dwellings decreased in island shorelines and increased in emergent vegetation, particularly in HAB 2.

Results supported predictions 1 and 2 which link population growth and distribution of muskrats to water level regime. However, I realize that the study lacked controls and replicates, and therefore the results should be interpreted with some caution (Hurlbert 1984; Hairston 1989). Demographic changes between years could have been
associated with other variables that fluctuated and interacted with water level, such as vegetative composition (i.e., habitat availability) and predator numbers. Although changes in habitat availability were accounted for between and within years; the effect of variation in predator numbers could not be determined reliably in this study. Future investigations determining the impact of changes in water level on muskrats should employ radio-implants to follow the fate of individuals.

Differences in population growth rate and distribution under contrasting water level regimes were due largely to differences in adult survival and juvenile recruitment rate during the summer breeding period. Dispersal movements among habitats appear to play a secondary role in the distribution of adult muskrats during summer. Near drought conditions in 1988 resulted in a low adult survival rate (ca 0.63 per 30 days) from June through August. In contrast, the survival rate of the adult population during the summer of 1992 was around 0.78 per 30 days.

Low adult survival rate during summer (June - August) 1988 was not distributed equally across all habitats. After correcting for dispersal movements among habitats, I found that the habitat-specific survival rate of individuals occupying island shorelines was 0.75, while survival rates of muskrats in habitats 2 and 3 were 0.59 and 0.34, respectively. Thus, adult muskrats inhabiting emergent
vegetation were exposed to high mortality despite the presence of suitable habitat in close proximity (i.e., island shorelines). Although some dispersal movements into HAB 1 did occur, constant density indicated that loss and gain rates were equivalent. The limited amount of temporal variability in density suggests that territoriality regulates the number of breeders in island shorelines (see also Messier and Virgl 1992). Other studies have also stressed the role of spacing behaviour in regulating the breeding density of small mammals in prime habitats (Taitt and Krebs 1985; Ostfeld et al. 1988; Lambin and Krebs 1991; Brandt 1992).

The low number of juveniles that entered the trappable population and the lack of lodge construction during autumn of 1988 was indicative of poor juvenile recruitment, which supports the third prediction. Assuming that the pregnancy rate of females was similar in both years, low juvenile recruitment in 1988 was likely the result of higher mortality rates. Like other altricial species, preweaned muskrats are susceptible to a host of different predators. During drought conditions, an increasing number of lodges became susceptible to predation, particularly those lodges in shallow water (i.e., prairie bulrush). For example, in addition to the increasing number of mink captured in habitats 2 and 3 during late summer 1988, 2 skunks were captured on muskrat lodges and many lodges were destroyed by
coyotes in the prairie bulrush habitat. During declining water level, other studies have indicated higher predation risk by mink and fox on muskrats inhabiting shallow water habitats (Danell 1978; Proulx et al. 1987; Hjältén 1991; Clark and Kroeker 1993). Although the mortality rate of adults occupying island shorelines was low, high mortality of adults in emergent vegetation and low recruitment of juveniles in all habitats generated negative population growth. Determining the impact that these and other demographic parameters (e.g., dispersal rate) have on local population size in spatially heterogeneous landscapes is necessary to assess current theories involving source-sink population dynamics (Hansson 1977; Pulliam 1988; Pulliam and Danielson 1991).

Results did not support our prediction that the nutritional condition of muskrats would be independent of water level regime, despite continued access to food resources. I found that individuals captured during the 1988 breeding period possessed approximately 5% less body fat than muskrats captured during the same period in 1992. Although several species of microtines appear to be food-limited (see Ostfeld 1985, 1992 for reviews), whether population size of muskrats is determined by the nutritional condition of individuals during the ice-free period is currently under investigation. However, some points warrant discussion here.
In the presence of predators, declining water level may cause muskrats to shift their foraging activities to food resources located in areas with water levels deep enough to minimize predation risk. Concurrent with a decline in water level was also a reduction in the operational habitat available (OHA). Due to the combination of this possible predator-induced habitat shift and reduction in OHA, there was a substantial increase in competitor density in the emergent vegetation. Studies have shown that increasing competitor density often results in greater interference competition and less foraging activity (Bowers et al. 1987; Hughes et al. 1994). Hypothetically, interference from conspecifics during low water level could have reduced foraging activity and decreased fat stores in muskrats.

Water level is the principal factor determining variation in population size of muskrats during the ice-free and freeze-over seasons and consequently, acts as an additive mortality factor (Caughley 1985). Recent studies have also stressed the connection between fluctuations in water level and muskrat numbers and distribution (Kroll and Meeks 1985; Thurber et al. 1991; Clark and Kroeker 1993), but no proximate mechanism has been provided. This study and our previous studies indicate that although water level drives variation in muskrat numbers, spacing behaviour tends to regulate the number of breeders in prime habitats (Messier et al. 1990; Messier and Virgl 1992; Marinelli and
Messier 1993). Consequently, spacing behaviour imposes a constraint on the distribution of muskrats among habitats under variable water levels (i.e., fluctuating environment).

I have also shown how variations in water level directly affect the absolute density of muskrats in emergent vegetation by changing the OHA. For example, the large and rapid decline in OHA in 1988 was met by an equal loss of individuals (through increased mortality and emigration) from habitat 3, but not from habitat 2. This caused a large and sudden increase in the density of muskrats occupying habitat 2 and was associated with an augmentation in predator numbers, especially mink. Such a response in predator numbers may be indicative of spatial density-dependence (Walde & Murdoch 1988; Stewart-Oaten and Murdoch 1990), but this feedback mechanism for muskrat population dynamics remains untested.

The results of this study clearly indicate that water level limits muskrat population size during the summer breeding period. However, the actual mortality agent(s) responsible for population variation between years could not be identified. I hypothesize that predation (especially by mink) is a key factor limiting population size of muskrats (Errington 1946, 1956). Specifically, I predict that muskrat density, water level, and predation interact to limit muskrat population size, particularly in marginal habitats. Determining the spatial and/or temporal level upon which
predation may be strictly additive or exhibit some regulatory influence on muskrat populations requires further investigation.
4. HABITAT SUITABILITY IN MUSKRATS: A TEST OF THE FOOD LIMITATION HYPOTHESIS

4.1 Introduction

An important aspect of landscape ecology is the ability to predict the distribution of animals inhabiting heterogeneous environments. Fretwell and Lucas (1970) developed the ideal free distribution model to explain patterns of habitat selection in animals. Given a choice of habitats, an individual should select the habitat that maximizes survival and reproductive success. Two key assumptions of the ideal free distribution model are: (1) the number of individuals in each habitat is proportional to resource availability, and (2) individual fitness is similar across all occupied habitats. Alternatively, the ideal despotic distribution model predicts that some animals may attain greater fitness by defending some critical resource(s) (Fretwell and Lucas 1970; Pulliam 1988).

As reproductive success is largely a function of breeding site quality, individuals should select habitats with the greatest likelihood of producing offspring that survive to reproduce (Morris 1991a). However, to understand the process of habitat selection it is essential to

1 Published in J. Zool., Lond. (1997; In press).
determine which factor or set of factors influence habitat
suitability. Because food resources are an important
limiting factor for most vertebrate populations (Lack 1954),
spatial differences in food quality and/or quantity should
be related to female reproductive parameters and juvenile
growth among habitats. The hypothesis that food at least
limits animal populations is supported by numerous food
manipulation studies on small mammals that have linked
forage quality and availability with demographic parameters
(Cole and Batzli 1978; Taitt 1981; Ostfeld et al. 1985;
Ostfeld and Klosterman 1986; Dobson 1988; Desy and Batzli
1989; Boutin 1990; Dobson 1995). Generally, these
investigations have shown that increasing food quality or
quantity resulted in females with higher fat indices, larger
body mass, earlier parturition dates, and larger litters.
Growth and recruitment rates of juveniles were also
positively correlated with food resources. However, studies
specifically addressing the limiting effect of food on
habitat suitability are lacking.

Other investigations have linked habitat-specific
recruitment and survival to predation risk (Desy and Batzli
1989; Kotler et al. 1993; Doncaster 1994; Hughes et al.
1994). Competitor density affects habitat suitability, but
is considered an implicit assumption of animal distribution
models (Rosenzweig 1991), and hence, interacts with food
resources and predation risk. Therefore an alternative, but
not mutually exclusive, hypothesis is that predation risk influences habitat suitability.

Considering that marshes are well structured spatially, muskrats (*Ondatra zibethicus*) provide a good model species to investigate habitat selection in heterogeneous environments. Previous studies have confirmed that habitat selection in muskrats is density-dependent, and that water level limits the distribution and population size of muskrats (Errington 1963; Messier et al. 1990; Messier and Virgl 1992; Clark and Kroeker 1993; Chapter 3). Water level influences access to food resources and predation risk, particularly during winter, causing differences in adult survival and juvenile recruitment among habitats (Messier et al. 1990; Clark & Kroeker 1993; Clark 1994).

Here, I test the hypothesis that food is a significant factor affecting habitat suitability for muskrats. Adult body condition, reproductive parameters, juvenile growth rate, and forage quality were compared among different habitats in a northern marsh environment. I first show which habitats represent prime and marginal habitats based on muskrat distribution and litter survival rate among habitats. Then, I tested the predictions that muskrats in prime habitats relative to marginal habitats (1) have greater adult body mass, body size, and fat content, (2) exhibit earlier parturition date, larger litter size, and
higher pregnancy rate, (3) show higher juvenile growth rate, and (4) produce feces with a higher crude protein content.

4.2 Methods

4.2.1 Capture-recapture

Six primary trapping periods were conducted from May through October each year. The total area trapped during 1992, 1993, and 1994 was 152, 133, and 144 ha, respectively, including zones of open water. HAB 1 accounted for 19 - 21 ha, HAB 2 for 22 - 23 ha, and HAB 3 for 14 - 20 ha. Each primary trapping period consisted of three trapping nights per muskrat dwelling carried out over a 2 or 3-week period. Dwellings were trapped every second day to reduce trap mortality. Three to four modified Tomahawk traps were set near each burrow system or lodge. Traps contained dry vegetation for bedding, were baited with a piece of carrot, and covered with vegetation or a wood box.

Upon capture, muskrats were checked for ear tags, sex, and reproductive condition (females: pregnant or not pregnant, males: scrotal or not scrotal). Body mass (BM) was recorded to the nearest 1 g with a portable electronic scale. Total body length (TBL) and tail length (TL) were measured to the nearest 1 mm, and body length (BL) was determined by subtracting TL from TBL. Unmarked animals were marked with two monel #1 ear tags (National Band and Tag
Co., Newport, Kentucky). Muskrats were then released near the capture site.

As the individual represents the unit of replication for each habitat, I classified adults as residents or nonresidents. This classification enabled me to be reasonably certain that an individual captured in a given habitat represented a sample from that subpopulation. A muskrat was judged "resident" if one of the following criteria were met: (1) captured a minimum of two consecutive times (either between primary sampling periods or within a primary sampling period) at the same dwelling, or (2) captured once at a dwelling that was occupied during the breeding period and no other same-sex individual was captured at the same dwelling, and young were produced. These criteria are reasonable considering that muskrats are territorial during the breeding period, and nonresidents (floaters) do not maintain access to a resident's homerange during the reproductive season (Marinelli and Messier 1993).

Population size for each habitat was estimated using the minimum number known alive (MNA) method (Krebs 1966). Habitat-specific population size estimates were adjusted for movement of individuals among habitats. If an individual was captured a minimum of two consecutive times in a different habitat than that of initial capture it was deemed to have changed habitats. In addition, if the dwelling originally occupied by a marked individual was no longer active, then a
single capture of this animal at a new dwelling in a
different habitat was indicative of a habitat change.
Habitat-specific density was calculated by dividing the MNA
estimate by the area of operational habitat (Chapter 3).
Operational habitat considers the effect of water level on
the availability of habitat. Operational habitat was defined
as the area in HAB 2 and HAB 3 that was located in water \( \geq 10 \)
cm deep. Habitat area along island shorelines (HAB 1) is not
dependent on water level as muskrats can adjust the entrance
of a burrow.

4.2.2 Dwelling numbers and distribution

During each year of the study, systematic surveys of
the entire marsh were conducted every two weeks during the
ice-free period (ca. 6 months) to determine the occupancy of
existing and newly constructed muskrat dwellings. Water
level in the marsh was also recorded from a permanent gauge
during each survey.

