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VARIATION IN MUSKRAT LIFE HISTORY: A COMPARISON OF NORTHERN AND SOUTHERN POPULATIONS.

BY

© MARK R. SIMPSON

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Variation in Muskrat Life History: A Comparison of Northern and Southern Populations" submitted by Mark R. Simpson in partial fulfilment of the requirements for the degree of Master of Science.

Stan Boutin
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Date: SEPTEMBER 24, 1987

ABSTRACT

Muskrats (Ondatra zibethicus) were studied at Old Crow flats, Yukon Territory and Tiny Marsh, Ontario during the summers of 1985-1986. Comparisons were made of the climate and muskrat life-history patterns exhibited at each study site. As well, comparisons of life-history parameters were made between populations over the muskrats geographic range.

Climatic comparisons assessed the variability and predictability of precipitation, temperature and snowfall patterns from 1981-1985 at both sites. As well, variability of growing season length was analyzed. Climatic patterns were generally more predictable and less variable at the northern study site (Old Crow) than at the southern site (Tiny Marsh).

Muskrats at Old Crow flats and Tiny Marsh were livetrapped to obtain data on patterns of weight change, growth, reproduction, and survival. Samples of muskrats were also obtained by removal methods to quantify annual reproduction. Litter size was not significantly difference between the two sites; however, annual production was significantly greater at Tiny Marsh where more litters were produced. Growth rates of juvenile and adult muskrats were significantly greater at Tiny Marsh, as was adult body weight. Juvenile body weight, when expressed as a percentage of mean fall adult weight, was significantly greater at Tiny Marsh than at Old Crow. Overwinter survival was significantly greater and less variable at Old Crow than at Tiny Marsh.

Life-history strategies between populations over the muskrats geographic range were compared using values derived from previous published studies in the literature. Litter size, number of litters, and adult body weight data were derived from 42 literature sources. Data were also collected on temperature, precipitation, growing season length and habitat type for each study site. Litter size and number of litters produced per season were highly correlated with temperature, precipitation and growing season length.. Removal of autocorrelated climatic parameters indicated that growing season length best explained the pattern of litter size and number of litters in muskrat populations. Body weight did not significantly affect reproduction in muskrats.

The results of this study are discussed within the framework of the r-K and bet-hedging models of life-history evolution. Northern muskrat populations are relatively K-selected when compared to southern populations, providing support for the r-K model of life-history evolution.

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VARIATION IN MUSKRAT LIFE HISTORY: A COMPARISON OF NORTHERN AND SOUTHERN POPULATIONS.

CHAPTER 1: ENVIRONMENTAL PREDICTABILITY AND VARIABILITY

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VARIATION IN MUSKRAT LIFE HISTORY: A COMPARISON OF NORTHERN AND SOUTHERN POPULATIONS.

GENERAL INTRODUCTION

A life history strategy is defined as the response of an animal to an ecological problem (Stearns 1976). A useful life-history model must predict, a priori, the type of strategy a species will follow in a given environment. Two existing theories of life-history tactics are r-K theory (MacArthur and Wilson 1967), and bet-hedging theory (Ch[illegible]nov and Schaffer 1973). Few studies of mammals have rigorously tested the predictions of these two theories. Most studies of mammalian life histories have been interspecific comparisons focusing on one prediction of life-history theory, such as litter size variation (Millar 1977, Armitage 1981, Dunham and Miles 1985, Harvey and Clutton-Brock 1985). Therefore, the question arises as to whether relationships which are evident in broad scale interspecific comparisons are also present at lower levels of biological organization. Comparisons at higher levels of organization may be confounded by the historical constraints of species design (Dobson and Murie 1987). At present, much atte[illegible]on is concentrated on making detailed intraspecific comparisons of life-history strategies within the framework of the r-K and bet-hedging models, especially for ground dwelling sciurids along elevational gradients (Bronson 1979, Zammuto and Millar 1985a, 1985b, Murie 1985, Dobson and Kjelgaard 1985). To date there have been no comparable studies of intraspecific life history variation on a latitudinal scale.

R-K theory was the first model proposed to explain the evolution of life-history strategies (Cody 1966, MacArthur and Wilson 1967, Pianka 1970, Pianka 1976, Boyce 1984). This theory considers the effect of population density on the fitness of an organism, where a compromise exists between the rate and efficiency of biological production (Smith 1976; Boyce 1984). In stable predictable environments where population density is