4.2.3 Litter survival rate

To determine litter survival rate, I first estimated
the number of litters produced per habitat. During the
breeding season (May through August), lodges were opened
with minimum disturbance and checked for young (Caley and
Boutin 1985). All young \( >40 \) g were marked with two ear tags.
Most young from litters produced in habitats 2 and 3 were
marked when individuals were around 30 days old (i.e., weaning age). Since nest chambers in burrows are less accessible, most young produced in HAB 1 were 50 days old at first capture. All young used to estimate the original number of litters weighed ≤550 g. As juveniles do not leave their natal homerange until autumn and generally attain a body mass >570 g before dispersing (Chapter 5), these estimates of litter production should be unbiased by dispersal movements.

Litter survival rate was calculated as the frequency of at least one individual from a litter surviving until the autumn trapping period (i.e., September or October). For those few litters that were only partially marked during summer and for which I did not recapture a marked individual in autumn, I determined the fate of the litter from the capture of an unmarked littermate. Grouping among littermates was determined by comparing the estimated birth date of the potential siblings (see Reproductive parameters for estimation of parturition date). The percentage of litters that had their fates determined in this manner was 11% (21 / 192). Litter survival rate should not be biased by differences in litter size or number of littermates marked as survival to weaning in muskrats is independent of litter size, and survival of littermates is strongly autocorrelated (Boutin et al. 1988). Thus, prior to weaning, litters either completely disappear or have a high probability of weaning.
at least one young. After weaning, juvenile survival becomes increasingly independent of littersmate survival (Boutin et al. 1988). I acknowledge that estimates of litter survival do not include litters that have failed before entering the trappable population (i.e., before weaning).

Litters were classified as first and second litters based on the frequency distribution (calculated for two-week intervals from May 1 - August 15) of parturition date (Fig. 4.1). Median parturition date for first and second litters was May 26 and July 3, respectively. Juveniles born before June 21 were designated as first litters and individuals born on or after June 21 were categorized as second litters. My classification of litter order should be unaffected by the production of third litters as I recorded only 4 females that were known to produce 3 litters during the entire study.

4.2.4 Adult body condition

BM and BL were used as a general indicator of the physiological condition and physical size of muskrats, respectively. BL rather than TBL was employed as a measure of size because adults often lose portions of their tail during aggressive interactions. For cases in which individuals were captured more than once during a primary trapping period the first capture was used as a measurement of BM and BL. The minimum interval between measurements for
Fig. 4.1. Frequency distribution of parturition date for muskrats at Indi lake (n = 221). Frequencies were calculated at two-week intervals from May 1 to August 15, 1992 - 1994.
a specific individual was 21 days. Since muskrats are not sexually dimorphic (Willner et al. 1980; Virgl and Messier 1995), the effect of sex on BM and BL was not considered in this study. Pregnant females were not included in the analysis of body mass.

An estimate of fat content in muskrats was determined via the isotopic dilution method using the following equation:

\[
Y = 71.88 - 1.03X
\]  

(4.1)

where \(Y\) is percent body fat and \(X\) is percent body water of ingesta-free body mass (\(r^2 = 0.93, P < 0.01\)). Fat concentration was estimated for adults among habitats during each primary trapping period in 1992 and 1993.

### 4.2.5 Juvenile growth rate and autumn mass

Growth rate of juveniles was determined using a linear derivation of the Gompertz growth function:

\[
G = -a \ln S + b
\]  

(4.2)

where \(G\) is mass-specific growth rate, \(S\) is body mass, \(-a\) is the slope (growth rate constant), and \(b\) is the intercept (specific growth rate when \(\ln S = 0\); see Kaufmann 1981; Boutin and Larsen 1993). Data were fit to the Gompertz growth model based on a recent study of 25 semi-captive muskrats (Virgl and Messier 1995). This enabled me to test for differences in slope among habitats and years using analysis of covariance (ANCOVA). Analyses were performed
separately for the preweaning (≤170 g) and postweaning periods (>170 g; Virgl and Messier 1995). Individual measurements were restricted to a minimum of 3 days during the preweaning period, and a minimum of 14 days during the postweaning period.

Juvenile muskrats born from May - July exhibit a growth diapause from October through April in northern environments, and attain similar asymptotic mass and length (Virgl and Messier 1995). Thus, measurements of BM and TBL from individuals captured in October were used to compare first year asymptotic body mass and size (i.e., autumn mass and size), and should not be biased by differential survival rate of first and second litters. Data for the analysis of growth, autumn mass and size, were recorded only for individuals that remained residents in a particular habitat.

4.2.6 Reproductive parameters

Parturition date was estimated by determining the age of individuals from the equation derived by Virgl and Messier (1995):

\[
AGE = 0.157 \times BM - 1.114
\]

Age estimates were then backdated to predict date of birth. Although the accuracy and precision of age estimates decreases with increasing BM, I felt that the equation would still provide a reasonable estimate of parturition date for weaned individuals. To test this assumption, the deviation
in parturition date as a function of BM was analyzed for individuals marked and aged prior to weaning, and subsequently weighed and aged upon consecutive recaptures \((n = 64)\). Deviation in parturition date was determined as the difference between "known" parturition date (i.e., age assessed during the preweaning period which is precise to 1-3 days; see Virgl and Messier 1995) and predicted parturition date from BM at recapture. The mean absolute deviation \((\pm 2 \text{ SD})\) was 4.4 \pm 10.4 days, which is well within the gestation period of muskrats (25 - 30 d). Thus, the likelihood of incorrectly assigning individuals to the wrong litter for a particular female was minimal.

Analysis of litter size included only those litters that were designated as "complete". Litters were considered complete if young were found in intact nests (i.e., no evidence that the dam was in the nest chamber prior to opening the lodge). This constraint precluded analysis of litter size for HAB 1, but allowed me to test for differences in litter size between habitats 2 and 3. Pregnancy rate was determined as the number of pregnant females divided by the total number of females captured within each primary trapping period during the breeding season (May 1 - August 31). The ratio was calculated for residents of each habitat and excludes repeated captures of individual females within a primary trapping period.
4.2.7 Fecal crude protein

Fresh muskrat feces were collected from captured individuals and fecal piles located near active dwellings. Samples were collected during each primary trapping period, placed in a plastic bag, identified with date and habitat, and stored at -20°C. Samples were then freeze-dried and ground to a homogenous mixture. Because most samples did not contain enough feces for accurate analysis, I randomly combined samples within each month and habitat to produce a maximum of 5 composite replicates (range, 2 - 5) for each month and habitat. Fecal samples were then analyzed for nitrogen content and values converted to percent crude protein at the Feed Testing Services Lab, University of Saskatchewan (Saskatoon, SK).

4.2.8 Statistical analyses

Due to low sample size, I could not accurately assess the effect of year on litter survival rate. However, water level from May - September was comparable among years (see Results), hence justifying the pooling of data across years for each habitat. Hierarchical log-linear analysis (SPSS for Windows) was used to examine the effects of habitat and litter order (first or second) on litter survival rate. Beginning with the full model, variables were removed through backward elimination if they did not contribute
significantly ($P > 0.05$) to the variation in litter survival probability.

A 3-way analysis of variance (ANOVA) was used to test for the effects of habitat, month, and year on adult BM and BL. In order to pool females and males for the analysis of fat content, I first tested for significant effects of sex (and all sex interactions) on fat content. Sample size did not permit testing for sex differences in fat content within habitats. Differences in fatness among habitat, month, and year was then analyzed with a 3-way ANOVA.

As mentioned above, juvenile growth rate was analyzed using ANCOVA to test the effect of habitat and year on the slope from the generated linear growth curves, and including parturition date as a covariable. I statistically controlled for the effect of parturition date because previous work has shown that growth rate in muskrats is dependent on date of birth (Virgl and Messier 1995). A 2-way ANOVA was performed to test the effects of habitat and year on juvenile body mass and size in autumn.

Two nonparametric 1-way ANOVAs (Kruskal-Wallis, $\chi^2$ approximation) were performed to test for differences in parturition date among years within each habitat, and among habitats. The first test was performed to check if data across years could be pooled for each habitat. To analyze the effect of habitat and year on litter size, I first determined if litter size was dependent on litter order. A
Wilcoxon two-sample test indicated that litter size was independent of litter order (Z = -1.33, n₁ = 39, n₂ = 23, P = 0.18), and subsequently, first and second litters were pooled. The Wilcoxon two-sample test was used to test for differences in litter size between 1992 and 1993 within habitats 2 and 3. Years were then pooled and the effect of habitat on litter size was tested using the same statistical procedure. Pregnancy rate among habitats within years was analyzed using log-likelihood ratios.

Friedman repeated measures ANOVA on ranks (SigmaStat for DOS) was used to test if the temporal distribution of fecal crude protein content differed among habitats. For each habitat, the average fecal crude protein content of a given month and year was used as the individual sample. Percent fat content was arcsine transformed prior to analysis (Zar 1984). For all statistical tests a P-value >0.05 was judged to be not significant. All statistical analyses (except those specified) were performed using the SAS statistical package for microcomputers.

4.3 Results

Water level (±1 SD) for 1992, 1993, and 1994 averaged 101.5 ± 7.7 cm, 95.2 ± 10.5 cm, and 96.4 ± 3.6 cm, respectively. Although mean water level did not differ markedly among years, variation in water level during 1993
was significantly greater than 1992 and 1994 (Bartlett's test for homogeneity of variances, $B_0 = 11.75$, df = 2, $P < 0.01$). During all three years, water level was relatively high and constant from spring through summer. However, during autumn of 1993 water level continued to decline and was 20 cm lower at the time ice formed than in 1992 and 1994.

Average ($\pm$1 SD) population density of muskrats (MNA / ha) in 1992, 1993, and 1994 was $4.4 \pm 1.7$, $4.2 \pm 1.0$, and $1.4 \pm 0.6$, respectively. The three fold decline in density in 1994 was the result of lower water level in autumn 1993 and poor survival of muskrats during the ensuing winter (Chapter 5).

### 4.3.1 Assessment of habitat suitability

At low density, muskrats tend to concentrate their dwellings predominately in island shorelines (HAB 1). For example, with fewer than 100 dwellings, the relative distribution of dwellings among habitats was about 60% in HAB 1, 35% in HAB 2, and less than 5% in HAB 3 (Fig. 4.2). As density increased, a greater proportion of dwellings were found in HAB 2. Muskrats colonized HAB 3 last as illustrated by the low but increasing proportion of dwellings found in this habitat with increasing population size (Fig. 4.2). The slope ($\pm$1 SE) of the regression line for these relationships was relatively steeper for HAB 1 ($b = -0.11 \pm 0.01$) than for
Fig. 4.2. Relative distribution of dwellings located in each habitat as a function of total number of dwellings (index of population size).
HAB 2 ($b = 0.06 \pm 0.01$) and HAB 3 ($b = 0.04 \pm 0.01$). These results indicate a preference by muskrats to colonize island shorelines first, followed by habitats 2 and 3, hence reflecting the relative suitability of each habitat.

Hierarchical log-linear analysis indicated that litter survival rate was dependent on habitat ($\chi^2 = 11.86, df = 2, P < 0.01$). After pooling first and second litters, the likelihood of at least one juvenile from a litter entering the autumn population was greatest in HAB 1 (91%, $n = 53$), followed by habitats 2 (75%, $n = 107$) and 3 (60%, $n = 32$; Fig. 4.3). These results provide strong support for the previous conclusion that habitat suitability declines from HAB 1 to HAB 3.

Litter survival was dependent on litter order ($\chi^2 = 19.31, df = 1, P < 0.01$), the decrease in survival rate between first and second litters was additive among habitats (i.e., habitat-litter interaction; $\chi^2 = 0.35, df = 2, P > 0.50$). Despite having a longer average exposure period, young from first litters (87%, $n = 122$) had a greater probability of surviving to autumn than young from second litters (59%, $n = 70$; Fig. 4.3). For example, the average ($\pm 1$ SE) number of days between initial capture and first autumn recapture for juveniles from first and second litters was 64 $\pm$ 2 days, and 48 $\pm$ 5 days, respectively. Survival rate per 30 days for first litters was 93% compared to 72% for second litters.
Fig. 4.3. Variation in litter survival rate among habitats for first and second litters. Survival rate was calculated as the proportion of litters with one surviving individual to the autumn trapping period. Numbers above bars represent number of litters monitored.
4.3.2 Nutrient-dependent body attributes

Results from the 3-way ANOVA indicated that habitat 
\( (E_{2,712} = 2.75, \, P = 0.06) \) and year 
\( (E_{2,712} = 2.69, \, P = 0.07) \) had 
a marginally significant effect on adult BM. In contrast, 
month explained the largest amount of the variation in adult 
BM \( (E_{5,712} = 21.62, \, P < 0.01) \). Habitat-month and habitat-year 
interaction terms were not significant \( (F < 0.70, \, P > 0.20) \), 
as was the 3-way interaction \( (E_{15,712} = 0.92, \, P > 0.20) \). 
However, there was a marginally significant interaction 
between month and year \( (E_{10,712} = 1.85, \, P = 0.05) \). Generally, 
adult BM increased from May through October with heavier 
muskrats occupying island shorelines, followed by habitats 2 
and 3 (Table 4.1). To specifically test for differences in 
adult BM among habitats, I pooled data across months and 
years. Results of a one-way ANOVA indicated that adult BM 
was statistically different among habitats \( (E_{2,758} = 5.77, \, P < 
0.01) \). Mean \((\pm 1 \text{ SE})\) BM of muskrats occupying habitats 1 
\( (975.3 \pm 6.1 \, g, \, n = 267) \) and 2 \( (967.3 \pm 4.7 \, g, \, n = 376) \) was 
greater than HAB 3 \( (940.3 \pm 9.0 \, g, \, n = 119) \).

Results from the 3-way ANOVA indicated that body size 
(i.e., BL) of resident adults was not statistically 
dependent on year at any level in the model (main effect, 2- 
and 3-way interactions, \( F < 1.41, \, P > 0.17) \). Subsequently, I 
reduced the model to examine the effects of habitat and 
month on adult BL. Similar to BM, body size of adults 
increased significantly from May through October.
Table 4.1. Mean (±1 SE) body mass (g) and percent fat content (%FAT) in resident adult muskrats among habitats during each primary trapping period at Indi lake. () = sample size. ND = no data.

<table>
<thead>
<tr>
<th>Month</th>
<th>HAB 1</th>
<th>HAB 2</th>
<th>HAB 3</th>
<th>HAB 1</th>
<th>HAB 2</th>
<th>HAB 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Body mass</td>
<td></td>
<td></td>
<td>%FAT</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>HAB 1</td>
<td>HAB 2</td>
<td>HAB 3</td>
<td>HAB 1</td>
<td>HAB 2</td>
<td>HAB 3</td>
</tr>
<tr>
<td></td>
<td>MEAN ± SD</td>
<td>MEAN ± SD</td>
<td>MEAN ± SD</td>
<td>MEAN ± SD</td>
<td>MEAN ± SD</td>
<td>MEAN ± SD</td>
</tr>
<tr>
<td></td>
<td>(N)</td>
<td>(N)</td>
<td>(N)</td>
<td>(N)</td>
<td>(N)</td>
<td>(N)</td>
</tr>
<tr>
<td>May</td>
<td>916.0 ± 18.0</td>
<td>911.5 ± 13.3</td>
<td>896.5 ± 23.5</td>
<td>4.9 ± 1.2</td>
<td>9.3 ± 2.0</td>
<td>ND</td>
</tr>
<tr>
<td></td>
<td>(36)</td>
<td>(51)</td>
<td>(20)</td>
<td>(10)</td>
<td>(9)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>963.5 ± 16.9</td>
<td>938.5 ± 9.5</td>
<td>907.3 ± 19.5</td>
<td>6.6 ± 1.0</td>
<td>5.7 ± 1.0</td>
<td>9.4 ± 0.8</td>
</tr>
<tr>
<td></td>
<td>(32)</td>
<td>(65)</td>
<td>(21)</td>
<td>(17)</td>
<td>(14)</td>
<td>(7)</td>
</tr>
<tr>
<td>July</td>
<td>935.5 ± 12.5</td>
<td>929.5 ± 8.9</td>
<td>934.3 ± 12.9</td>
<td>5.3 ± 1.2</td>
<td>4.2 ± 0.7</td>
<td>3.7 ± 1.4</td>
</tr>
<tr>
<td></td>
<td>(49)</td>
<td>(65)</td>
<td>(23)</td>
<td>(15)</td>
<td>(20)</td>
<td>(10)</td>
</tr>
<tr>
<td>Aug</td>
<td>954.1 ± 12.8</td>
<td>976.8 ± 9.5</td>
<td>956.6 ± 16.8</td>
<td>2.5 ± 0.9</td>
<td>4.5 ± 1.0</td>
<td>4.8 ± 1.9</td>
</tr>
<tr>
<td></td>
<td>(53)</td>
<td>(82)</td>
<td>(27)</td>
<td>(14)</td>
<td>(23)</td>
<td>(10)</td>
</tr>
<tr>
<td>Sep</td>
<td>1016.4 ± 11.2</td>
<td>1004.1 ± 9.5</td>
<td>992.4 ± 16.4</td>
<td>4.7 ± 0.9</td>
<td>5.8 ± 1.3</td>
<td>8.3 ± 2.8</td>
</tr>
<tr>
<td></td>
<td>(57)</td>
<td>(62)</td>
<td>(13)</td>
<td>(18)</td>
<td>(17)</td>
<td>(4)</td>
</tr>
<tr>
<td>Oct</td>
<td>1047.9 ± 11.9</td>
<td>1041.4 ± 11.7</td>
<td>980.8 ± 17.4</td>
<td>5.9 ± 1.7</td>
<td>7.9 ± 1.4</td>
<td>ND</td>
</tr>
<tr>
<td></td>
<td>(44)</td>
<td>(56)</td>
<td>(15)</td>
<td>(11)</td>
<td>(19)</td>
<td></td>
</tr>
</tbody>
</table>
(E_{s,553} = 2.73, P = 0.02), and the increase was additive across habitats (i.e., habitat-month interaction, E_{10,553} = 0.83, P > 0.50). For example, mean BL (±1 SE) of adults in May and October was 314 ± 1 mm (n = 124) and 324 ± 1 mm (n = 57), respectively. The variation in body size was also statistically different among habitats (E_{2,553} = 5.09, P = 0.01). Mean (±1 SE) BL of muskrats in habitats 1 (319 ± 1 mm, n = 179) and 2 (319 ± 1 mm, n = 307) was greater than HAB 3 (314 ± 1 mm, n = 85).

Fat content in adults did not vary significantly between sexes (E_{1,197} = 0.37, P > 0.50), and sex did not interact with month or year (F < 1.04, P > 0.30). Subsequently, I pooled sexes and analyzed the effect of habitat, month, and year on fat content. Fat concentration of muskrats did not differ among habitats (E_{2,189} = 0.27, P > 0.50). However, fat content did vary significantly among months (E_{5,189} = 3.44, P = 0.01) and years (E_{1,189} = 20.08, P < 0.01). Habitat did not interact with year (E_{2,189} = 2.00, P = 0.14), but there was a marginally significant habitat-month interaction (E_{5,189} = 1.86, P = 0.06). There was also a significant interaction between month and year (E_{4,189} = 4.58, P < 0.01), but the 3-way interaction term was not significant (E_{6,189} = 0.85, P > 0.50). Fat content in muskrats declined from May through August, and then increased in autumn (Table 4.1), which was similar to previous results of
chemical analysis of body composition (Virgl and Messier 1992a).

Because few juveniles from island shorelines were captured during the preweaning period, analysis of growth rate was performed only on preweaned young from HAB 2 and HAB 3, for 1992 and 1993. All least squared regressions for estimating the slope (-a) and intercept (b) were significant \( (r^2 > 0.46, P < 0.01) \). A 2-way ANCOVA (with parturition date as the covariable) generated a significant interaction between habitat and year \( (F_{1,127} = 10.26, P < 0.01) \). Partitioning the analysis by year indicated that there was no difference in preweaning growth rate between HAB 2 \((-a = -0.062, b = 0.46, \bar{n} = 22)\) and HAB 3 \((-a = -0.053, b = 0.33, \bar{n} = 22)\) in 1992 \( (F_{1,40} = 1.32, P > 0.20) \). However, in 1993, there was a marginal statistical difference between the growth rate of individuals in HAB 2 \((-a = 0.058, b = 0.26, \bar{n} = 71)\) and HAB 3 \((-a = 0.037, b = 0.19, \bar{n} = 18; F_{1,85} = 4.40, P = 0.04)\).

A 2-way ANCOVA for analyzing the effect of habitat and year on growth rate during the postweaning period generated a significant interaction \( (F_{3,399} = 2.85, P = 0.04) \). Subsequent analysis, by year, indicated that postweaning growth rate among habitats was not statistically different \( (F < 2.88, P > 0.09; \text{Table 4.2}) \). However, growth rate among years was markedly different \( (F_{2,404} = 8.44, P < 0.01) \). Growth of juveniles during the postweaning period was highest in
Table 4.2. Postweaning growth rate constant (-\(a\)) and intercept (\(b\)), and autumn mass (MASS ± 1 SE) of juvenile muskrats among habitats (HAB) and years at Indi lake. The estimates \(-a\) and \(b\) were determined by least squares regression of the linearly derived Gompertz equation after controlling for parturition date (see Methods). All regressions were significant \((r^2 > 0.60, P < 0.01)\). Autumn mass represents the mass of juveniles captured in October. () = sample size. ND = no data.

<table>
<thead>
<tr>
<th>Year</th>
<th>HAB 1 -a (HAB 2 b)</th>
<th>HAB 2 -a (HAB 3 b)</th>
<th>HAB 1 MASS 13.2 (HAB 2 MASS 8.4 (HAB 3 MASS 15.9)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>-0.020 0.14 (49)</td>
<td>-0.027 0.19 (103)</td>
<td>-0.030 0.21 (32)</td>
</tr>
<tr>
<td>1993</td>
<td>-0.017 0.12 (32)</td>
<td>-0.026 0.19 (89)</td>
<td>-0.018 0.11 (15)</td>
</tr>
<tr>
<td>1994</td>
<td>-0.023 0.17 (72)</td>
<td>-0.025 0.18 (17)</td>
<td>ND</td>
</tr>
</tbody>
</table>
1994, followed by 1992 and 1993 (Table 4.2).

Data for mass of juveniles captured in October (i.e., first year asymptotic mass) suggested that individuals occupying HAB 1 and HAB 2 attained greater BM than muskrats in HAB 3 (Table 4.2). Results of a 2-way ANOVA indicated that the effects of habitat and year on juvenile autumn mass were not additive ($F_{1,231} = 3.54, P = 0.02$). Subsequent analysis indicated that autumn mass did not differ among habitats in 1992 ($F_{2,99} = 1.34, P > 0.20$) or 1993 ($F_{2,79} = 0.47, P > 0.20$). However, in 1994, the average mass of juveniles captured in October was greater in island shorelines than HAB 2 ($F_{1,53} = 11.69, P < 0.01$; Table 4.2).

Mean autumn size (TBL; ±1 SE) of juveniles in HAB 1 (499 ± 2 mm, $n = 81$) was greater than individuals in HAB 2 (487 ± 2 mm, $n = 126$) and HAB 3 (485 ± 3 mm, $n = 31$), but the difference was just beyond significance ($F_{2,230} = 2.74, P = 0.07$). Body size of juveniles in October was independent of year ($F_{2,230} = 2.31, P = 0.10$), and additive across habitats for each year ($F_{1,230} = 2.23, P = 0.09$).

### 4.3.3 Nutrient-dependent reproductive parameters

Parturition date did not differ significantly among years within habitats ($\chi^2 < 1.71, P > 0.40$). Subsequently, I pooled the data across years and specifically tested for habitat effects. There was no difference in parturition date among habitats ($\chi^2 = 2.86, df = 2, P > 0.20$). The earliest
recorded date of birth was on May 4 in 1992, while the latest recorded parturition date was on August 6 in 1993.

Analysis of litter size between years (1992 and 1993) within habitats 2 and 3 generated the following results. For HAB 2, average litter size was larger in 1993 than in 1992 ($Z = -2.14, n_1 = 11, n_2 = 24, P = 0.03$). Similarly, for HAB 3, mean litter size was larger in 1993 than in 1992, but the result was just beyond significance ($Z = 1.86, n_1 = 8, n_2 = 7, P = 0.06$). Since the increase in litter size between years was additive for habitats 2 and 3 (Table 4.3), I pooled the data across years and tested for a difference in litter size between habitats. Results indicated that there was no statistical difference in the size of litters produced in habitats 2 and 3 ($Z = -1.58, n_1 = 35, n_2 = 15, P = 0.11$).

Data for the proportion of pregnant females captured during the reproductive period suggested that pregnancy rate was lower in island shorelines than habitats 2 and 3 (Table 4.3). However, statistical analysis indicated that there was no difference in pregnancy rate among habitats for each year ($\chi^2 < 3.20, P > 0.10$).
Table 4.3. Mean litter size and proportion of pregnant female muskrats captured from May through August (i.e., ratio of pregnant to total number of females captured; \%PREG) among habitats and years at Indi lake. The ratio was based on a single capture event for each primary sampling period. () = sample size. ND = no data.

<table>
<thead>
<tr>
<th>Year</th>
<th>Litter size</th>
<th>%PREG</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HAB 1</td>
<td>HAB 2</td>
</tr>
<tr>
<td>1992</td>
<td>ND</td>
<td>6.5 (11)</td>
</tr>
<tr>
<td>1993</td>
<td>ND</td>
<td>7.7 (24)</td>
</tr>
<tr>
<td>1994</td>
<td>ND</td>
<td>8.2 (10)</td>
</tr>
</tbody>
</table>
4.3.4 Food quality

Because I could not collect fecal samples from HAB 3 in all years (particularly in 1994 when this habitat was generally unoccupied), I first compared fecal crude protein (FCP) content among all three habitats, and then between HAB 1 and HAB 2. Friedman repeated measures ANOVA on ranks indicated that FCP was homogenous among habitats 1, 2, and 3 (n = 12, $E_r = 1.83$, df = 2, $P = 0.45$; Table 4.4). Crude protein content of feces collected from muskrats in HAB 2 appeared to be greater than individuals occupying HAB 1 (Table 4.4), but the results were just beyond significance (n = 18, $E_r = 3.56$, df = 1, $P = 0.06$). Overall, the temporal variation in FCP appeared to be similar across habitats. There was a trend for fecal crude protein content to increase from May through July with little change in August, decline in September, and then increase in October (Fig. 4.4).

The above results on variation in fecal crude protein content among habitats does not support the food limitation hypothesis. Although a marginal difference in FCP was detected between HAB 1 and HAB 2, the direction of the difference was inconsistent with the prediction relating habitat suitability with food quality.
Table 4.4. Mean (±1 SE) crude protein content of feces collected from muskrats among habitats during each month and year. Fecal crude protein content is expressed as a percentage of dry mass. () = sample size. ND = no data.

<table>
<thead>
<tr>
<th>Month</th>
<th>Year</th>
<th>HAB 1</th>
<th>NIAD 2</th>
<th>HAB 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>1992</td>
<td>11.4 ± 0.8 (5)</td>
<td>9.2 ± 1.3 (2)</td>
<td>8.7 ± 0.1 (5)</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>14.0 ± 0.7 (5)</td>
<td>12.9 ± 0.7 (5)</td>
<td>12.5 ± 1.0 (5)</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>11.5 ± 1.5 (5)</td>
<td>12.8 ± 1.7 (4)</td>
<td>ND</td>
</tr>
<tr>
<td>June</td>
<td>1992</td>
<td>13.5 ± 0.5 (5)</td>
<td>15.4 ± 0.7 (5)</td>
<td>11.5 ± 0.7 (5)</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>11.9 ± 1.5 (5)</td>
<td>15.8 ± 1.0 (5)</td>
<td>15.8 ± 1.4 (5)</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>13.0 ± 1.4 (5)</td>
<td>15.9 ± 1.0 (5)</td>
<td>ND</td>
</tr>
<tr>
<td>July</td>
<td>1992</td>
<td>14.8 ± 0.6 (5)</td>
<td>12.6 ± 2.2 (5)</td>
<td>13.2 ± 2.8 (5)</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>14.8 ± 0.5 (5)</td>
<td>18.6 ± 1.0 (5)</td>
<td>22.2 ± 1.8 (5)</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>21.0 ± 0.5 (5)</td>
<td>20.9 ± 0.6 (4)</td>
<td>ND</td>
</tr>
<tr>
<td>Aug</td>
<td>1992</td>
<td>16.1 ± 0.7 (5)</td>
<td>17.2 ± 0.9 (5)</td>
<td>17.9 ± 0.9 (5)</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>15.1 ± 0.8 (5)</td>
<td>19.4 ± 1.7 (5)</td>
<td>20.7 ± 2.1 (5)</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>18.8 ± 0.9 (5)</td>
<td>17.3 ± 2.6 (5)</td>
<td>ND</td>
</tr>
<tr>
<td>Month</td>
<td>Year</td>
<td>HAB 1</td>
<td>HAB 2</td>
<td>HAB 3</td>
</tr>
<tr>
<td>-------</td>
<td>------</td>
<td>-----------</td>
<td>-----------</td>
<td>-----------</td>
</tr>
<tr>
<td>Sep</td>
<td>1992</td>
<td>12.0 ± 1.8 (5)</td>
<td>15.5 ± 0.8 (5)</td>
<td>15.9 ± 1.0 (5)</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>15.4 ± 1.8 (5)</td>
<td>18.7 ± 0.7 (5)</td>
<td>13.8 ± 3.3 (2)</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>15.6 ± 0.5 (5)</td>
<td>17.4 ± 1.1 (5)</td>
<td>ND</td>
</tr>
<tr>
<td>Oct</td>
<td>1992</td>
<td>20.2 ± 1.7 (5)</td>
<td>20.4 ± 1.6 (5)</td>
<td>19.1 ± 1.1 (5)</td>
</tr>
<tr>
<td></td>
<td>1993</td>
<td>17.8 ± 1.1 (5)</td>
<td>23.9 ± 2.0 (5)</td>
<td>ND</td>
</tr>
<tr>
<td></td>
<td>1994</td>
<td>13.6 ± 1.2 (5)</td>
<td>19.8 ± 1.6 (5)</td>
<td>18.9 ± 1.7 (3)</td>
</tr>
</tbody>
</table>
Fig. 4.4. Mean crude protein content of feces collected among habitats and months. Error bars represent 1 SE. Numbers above bars indicate number of composite samples (see Methods).
4.4 Discussion

4.4.1 Habitat selection and suitability

To circumvent a potential tautological argument when testing the influence of food quality on habitat suitability in muskrats, I first showed which habitats represented "prime" and "marginal" habitat. Results of this and previous studies provide strong evidence that habitat selection in muskrats is density-dependent, and that some habitats are preferred while others are avoided (Fig. 4.2; Messier et al. 1990; Messier and Virgl 1992; Clark 1994). At Indi lake, individuals prefer to settle in island shorelines (HAB 1), and secondarily in habitats associated with common bulrush and broadleaf cattail (HAB 2). Muskrats tend to avoid occupying areas with prairie bulrush (HAB 3), but are forced to settle in this habitat at high density. Spacing behaviour appears to be a strong mechanism for regulating the breeding density of many small mammals, including muskrats, in prime habitats (Taitt and Krebs 1985; Ostfeld et al. 1988; Lambin and Krebs 1991; Brandt 1992; Chapter 3). Evidence suggests that muskrat populations occupying marsh systems do not conform to an ideal free distribution (Messier et al. 1990), but better fit the ideal despotic model where some individuals achieve greater fitness by monopolizing some critical resource(s) (Fretwell and Lucus 1970; Pulliam 1988; Morris 1989).
In this study, survival of at least one juvenile from a litter into the autumn population was markedly different among habitats. Litter survival rate was consistently higher in habitats 1 and 2 than in HAB 3 (Fig. 4.3). Messier et al. (1990) also showed that overwinter survival was greatest in island shorelines followed by HAB 2 and HAB 3. Similarly, analysis of demographic parameters from June through August indicated that during periods of variable water level, adult survival rate was greater in HAB 1 followed by habitats 2 and 3 (Chapter 3). The results of these studies indicate unequivocally that island shorelines, cattail, and common bulrush represent more suitable habitats than prairie bulrush. My objective was to determine if food may explain such differences in habitat suitability.

4.4.2 Food resources and habitat suitability

If food resources are a factor affecting the suitability of breeding sites, then measurements of nutrient-dependent phenotypic variables such as adult body condition, reproductive performance, and juvenile growth rate should be positively correlated with the spatial pattern of habitat quality (Boutin 1990; Dobson 1992; Campbell and Slade 1995; Dobson and Michener 1995). This is particularly true for small rodents that have a limited capacity to accumulate large fat stores and depend on exogenous sources of energy (Gittleman and Thompson 1988;
Thompson 1992). Based on a rigorous analysis of nine nutrient-dependent phenotypic variables and an independent assessment of diet quality, I reject the hypothesis that food resources represent a significant factor affecting habitat selection and suitability in muskrats. I tested ten predictions of the food limitation hypothesis (FLH) and found partial support for only four predictions. None of the predictions relating habitat quality with nutrient-dependent reproductive parameters (parturition date, litter size, and pregnancy rate) could be confirmed statistically, despite relatively large sample sizes.

Adult body mass and length (i.e., size) was significantly greater in HAB 1 and HAB 2 than in HAB 3. However, since fat content of individuals did not differ among habitats, much of the variation in body mass was likely due to the amount of lean body mass possessed by adults. Indeed, Virgl & Messier (1993) found that lean mass accounted for over 80% of the variation in body mass, while fat content could not be predicted from body mass in muskrats. Although some vertebrate species may store small amounts of energy as protein tissue, most of the lean mass of an animal relates to structural size (van der Meer and Piersma 1994). Since competitive ability and physical prowess are highly correlated (Clutton-Brock and Harvey 1978; Brandt 1992), the difference in body mass between adult residents of prime and marginal habitats probably
reflects the outcome of competition for quality breeding sites (i.e., smaller individuals were forced into inferior habitats).

In 1992 and 1993, asymptotic mass of juveniles in HAB 1 and HAB 2 appeared to be greater than HAB 3, but the difference was not significant (Table 4.2). In 1994, asymptotic mass of juveniles in island shorelines was significantly greater than in HAB 2, providing partial support for the FLH. Some additional support for the FLH came from the result that juveniles attained a larger asymptotic size in island shorelines compared to other habitats, but the effect was just beyond significance ($\beta = 0.07$). Furthermore, growth rate of juveniles between habitats 2 and 3 during the preweaning period was marginally different in 1993 ($\beta = 0.04$), but not in 1992.

Perhaps the strongest negative result against the FLH was the fact that I could detect no significant difference in the growth rate of juveniles among habitats during the postweaning period. Several studies have shown that growth in birds and mammals exhibits a high degree of phenotypic plasticity, and is linked to environmental conditions such as food quality and quantity (see Ricklefs 1983; Zullinger et al. 1984; Bronson 1989). The power of detecting a habitat effect should have been high given the large sample sizes, and therefore, I feel confident in the strength of this conclusion.
Studies of small and large herbivorous mammals have documented the strong correlation between dietary nitrogen and fecal nitrogen content (Sinclair et al. 1982; Loeb et al. 1991; see Cook et al. 1994). Analysis of fecal nitrogen content (fecal crude protein) therefore provides a reliable estimate of the quality of food consumed by individuals. I found that the temporal distribution of fecal crude protein (FCP) obtained from muskrats was relatively homogenous among all three habitats. Although median FCP content was marginally higher in HAB 2 than HAB 1 ($P = 0.06$), the direction of the difference was inconsistent with the prediction relating habitat suitability with food quality. Overall, the spatial and temporal distribution of fecal crude protein obtained from muskrats indicated that food quality was relatively homogenous among all three habitats during the ice-free period.

Rejection of the food limitation hypothesis suggests that food resources are distributed more or less homogenously among habitats, and consequently, is not the key factor driving territoriality in muskrats. Selection for maintaining exclusive access to food resources within a breeding area would occur only if the distribution of food is sufficiently heterogenous to compensate for the cost of defence (Ostfeld 1985, 1992). Although defence of food resources may occur, some other factor(s) responsible for differential adult and litter survival rate (i.e., fitness)
among habitats must be associated with the evolution of spacing behaviour in muskrats. I hypothesize that predation risk is the principal factor responsible for differences in habitat suitability, and the evolution of territoriality in muskrats. During years of high density, defence of breeding sites may also be selectively adaptive to reduce the risk of infanticide (Caley and Boutin 1985; Wolff 1989).

In heterogeneous environments, predation risk can directly and indirectly affect the selection and suitability of a habitat. Increased mortality rate in high-risk habitats will obviously influence habitat selection and suitability directly. However, recent studies have shown that predation risk can indirectly reduce foraging time by forcing individuals to feed in lower-risk habitats which causes an increase in density and associated interference competition (Kotler et al. 1993; Koskela and Ylönen 1995; Bouskila 1995). Predation risk can therefore influence the abundance and distribution of individuals inhabiting a heterogeneous environment (Doncaster 1992, 1994). The strength of such indirect effects of predators on changes in prey movement and foraging behaviour among habitats likely varies with the population density of prey.

An aspect of the food limitation hypothesis I did not measure directly was the quantity of forage available to muskrats in each habitat. The principal explanation for not measuring food quantity was that although muskrats prefer to
eat the roots and shoots of emergent hydrophytes, they also feed on terrestrial forbs and submergent vegetation. In addition, there appears to be a large amount of temporal variation in the part of the plant that individuals select to eat (pers. obs.), which would make quantifying food availability problematic. Furthermore, I never observed any "eat-outs" in which exceptionally large areas of vegetation were removed and would have resulted in significant spatial and temporal differences in food quantity (Errington 1963). I believe that the concurrent measurement of numerous life history and physical characteristics of muskrats provided a better test of the effect of food quality and quantity on habitat suitability.

I do not contend that muskrat populations are not food-limited. On the contrary, in temperate environments with variable water level, food accessibility can be severely restricted during winter, hence causing high overwinter mortality (Messier and Virgl 1992; Clark 1994). The three-fold decline in density between the autumn of 1993 and spring of 1994 demonstrates the limiting effect of water level on muskrat population size. The most important and striking result of this study was that muskrats, either at a habitat-specific or population level, were not limited by food during the ice-free period. High fat concentration and forage quality during winter also suggest that the quality of food available to muskrats should not limit population
size (Virgl and Messier 1992). Consequently, I predict that competition for quality food is a weak mechanism regulating population size of muskrats in marsh environments.
5. HABITAT SELECTION, DEMOGRAPHY, AND SOURCE-SINK DYNAMICS OF MUSKRATS

5.1 Introduction

Population dynamics is the result of interactions between density-dependent (regulatory) and density-independent (stochastic) factors. Both processes limit population size, but only regulatory mechanisms create density dependence which maintains populations around some dynamic equilibrium density (Hestbeck 1987; Messier 1991; Sinclair and Pech 1996). Spacing behaviour, which induces emigration, is an integral part of current models that describe the regulation of small mammals in heterogeneous landscapes (Hestbeck 1987; Stenseth and Lidicker 1992; Krebs 1996). However, temporal changes in habitat availability, caused by environmental stochasticity, can create temporary shifts in demographic structure and alter population dynamics (Adler and Wilson 1987; Ostfeld 1992).

In the "source-sink" model, spatial variation in habitat suitability and defence of resources by residents generate differential population growth among habitats (Pulliam 1988; Pulliam and Danielson 1991). Over ecological time, births exceed deaths in prime (source) habitats, while reproduction is lower than mortality in marginal (sink) habitats. This results in a surplus of individuals in source
habitats and a deficit in sink habitats. Spacing behaviour forces surplus individuals from prime habitats to immigrate into marginal habitats, providing stability in source habitats and variable population numbers in sink habitats (Pulliam 1988; 1996). In highly fluctuating environments, however, movement from source to sink habitat should occur only during "increasing" phases of the local population. During a "decreasing" phase one should expect net emigration from sink to source habitats, as postulated by Morris (1991b).

Recent demographic studies with birds and small mammals have tested some of the predictions of the source-sink model (Pulliam et al. 1992; Keith et al. 1993; Diffendorfer et al. 1995; Paradis 1995; Brawn and Robinson 1996; Curnutt et al. 1996). Spatial variation in population size and survival rate, and the immigration of unmarked individuals from surrounding areas into sink habitats suggest that source-sink dynamics occur in natural populations. However, few studies have demonstrated the relative importance of emigration and mortality to habitat-specific population changes (Ostfeld and Klosterman 1986; Gliwicz 1989; Keith et al. 1993). More research on the functional significance of emigration among habitats is necessary for understanding the role of spacing behaviour in the regulation of small mammals.
I carried out an intensive mark-recapture programme on a single population of muskrats (*Ondatra zibethicus*) to estimate several demographic parameters among three contiguous habitats. The strong spatial structure of this northern marsh, coupled with its isolation from other marshes, makes this population particularly suitable to investigate source-sink dynamics. Previous studies indicate that: (1) habitat selection is density-dependent, (2) there is differential fitness among habitats, and (3) water level is the principal factor limiting population size (Messier et al. 1990; Messier and Virgl 1992; Chapter 3). In particular, during a population expansion, construction of dwellings occurs first in island shorelines (HAB 1), followed by areas dominated by cattail (*Typha latifolia*) and common bulrush (*Scirpus validus* HAB 2). The establishment of lodges in HAB 3 (dominated by prairie bulrush; *Scirpus paludosus*) is observed at high population size. Higher survival in HAB 1 appears to explain the observed pattern of habitat use (Messier et al. 1990; Chapter 3). Based on these results, I view HAB 1 as the prime habitat, while HAB 2, and particularly HAB 3, are more marginal habitats for muskrats.

My primary objective was to test the hypothesis that habitat-specific demography of muskrats follows a source-sink model (Pulliam 1988). Habitat-specific demographic parameters were examined separately during the breeding (May - October) and non-breeding (October - May) periods. As a
second objective, I determined the effect of temporal variation in habitat availability, due to water fluctuations, on muskrat demography.

With respect to the first objective, I made the following predictions. Prime habitats relative to marginal habitats should: (1) display smaller temporal changes in population size and density, and (2) have greater juvenile and adult survival rates. Such differences in survival should be manifested as positive population growth ($\lambda > 1$) in prime habitats and negative growth ($\lambda < 1$) in sink habitats. At the onset of the breeding season, spacing behaviour in prime habitats should force surplus individuals from source habitats into sink habitats. In contrast, near the end of the breeding period, adults in more marginal habitats should attempt to fill any vacancies in prime habitats (due to mortality). Among juveniles, high autumn recruitment in source habitats should be associated with directional emigration from prime to marginal habitats.

5.2 Methods

5.2.1 Capture-recapture

Trapping areas, capture protocol and techniques were explained in Chapter 4 (see Page 49). However, some additional information is required for this Chapter. All juveniles captured and marked at a dwelling from May through
August were designated as residents of that habitat. In addition, unmarked juveniles captured in September that weighed ≤550 g were considered residents. This enabled me to consider young that did not enter the trappable population until autumn (i.e., born from mid to late summer) in estimates of juvenile recruitment and survival. These estimates should be little biased by movement of this cohort within and among habitats before September. Only 6% (4/67) of the juveniles that dispersed from their natal site weighed ≤550 g (range: 532-542 g), and the mean (±1 SD) body mass of juveniles that dispersed was 664 ± 78 g (n = 67).

To estimate mortality and dispersal during the breeding period, all active dwellings outside the intensively sampled areas (i.e., remaining marsh area) were also trapped at least twice during the last two weeks of September in 1992 - 1994. To separate mortality from dispersal during winters of 1992-93 and 1993-94, all active dwellings outside the intensive area were trapped twice per month during May, June, and July of 1993 and 1994, respectively. Finally, for the winter of 1994-95, all active dwellings in the entire marsh were trapped at least twice over a 5-week period during April and May of 1995.

Movement of muskrats among habitats was determined using the following criteria. If an individual was captured a minimum of two consecutive times in a habitat different than that of initial capture it was deemed to have changed
habitats. Also, if the dwelling originally occupied by an individual was no longer active, then a single capture of this animal at a new dwelling in a different habitat was indicative of a habitat change (Chapter 3). I considered any settlements >100 m from a breeding/natal site that occurred within a habitat as representing "within-habitat" dispersal.

5.2.2 Recapture Rate

I used the program SURGE (Pradel and Lebreton 1991) to estimate recapture rates of resident adults and juveniles for the population. Because movement of individuals among habitats can not be modeled within SURGE, I could not estimate habitat-specific recapture rates. Here, SURGE was used to model the effect of sex, trapping period, and year on adult recapture rate, and the effect of litter number (first or second), trapping period, and year on juvenile recapture rate. Models were selected based on parsimony criteria and biological significance (Lebreton et al. 1993). Variables were removed in a stepwise fashion and sequential models compared with likelihood ratio tests.

5.2.3 Demography

Population size for each habitat was estimated using the minimum number known alive (MNA) method (Krebs 1966). Absolute density was determined by dividing habitat-specific population size by the area of operational habitat. The
finite rate-of-increase \( (\lambda) \) for each habitat during the breeding or non-breeding period was calculated as:

\[
\lambda = \frac{\text{MNA}_{t+1}}{\text{MNA}_t}
\]  

(5.1)

For the breeding period, \( \text{MNA}_t \) was the population size in May, and \( \text{MNA}_{t+1} \) was the estimated number of adults in October plus the average number of juveniles for September and October. For the non-breeding period (i.e., overwinter), \( \text{MNA}_t \) and \( \text{MNA}_{t+1} \) refers to the number of animals present in October and the following spring, respectively. Habitat-specific change in population size (\( \Delta N \)) and absolute density (\( \Delta D \)) for the breeding or non-breeding period was calculated using the same MNA estimates for each time interval.

Survival rate of adults over the breeding period was calculated as the proportion of May residents that were still alive in September or October. Resident adults captured in June - August were assumed present in May. Survival rate of juveniles over the breeding period was calculated as the proportion of juveniles marked in summer that were still alive in September or October. Juveniles were categorized as first or second litters based on the frequency distribution of parturition date (Chapter 4). Parturition date was determined by first estimating age from body mass (Virgl and Messier 1995), and then backdating to determine date of birth. Based on median parturition date for first (May 26) and second (July 3) litters, I designated young born before June 21 as first litters and individuals
born on or after June 21 as second litters. Juveniles from third litters (only 4 females were known to produce 3 litters during the entire study) were excluded from the analysis.

Survival rate during the non-breeding period was estimated as the proportion of muskrats known to be present in autumn (September or October) and recaptured during the following spring/summer trapping periods. These estimates were based on the number of marked individuals in the entire marsh so that survival estimates were not confounded by movements of muskrats in or out of the intensively trapped area.

Habitat-specific survival rates were corrected for movement of individuals among habitats. Muskrats that changed habitats between primary sampling periods were considered to have survived in the previous habitat. For example, an individual that emigrated from HAB 1 to HAB 3 between August and September was considered to have survived that period in HAB 1. Habitat-specific juvenile recruitment rate was calculated as the number of resident juveniles alive in September divided the number of resident adults alive in May.

During the breeding period, habitat-specific immigration and emigration rates were determined for the August - September and September - October trapping intervals (i.e., i to i+1). I did not analyze movement of
muskrats between May and August as less than 4% of adults (9/253) and 1% of juveniles (4/777) changed habitats during this period over the entire study. Rates for adults and juveniles were calculated independently. Immigration rate from $i$ to $i+1$ was calculated as:

$$I / (MNA_{i+1} + I) \quad (5.2)$$

where $I$ is the number of immigrants in a specific habitat, and $MNA_{i+1}$ is the number of residents known alive in that habitat at time $i+1$. Conversely, emigration rate from $i$ to $i+1$ was calculated as:

$$E / (MNA_i + E) \quad (5.3)$$

where $E$ is the number of emigrants from a specific habitat, and $MNA_i$ is the number of residents known alive in that habitat at time $i$.

Habitat-specific immigration and emigration rates during spring (April - May) were calculated using the same equations. The calculation was based on the segment of the marked population from the previous year that survived the winter, and assumed that dispersal movements occurred in the spring. No age classification was necessary in spring as all muskrats were sexually mature at this time.

5.2.4 Statistical Analysis

Due to slight variation in the number of days between primary trapping periods, immigration and emigration rates of adults and juveniles were standardized to rates per 30-
day intervals during the breeding period. For survival (or mortality) rates, the geometric mean (GM), and SE or 95% confidence interval was used as a measure of central tendency and dispersion, respectively. The 95% confidence intervals were calculated as antilog \((GM \pm 1.96 \times SE (\text{log-values}))\). Due to mathematical limitations (i.e., presence of zeros), the arithmetic mean was used to calculate average \(\lambda\), immigration, and emigration rates for each habitat.

Using population estimates from all primary sampling periods \((n = 19)\), the relationship between habitat-specific population density and total population density was determined using least-squared regression. Significant differences in the slope and y-intercept of each habitat line was tested using ANCOVA.

Hierarchical log-linear analysis (SPSS for windows) was used to examine the effects of habitat, sex, and year on survival of adults from May through autumn. A similar analysis was performed to analyze the effects of habitat, litter number, and year on survival of juveniles until autumn. Finally, I analyzed the interaction between overwinter survival (response variable) and habitat, sex, and year. For all these hierarchical models, variables were removed from the full model through backward elimination if they did not contribute significantly \((P > 0.05)\) to the model. If a significant interaction between two explicative variables (e.g., habitat, sex, or year) was found, the model
was reduced and data were analyzed using standard log-linear methods.

I used \( \chi^2 \) analysis to contrast emigration and immigration rates, independently, among habitats during the autumn or spring. A multiple regression model was used to determine the contribution of several demographic parameters to changes in population size within each habitat for the breeding or non-breeding period. For the breeding period, independent variables included the number of resident juveniles produced, adult mortality, juvenile mortality, and the number of emigrants and immigrants (adults and juveniles combined). For the non-breeding period, estimates of mortality, emigration, and immigration of individuals within each habitat were used as independent variables. Although these models are partly circular in their representation of population dynamics, the use of partial correlation analysis controlled for statistical interdependence among the demographic variables. For all statistical tests, a \( P \)-value >0.05 was judged to be not significant. All statistical analyses (except those specified) were performed using the SAS statistical package for microcomputers.
5.3 Results

5.3.1 Variation in water level and habitat availability

Mean water level (±1 SD) during the breeding period of 1992, 1993, and 1994 was 102 ± 8 cm, 95 ± 11 cm, and 96 ± 4 cm, respectively. Although average water level did not differ markedly among years, variation in water level during 1993 was significantly greater than during 1992 and 1994 (Bartlett’s test for homogeneity of variance, \( B_c = 11.75, \ df = 2, P < 0.01 \)). Water level was relatively high and constant during May - August for all years (Fig. 5.1). However, during the autumn of 1993, water level was forced to decline by 20 cm at the time of ice formation compared to levels in 1992 and 1994.

In the spring of each year, the maximum proportion of emergent vegetation that was operational (i.e., with >10 cm of water) to muskrats was 95% of HAB 2, and 60% of HAB 3. During the breeding period of 1992 and 1994, the operational habitat available (OHA) to muskrats in HAB 2 and 3 did not change more than 5%. Similarly, from May - August of 1993 the OHA for muskrats in emergent vegetation was normal (i.e., ≈95% and 60% for HAB 2 and 3, respectively). However, the decline in water level during the autumn of 1993 resulted in a 18% (95→77%) and 41% (60→19%) decrease in OHA between August and October in HAB 2 and HAB 3, respectively. Thus, the effect of temporal changes in water level on
Fig. 5.1. Monthly variation in total population density of resident muskrats (No./ha) and water level (cm) from May 1992 through May 1995 at Indi lake. Density was estimated from the minimum number known alive (MNA) method and adjusted for changes in habitat availability (see Methods). Shaded areas represent winter periods when the marsh was frozen.
habitat availability, and consequently muskrat density, was relatively greater in HAB 3 than HAB 2. For example, although the number of muskrats in HAB 3 decreased 43% (40 to 23 animals) between August and September of 1993, density increased by 24% due to the decline in water level and subsequent loss of operational habitat.

5.3.2 Capture data

During this study, 1462 individual muskrats were captured 2425 times in the intensively trapped areas. In addition, 751 individuals were captured outside the intensive trapping areas to record dispersal movements across the entire population.

Recapture rate of adult residents was independent of sex and trapping period ($\chi^2 < 1.40$, $P > 0.20$). However, recapture probability of adults did vary significantly among years ($\chi^2 = 11.69$, $df = 2$, $P < 0.01$). Recapture rate for 1992, 1993, and 1994 was 70%, 77%, and 88%, respectively. For juveniles, the final model indicated that there was no interactions among recapture rate, litter number, trapping period, and year ($\chi^2 = 26.33$, $df = 20$, $P = 0.16$). Average recapture rate of juveniles in August - September of 1992, 1993, and 1994 was 53%, 65%, and 63%, respectively. Overall, high recapture probabilities for both adults and juveniles suggest that MNA estimates (described below) should be reliable (Hilborn et al. 1976).
5.3.3 Spatial and temporal variation in population size

At the population level, spring density (muskrats/ha) of muskrats was approximately 2.0 in 1992 and 1993 (Fig. 5.1). However, muskrat density decreased to 0.5 in May 1994 following a 20-cm reduction in water level during autumn 1993. As a result of more normal water levels during the breeding period of 1994, muskrat density then increased to 0.9 in May 1995 (Fig. 5.1).

At the habitat-specific level, the density of adult muskrats in the spring of each year was less variable in island shorelines (HAB 1) than HAB 2 and 3 (Fig. 5.2). For example, mean (+1 SD) density for May, 1992 - 1995, was 1.3 ± 0.7, 1.6 ± 1.2, and 1.2 ± 1.4 for HAB 1, 2, and 3, respectively. Monthly variation in density during the breeding period was also greater in HAB 2 and 3 than HAB 1. HAB 2 and 3 contained the highest densities (6-8 muskrats/ha) during the breeding period of 1992 and 1993, but were also associated with the lowest density in 1994 (Fig. 5.2).

Regressions of habitat-specific density on total population density demonstrated that changes in population density were not distributed equally across habitats (Fig. 5.3). All relationships were significant (F<sub>1,17</sub> > 15.0, P < 0.01), and ANCOVA indicated that there was a difference among slopes (F<sub>2,51</sub> = 20.14, P < 0.01) and intercepts (F<sub>2,51</sub> = 6.14, P < 0.01). The slope (+1 SE) of the regression for
Fig. 5.2. Monthly variation in population density of resident muskrats among the three contiguous habitats from May 1992 through May 1995. Density in HAB 2 and HAB 3 was adjusted for changes in habitat availability. HAB 1 = island shorelines, HAB 2 = common bulrush and cattail, HAB 3 = prairie bulrush. Shaded areas represent winter periods when the marsh was frozen.
Fig. 5.3. Relationship between habitat-specific density and total population density of muskrats during the ice-free period from 1992 - 1995.
HAB 1 (0.52 ± 0.13) was less than the slope for HAB 2 (1.44 ± 0.10) and HAB 3 (1.33 ± 0.10). The intercept (±1 SE) was greatest for HAB 1 (0.65 ± 0.46), followed by HAB 2 (-0.25 ± 0.36), and HAB 3 (-1.31 ± 0.37). These results indicated that the relative distribution of muskrats among habitats depended on total population size, and as density increased, a larger proportion of individuals occupied habitats 2 and 3 than HAB 1. In addition, at low population density (i.e., <1 muskrat/ha), animals first settled in HAB 1, followed by HAB 2. Muskrats tended to avoid HAB 3 unless population density exceeded ≈2 muskrats / ha (Fig. 5.3).

5.3.4 Demography during the breeding period

With the notable exception of HAB 3 in 1993 and 1994, all habitats exhibited positive population growth rate ($\lambda$) during the breeding period (Table 5.1). For 1992 - 1994, the average change in population size ($\Delta N$) was 33 muskrats in HAB 1, compared to 54 muskrats in HAB 2 and only 9 muskrats in HAB 3. Respective values for change in density ($\Delta D$) was 1.4, 2.9, and 1.6 for HAB 1, 2, and 3. Changes in density in emergent vegetation were modulated by reduced operational habitat availability which tended to increase density, particularly in HAB 3. Variation in $\Delta N$, $\Delta D$, and juvenile recruitment across habitats differed markedly over the three years of this study. For example, the coefficient of variation (CV) of $\Delta N$ and $\Delta D$ for HAB 1 and 2 did not exceed
Table 5.1. Habitat-specific demographic parameters during the breeding period (May - October) at Indi lake, 1992 - 1994. λ and ΔD represent the finite rate-of-increase and difference in density (No./ha) from May to October. JUV:AD was calculated as the number of resident juveniles known to be alive in September per resident adult in May. H1 = island shorelines, H2 = common bulrush and cattail, H3 = prairie bulrush. na = not applicable.

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<th>λ</th>
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<th>ΔD</th>
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<th>JUV:AD</th>
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<td>H2</td>
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<td>1.67</td>
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<td>1.3</td>
<td>2.2</td>
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<td>1993</td>
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<td>1.8</td>
<td>1.8</td>
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<td>1994</td>
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<td>1.9</td>
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<td>3.3</td>
<td>2.4</td>
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<td>2.57</td>
<td>1.61</td>
<td>1.4</td>
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<td>1.6</td>
<td>2.0</td>
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<td>(SD)</td>
<td>(1.26)</td>
<td>(0.58)</td>
<td>(1.32)</td>
<td>(0.7)</td>
<td>(1.6)</td>
<td>(1.5)</td>
<td>(1.6)</td>
<td>(1.2)</td>
<td>(2.0)</td>
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65%, while the CV of ∆N and ∆D was 275% and 94% for HAB 3. Similarly, juvenile recruitment in HAB 3 was relatively high in 1992, but was less than 0.8 in 1993 and 1994 (Table 5.1).

Analysis of adult survival from spring to autumn generated no significant two- or three-way interactions among habitat, sex, and year (χ² < 4.40, P > 0.30). Survival of adults was independent of sex (χ² = 0.00, df = 1, P > 0.50) and habitat (χ² = 0.41, df = 2, P > 0.50), but was significantly influenced by year (χ² = 10.52, df = 2, P = 0.01; Fig. 5.4a). Survival rate (±1 SE) over the breeding period was higher in 1994 (0.86 ± 0.07), when muskrat numbers were lowest (Fig. 5.1), compared to 1992 (0.58 ± 0.04) and 1993 (0.53 ± 0.05). Overall, adult survival appeared to contribute little to habitat-specific change in population size during the breeding period.

Analysis of juvenile survival during the breeding period produced no significant interaction among habitat, litter number, and year (χ² = 5.49, df = 4, P = 0.24). However, there was a marginally significant interaction between habitat and litter number (χ² = 6.59, df = 2, P = 0.04). Survival rate of juveniles from first litters for HAB 1, HAB 2, and HAB 3 was 0.73 (n = 171), 0.57 (n = 320), and 0.58 (n = 78), respectively, and 0.82 (n = 49), 0.47 (n = 117), and 0.38 (n = 42) for young from second litters. When I pooled young from first and second litters I found a significant habitat-year interaction (χ² = 29.97, df = 4,
Fig. 5.4. Survival rate of resident adult (a) and juvenile (b) muskrats among habitats during the ice-free period of 1992 - 1994. Survival rate was corrected for movement of individuals among habitats (see Methods). HAB 3 was unoccupied in 1994. Numbers in parentheses indicate sample size.
$P < 0.01$). An analysis by year indicated that juvenile survival rate was independent of habitat in 1992 ($\chi^2 = 0.69, df = 2, P > 0.50$), but was significantly higher in HAB 1, followed by HAB 2 and HAB 3 in 1993 ($\chi^2 = 21.38, df = 2, P < 0.01$). Juvenile muskrats also exhibited higher survival in HAB 1 than HAB 2 during 1994 ($\chi^2 = 29.85, df = 1, P < 0.01$; Fig. 5.4b). Spatial variation in juvenile survival, therefore, influenced habitat-specific change in population size during the breeding period.

If adult muskrats perceive island shorelines as more suitable, then autumn vacancies in HAB 1 (caused by summer mortality) should be filled quickly by animals from more marginal habitats. Thus, immigration should be highest in HAB 1, and emigration should be highest in HAB 3. As predicted, the rate of emigration from HAB 2 and 3 was greater than HAB 1 ($\chi^2 = 15.89, df = 2, P < 0.01$). Although immigration rate was greater in HAB 1 than HAB 2 and 3 (Table 5.2), the results were just beyond statistical significance ($\chi^2 = 5.32, df = 2, P = 0.07$).

Source-sink theory predicts that high survival of juveniles in HAB 1 during the breeding period should be associated with high emigration. Alternatively, low juvenile survival in HAB 3 should be associated with high immigration. Analysis indicated that emigration of juveniles from HAB 1 and 3 was greater than HAB 2 ($\chi^2 = 5.56, df = 2, P = 0.04$; Table 5.3). Immigration rate, however, was not statistically
Table 5.2. Immigration and emigration rate of adult muskrats (per 30 days) among habitats at Indi lake, during autumn of 1992 - 1994. Values represent the proportion of marked adults in a habitat that immigrated or emigrated between primary sampling periods (see Methods). n.a. = not applicable. () = number moved.

<table>
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</table>
Table 5.3. Immigration and emigration rate of juvenile muskrats (per 30 days) among habitats during autumn of 1992 - 1994. Values indicate the proportion of marked juveniles in habitat that immigrated or emigrated between primary sampling periods (see Methods). n.a. = not applicable. () = number moved.

<table>
<thead>
<tr>
<th>Interval</th>
<th>Immigration</th>
<th>Emigration</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>HAB 1</td>
<td>HAB 2</td>
</tr>
<tr>
<td>Aug-Sep 1992</td>
<td>0.00</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>(1)</td>
<td>(5)</td>
</tr>
<tr>
<td>Sep-Oct 1992</td>
<td>0.08</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>(5)</td>
<td>(5)</td>
</tr>
<tr>
<td>Aug-Sep 1993</td>
<td>0.00</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>(7)</td>
<td>(3)</td>
</tr>
<tr>
<td>Sep-Oct 1993</td>
<td>0.05</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>(1)</td>
<td>(8)</td>
</tr>
<tr>
<td>Aug-Sep 1994</td>
<td>0.05</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>(6)</td>
<td>(2)</td>
</tr>
<tr>
<td>Sep-Oct 1994</td>
<td>0.03</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>(1)</td>
<td>(10)</td>
</tr>
<tr>
<td>Mean (SE)</td>
<td>0.04</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>(0.01)</td>
<td>(0.05)</td>
</tr>
</tbody>
</table>
different among habitats ($\chi^2 = 3.25$, $df = 2$, $P = 0.20$). During autumn of 1992 and 1994, no muskrats (adults or juveniles) dispersed (settled >100 m) from their breeding/natal site within the same habitat. In 1993, when water level was lower, 13 individuals dispersed within the same habitat (1 moved within HAB 1, and 12 moved within HAB 2).

5.3.5 Demography during the non-breeding period

All habitats exhibited negative population growth (i.e., $\lambda < 1$) during winter (Table 5.4). The exception was HAB 3 during the 1994-95 winter which remained unoccupied by muskrats. The average rate of population decline in HAB 1 and 2 was less than in HAB 3 (Table 5.4). Similar to the breeding period, HAB 3 displayed the largest variation in $\lambda$ and $\Delta D$. For example, the coefficient of variation for $\Delta D$ was 64%, 83%, and 101% for HAB 1, 2, and 3, respectively.

Survival rate at the population level for the winters of 1992-93, 1993-94, and 1994-95 was 9.3%, 4.5%, and 10.3%, respectively. But survival of individuals was not distributed equally among habitats during all three years. Analysis of survival rate generated a significant interaction among habitat, sex, and year ($\chi^2 = 12.10$, $df = 4$, $P = 0.02$). Reduction of the model to sex and year produced no significant interaction or sex effect ($\chi^2 < 0.35$, $P > 0.50$), but indicated that overwinter survival
Table 5.4. Habitat-specific demographic parameters during the non-breeding period (October - May), 1992 - 1995. $\lambda$ and $\Delta D$ represent population growth rate and change in density (No./ha) between October and May. Mortality rate (MR) from October to May was calculated for adults and juveniles combined, after correcting for emigration. n.a. = not applicable. () = SD for $\lambda$ and $\Delta D$; 95% CI for MR.

<table>
<thead>
<tr>
<th></th>
<th>$\lambda$</th>
<th>$\Delta D$</th>
<th>MR</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>H1</td>
<td>H2</td>
<td>H3</td>
</tr>
<tr>
<td>92-93</td>
<td>0.24</td>
<td>0.48</td>
<td>0.36</td>
</tr>
<tr>
<td>93-94</td>
<td>0.61</td>
<td>0.09</td>
<td>0.00</td>
</tr>
<tr>
<td>94-95</td>
<td>0.44</td>
<td>0.40</td>
<td>n.a.</td>
</tr>
<tr>
<td>Mean</td>
<td>0.43</td>
<td>0.32</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>(0.19)</td>
<td>(0.21)</td>
<td>(0.25)</td>
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<tr>
<td></td>
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</tbody>
</table>
varied significantly among years ($\chi^2 = 35.22, \text{df} = 2, \ P < 0.01$).

A similar analysis with habitat and year as main effects indicated that survival (or mortality) was affected by year ($\chi^2 = 35.21, \text{df} = 2, \ P < 0.01$), but there was also a significant habitat-year interaction ($\chi^2 = 219.69, \text{df} = 4, \ P < 0.01$). Partitioning the analysis by year indicated that survival was similar among habitats during autumn 1992 to spring 1993 when water level was relatively high ($\chi^2 = 0.10, \text{df} = 2, \ P > 0.50$: HAB 1 = 8.7%, $n = 161$; HAB 2 = 9.6%, $n = 281$; HAB 3 = 9.2%, $n = 130$). However, during the winter of 1993-94 when water level was 20% lower, survival in HAB 1 (8.5%, $n = 141$) was higher than HAB 2 (2.6%, $n = 270$) and HAB 3 (2.8%, $n = 36$; $\chi^2 = 7.85, \text{df} = 2, \ P = 0.02$). Although survival during the winter of 1994-95 was higher in HAB 1 (20.9%, $n = 172$) than HAB 2 (11.8%, $n = 68$), the difference was not statistically significant ($\chi^2 = 2.73, \text{df} = 1, \ P = 0.10$).

During the spring, analysis indicated a significant difference in emigration rate among habitats ($\chi^2 = 6.53, \text{df} = 2, \ P = 0.04$), but no difference in immigration rate ($\chi^2 = 1.13, \text{df} = 2, \ P > 0.50$). Emigration rate of muskrats from HAB 2 and 3 was greater than from HAB 1 (Table 5.5).

The proportion of muskrats that dispersed within a habitat was not distributed equally among habitats, and varied across years (Table 5.6). In the spring of 1993, the
Table 5.5. Immigration and emigration rate of muskrats among habitats during the spring (April - May) of 1993 - 1995. Values represent the proportion of marked individuals in a habitat that immigrated into or emigrated from a different habitat than the previous autumn. \( n \) = total number of marked animals that survived the non-breeding period (autumn - May). n.a. = not applicable. () = number moved.

<table>
<thead>
<tr>
<th>Year</th>
<th>( n )</th>
<th>Immigration</th>
<th></th>
<th></th>
<th>Emigration</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>HAB 1</td>
<td>HAB 2</td>
<td>HAB 3</td>
<td>HAB 1</td>
<td>HAB 2</td>
<td>HAB 3</td>
</tr>
<tr>
<td>1993</td>
<td>53</td>
<td>0.44</td>
<td>0.21</td>
<td>0.20</td>
<td>0.36</td>
<td>0.37</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(11)</td>
<td>(7)</td>
<td>(3)</td>
<td>(5)</td>
<td>(10)</td>
<td>(6)</td>
</tr>
<tr>
<td>1994</td>
<td>19</td>
<td>0.35</td>
<td>0.30</td>
<td>0.50</td>
<td>0.36</td>
<td>0.71</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(6)</td>
<td>(3)</td>
<td>(1)</td>
<td>(4)</td>
<td>(5)</td>
<td>(1)</td>
</tr>
<tr>
<td>1995</td>
<td>43</td>
<td>0.10</td>
<td>0.38</td>
<td>1.00</td>
<td>0.17</td>
<td>0.50</td>
<td>n.a.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(4)</td>
<td>(5)</td>
<td>(1)</td>
<td>(6)</td>
<td>(4)</td>
<td></td>
</tr>
</tbody>
</table>

Mean (SE) | 0.30 | 0.30 | 0.57 | 0.30 | 0.53 | 0.75 |
|          | (0.10) | (0.05) | (0.23) | (0.06) | (0.10) | (0.25) |
Table 5.6. Proportion of muskrats that dispersed within a habitat (i.e., settled >100 m within the same habitat) during the spring of 1993 - 1995. Values represent the number of marked individuals that dispersed within a particular habitat divided by the number of muskrats that dispersed within all habitats. () = number dispersed within each habitat.

<table>
<thead>
<tr>
<th>Year</th>
<th>HAB 1</th>
<th>HAB 2</th>
<th>HAB 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>0.24</td>
<td>0.59</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>(4)</td>
<td>(10)</td>
<td>(3)</td>
</tr>
<tr>
<td>1994</td>
<td>0.80</td>
<td>0.20</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>(4)</td>
<td>(1)</td>
<td></td>
</tr>
<tr>
<td>1995</td>
<td>0.88</td>
<td>0.12</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>(21)</td>
<td>(3)</td>
<td></td>
</tr>
<tr>
<td>Mean</td>
<td>0.64</td>
<td>0.30</td>
<td>0.06</td>
</tr>
</tbody>
</table>
percentage of individuals that moved within HAB 2 was
greater than HAB 1 ($Z = 3.50, P < 0.01$). During the spring
of 1994 and 1995, when total population density was lower, a
significantly higher proportion of muskrats dispersed within
HAB 1 relative to HAB 2 ($Z > 3.30, P < 0.01$).

Overall, the pattern of population growth in HAB 1 and
2 indicated that production and survival during the breeding
period exceeded overwinter mortality. Average ($\pm 1$ SE)
population growth rate ($\lambda$) for the breeding and non-breeding
period in HAB 1 and HAB 2 was $1.41 \pm 0.55 (n = 6)$, and $1.45
\pm 0.54 (n = 6)$, respectively. In contrast, in HAB 3, mean
population growth rate was $0.90 \pm 0.57 (n = 4)$.

5.3.6 Habitat-specific population dynamics

Partial correlation analysis indicated that the
principal demographic variable influencing change in
population size within each habitat from spring to autumn
was the number of juveniles produced (partial $r^2 = 0.65, P =
0.02$). Habitat-specific change in population size was
negatively correlated with adult and juvenile mortality, but
less dependent on these two variables (partial $r^2 = 0.12, P
= 0.04$ for adults; partial $r^2 = 0.18, P = 0.07$ for
juveniles). Immigration and emigration of individuals
(adults and juveniles combined) did not influence
significantly population growth within each habitat during
the breeding period.
Mortality during the winter was the principal factor influencing change in habitat-specific population size from autumn to spring (partial $r^2 = 0.77$, $P < 0.01$). The strong positive relationship between mortality and decreasing population size was not unexpected. However, after statistically controlling for mortality, analysis also indicated that emigration influenced change in population size within each habitat (partial $r^2 = 0.19$, $P = 0.01$). The magnitude of the decline in population size was inversely related to the number of emigrants from each habitat.

5.4 Discussion

5.4.1 Factors limiting population size

Manipulation of water level has demonstrated that water level is the principal environmental factor influencing population growth of muskrats at Indi lake. Variation in water level acts independent of density to limit population size during both the breeding and non-breeding period. For example, in Chapter 3, I contrasted two years with similar spring density, but significantly different water level regimes from May through August. Results indicated that unstable and declining water level negatively affected adult survival and juvenile recruitment rate. In this Chapter, I have shown that overwinter survival was strongly dependent on the depth of water prior to freezing. Compared to 1992
and 1994, the 20-cm decline in water level during autumn of 1993 was associated with significantly lower overwinter survival rate. Other studies have demonstrated the link between population growth of muskrats and water level stability in northern marsh environments (Errington 1963, Donohoe 1966, Danell 1978, Proulx and Gilbert 1983, Clark and Kroeker 1993).

The effect of water level on the rate-of-increase of muskrat populations is clear, but the principal mortality agent responsible for limiting population size remains to be fully determined. Although access to forage during winter may be restricted, due to variability in ice thickness, muskrats do not appear to be limited by food resources per se. The accumulation of body fat during winter, and similarity in nutrient-dependent phenotypic variables among habitats during the breeding period indicate that nutritional stress is a function of food accessibility, and not quality or quantity (Virgl and Messier 1992, Chapter 4).

I hypothesize that predation by mink increases as water level decreases, and is the chief mortality agent limiting muskrat populations. Other investigators have suggested that predation risk from mink increased with declining water level (Danell 1978, Proulx et al. 1987, Hjältén 1991, Clark and Kroeker 1993). Furthermore, studies in terrestrial systems have linked predation and vegetative cover as factors limiting the population growth of several microtine
species (voles and lemmings) and snowshoe hares (Lepus americanus; Hansson 1984, Hansson and Henttonen 1985, Koprimäki et al. 1991, Keith et al. 1993, Hik 1995, Krebs et al. 1995, Reid et al. 1995). Further studies using radio telemetry or predator exclosures are needed to assess the interaction between water level and predation on muskrat population dynamics.

5.4.2 Demography among habitats

Water level, through its effect on population size, also determined the distribution of muskrats among habitats. With increasing population density fewer individuals settled in HAB 1 and a larger proportion occupied HAB 2 and 3 (Fig. 5.4). In addition, muskrats generally did not settle in HAB 3 until population density exceeded 2/ha. These results verify a previous conclusion that habitat selection in muskrats is density-dependent, and that HAB 1 is preferred, followed by HAB 2 and 3 (Messier et al. 1990, Messier and Virgl 1992).

Habitat-specific demographic patterns for this local muskrat population were generally consistent with the predictions of Pulliam’s source-sink model (Pulliam 1988). Although local population size declined during this study, average population growth rate in HAB 1 and 2 was positive ($\lambda > 1$). Consequently, HAB 1 and 2 contained persistent populations that exhibited low and moderate variation in
density, respectively. In contrast, negative population growth ($\lambda < 1$) in HAB 3 resulted in highly variable density, which eventually lead to a temporary "extinction" of muskrats in this habitat. Such dynamics are exemplary of sink habitats (Pulliam 1988, 1996).

Adult survival rate during the breeding period was independent of habitat, which is contrary to the model's prediction and previous studies of *Microtus* occupying heterogeneous landscapes (Ostfeld et al. 1985, Ostfeld and Klosterman 1986, Paradis and Croset 1995). One possible explanation for this result is the difference in factor(s) that determine habitat suitability in terrestrial versus semi-aquatic systems. Experimental studies of *Microtus* have demonstrated that habitat suitability is linked to vegetative cover which influences predation risk (Adler and Wilson 1989, Desy and Batzli 1989). In contrast, for muskrats, habitat suitability and predation risk are strongly correlated with water level. For terrestrial small herbivores, slight differences in vegetative cover may be associated with significant variation in survival, while relatively larger deviations in water level are necessary to cause habitat-specific differences in survival of adult muskrats. For example, results of this study suggested that the 20-cm decline (100$\rightarrow$80 cm) in water level during autumn 1993 was not sufficient to affect adult survival rate among habitats during the breeding period. Yet, results of Chapter
3 demonstrated that adult survival was significantly higher in HAB 1, followed by HAB 2 and 3 when water level was decreased by 40 cm (80–40 cm) between May and August.

Survival rate of juveniles among habitats did not differ in 1992, but spatial variation in survival was detected during the breeding period of 1993 and 1994. In 1993, individuals from first and second litters occupying island shorelines (HAB 1) had a higher probability of being recruited into the autumn population than juveniles produced in emergent vegetation (HAB 2 and 3). Similarly, in 1994, survival rate of juveniles from first and second litters was significantly higher in HAB 1 than HAB 2. These results support the source-sink model, and other studies that have linked habitat suitability with juvenile survival in small herbivorous mammals (Ostfeld et al. 1985, Adler and Wilson 1987, Paradis 1995).

The correlation between autumn water level and overwinter survival rate supports a previous hypothesis that mortality agents associated with water level differentially affect habitat suitability in muskrats (Messier et al. 1990). For example, survival rate during the non-breeding period was similar among habitats when autumn water level was high (1992 and 1994). But in autumn 1993, a 20-cm decline in water level resulted in residents of island shorelines having a significantly higher survival rate than individuals occupying habitats in emergent vegetation.
Spatial variation in juvenile survival during the breeding period, and overwinter survival of all individuals provide unequivocal evidence that habitat suitability was greatest in HAB 1, followed by HAB 2 and 3.

Movement patterns of adults during autumn and spring also indicated that expected fitness in island shorelines was equal or greater than fitness in habitats comprised of emergent vegetation. The significant emigration of adults from HAB 2 and 3 to HAB 1 during autumn supported my prediction, and the results of other studies investigating habitat suitability and directional emigration in microtines (Ostfeld and Klosterman 1986, Gliwicz 1989, Paradis 1995, Johannesen and Ims 1996). Autumn vacancies in island shorelines, caused by mortality of residents, were quickly filled by immigrants from the emergent vegetation. These results indicate that spacing behaviour plays a role in regulating the density of adult muskrats in island shorelines during the breeding period.

Analysis of juvenile dispersal movements during autumn generated ambivalent results. Although immigration rate was similar among habitats, emigration rate was greater in HAB 1 and 3 than in HAB 2. Emigration of juveniles from island shorelines was predicted given the high recruitment rate of juveniles in this habitat (Pulliam 1988). However, high emigration rate of juveniles from HAB 3 was not expected. Closer analysis of juvenile dispersal in the more marginal
habitats (i.e., HAB 2 and 3) may explain this phenomenon. In 
autumn 1992, immigration exceeded emigration rate in HAB 3, 
but in 1993 the opposite pattern occurred (Table 5.3). Also, 
in 1993, 54% (7/13) of the juveniles that dispersed from 
their natal site in HAB 2 settled within that habitat. Such 
episodes of dispersal within a habitat were not observed 
during the autumn of 1992 or 1994. I believe that these 
patterns of movement in the emergent vegetation, during 
1993, represent a response to declining water level and 
concurrent loss of habitat. The significant bias in the 
frequency of within-habitat dispersal may represent a form 
of frustrated dispersal (Lidicker 1975, Stenseth and 
Lidicker 1992, Ostfeld 1992). High emigration from HAB 3 may 
also be a reaction to a decrease in habitat suitability 
(Gliwicz 1992).

Before breeding is initiated, source-sink theory 
predicts that spacing behaviour in prime habitats should 
force surplus individuals into more marginal habitats 
(Pulliam 1988, Pulliam and Danielson 1991). Therefore, 
during a period of population increase, prime habitats 
should exhibit high emigration and low immigration rates 
compared to marginal or sink habitats. In this study, 
however, local population size declined from May 1992 
through May 1994, and then increased moderately through May 
1995 (Fig. 5.2). Declining population size likely produced a 
large number of available breeding sites in all habitats and
resulted in the directional emigration of individuals from HAB 2 (marginal habitat) and HAB 3 (sink habitat) to island shorelines (source habitat). These results stress the need for long-term or experimental studies that measure emigration rate from habitats during the declining and increasing phase of population cycles (Watkinson and Sutherland 1995, Pulliam 1996).

Nonetheless, stable population density of muskrats in HAB 1, and dispersal movements during spring, provide support for the role of spacing behaviour in regulating the breeding density of small mammals in prime habitats (Hestbeck 1987, Lambin and Krebs 1991, Stenseth and Lidicker 1992, Krebs 1996). Net emigration from sink or marginal habitats to source habitat is expected during a period of decline in local population size (Morris 1991b). In addition, the proportion of individuals that dispersed within HAB 1 was inversely correlated with total population size. Multiple regression analysis further indicated that overwinter change in population size within a habitat was dependent on the interaction between mortality and emigration. Increased mortality, which emancipates breeding space, was associated with a decrease in the number of emigrants from each habitat.

Selection by muskrats for island shorelines probably represents an evolutionary stable strategy for achieving the highest possible fitness in an environment with high
temporal stochasticity and a marked spatial structure. Much of the temporal variation in population size in HAB 2 and 3 appeared to be due to density-independent factors operating on dispersal and survival rates (i.e., mortality agents associated with changes in water level). In contrast, the relative stability of population size in island shorelines during this study suggests that demographic parameters were influenced more by density, and were less susceptible to the density-independent effects of water level. The influence of differential density-dependence on populations inhabiting heterogeneous landscapes has been studied in insect predator-prey systems (see Murdoch 1994), but evidence for the affect of this phenomenon in vertebrates is limited (Adler and Wilson 1987, Clark and Kroeker 1993, Pulliam 1996). Alternatively, the physical nature of burrows in island shorelines may have a greater capacity to buffer the effects of changes in water level.
6. GENERAL DISCUSSION

Similar to other small mammals, year-to-year changes in population size of muskrats was quite variable (Fig. 2.2). In many vertebrate species there is an association between relatively short generation time and sensitivity to environmental stochasticity. In such systems, density-independent factors often explain a large amount of the variation in population size. Although density-dependence may be infrequent, the response of demographic parameters to changes in density is necessary for population persistence (Murdoch 1994; Turchin 1995; Hanski et al. 1996; Sinclair and Pech 1996). My goal was to determine the factors that limit population growth of muskrats, and postulate which demographic parameters may vary with density to regulate population size.

For populations that occupy heterogeneous landscapes, habitat suitability often plays an important role in local population size (Pulliam 1988; Pulliam and Danielson 1991; Morris 1996). As demographic rates are linked to habitat suitability, spatial and temporal variation in food resources and/or predation risk among habitats affect habitat-specific abundance, which determines local population size. In this study, differences in habitat suitability were related to survival rate of juveniles
during the breeding period, and the probability of an individual surviving the winter (Chapter 5). Island shorelines represented prime habitat, while more marginal habitats were located in emergent vegetation. Emigration rate of adults from HAB 3 also indicated that expected fitness was less there than in the other two habitats (see also Morris 1991b). The distribution of emigration and survival rates among habitats explains the pattern of density-dependent habitat selection previously reported in this population (Messier et al. 1990; Messier and Virgl 1992). Muskrats preferred to settle in island shorelines (HAB 1), followed by habitats with cattail and common bulrush (HAB 2). Individuals tended to avoid occupying areas with prairie bulrush (HAB 3), but were forced to settle in this habitat when density was greater than ~2 muskrats/ha.

Previous studies have suggested that habitat suitability for muskrats was influenced by the interaction of water level, food resources, and predation risk (Errington 1963; Proulx et al. 1987; Messier et al. 1990; Clark and Kroeker 1993). Yet no study has isolated the principal biotic factor(s) responsible for differences in suitability among habitats. To test the hypothesis that food resources significantly influenced habitat suitability (food limitation hypothesis), I measured several nutrient-dependent life history attributes of muskrats. Although fat content of adults, postweaning growth rate of juveniles,
pregnancy rate, and litter size varied temporally, no statistical difference in the spatial variation of these phenotypic attributes was detected (Chapter 4). These results, combined with analysis of fecal crude protein (index of quality of food consumed) indicated that the distribution of food resources was more or less homogenous among habitats during the breeding period. Estimates of body fat and crude protein content in stomach samples from individuals collected during the winter (October - February) also indicated the presence of energy-rich forage (Virgil and Messier 1992a).

In view of these results, I contend that habitat suitability is not linked directly to food resources. Consequently, food does not limit demography among habitats, and competition for quality food would play a weak role in population regulation, and the evolution of spacing behaviour in muskrats. This is contrary to terrestrial systems in which variation in food quality appears to have a strong limiting effect on mammalian populations (Boutin 1990; Dobson 1995). The limiting effect of food on population growth in muskrats is likely due to the interplay between water level and food accessibility. For example, nutritional stress during winter may vary with autumn water level as access to roots and tubers will depend partially on the amount of free water. Residents occupying areas with low water level (e.g., HAB 3) would be more susceptible to
"freeze-out" conditions and decreased food accessibility than individuals residing in habitats with higher water levels (e.g., HAB 1 and 2).

The lack of support for the food limitation hypothesis suggests that predation risk was the principal mortality agent generating differences in survival rate among habitats. Clark and Kroeker (1993) also suggested that predation, especially by mink, was a key factor influencing muskrat demography. However, predation risk may be mediated by water level (Danell 1978; Hjältén 1991). Decreasing water level likely results in greater predation risk (Chapter 3). A similar link between predation and vegetative cover in terrestrial systems has been documented in other small mammals (Hansson and Henttonen 1985; Kopriváki et al. 1991; Keith et al. 1993; Hik 1995, Krebs et al. 1995; Reid et al. 1995). I hypothesize that predation is the principal mortality agent limiting muskrat populations, and that differences in predation risk among habitats has played a large role in the evolution of spacing behaviour.

Water level also influenced the operational habitat available to individuals occupying emergent vegetation. Such changes in habitat availability moderated competitor density, independent of changes in animal abundance. For example, a concurrent reduction in habitat area and marginal change in muskrat numbers resulted in a significant increase in density in HAB 2 and 3 (Chapter 3 and 5). However, the
spatial variation in demography indicated that temporal changes in water level did not affect suitability among habitats equally. For example, during drought-like conditions in the summer of 1988, adult survival rate was greater in island shorelines than habitats in emergent vegetation (Chapter 3). Similarly, survival rate of juveniles during the breeding period was less dependent on water level in HAB 1 than HAB 2 and 3 (Chapter 5). In addition, dispersal movements of individuals into and out of HAB 3 was partially dependent on changes in water level (Chapter 3 and 5). Thus, demography in habitats comprised of emergent vegetation appeared to be more susceptible to the density-independent effects of water level than island shorelines.

Factors affecting demographic rates include population density, environmental (extrinsic) and demographic (intrinsic) stochasticity (Pulliam 1996). This study indicated that much of the variation in habitat-specific demographic rates was due to the density-independent effects of changes in water level, particularly in habitats 2 and 3. The differential response of survival and movement rate among habitats to temporal changes in water level may be correlated with the strength of density dependence. Populations with strong regulatory mechanisms are more resistant to temporary stochastic events than populations with weak density dependence (Sinclair and Pech 1996).
Stable population size of muskrats in island shorelines, and the tenuous relationship between density and juvenile survival rate (compare Fig. 5.2 and 5.4) suggests that regulatory mechanisms were stronger in HAB 1 than in HAB 2 and 3. In addition, adult immigration rate during autumn and spring, and the frequency of dispersal within HAB 1 indicated that spacing behaviour was regulating population size in island shorelines. Thus, the spatial variation in demographic parameters exhibited by this muskrat population may be due to heterogeneity in the strength of density dependence among habitats.
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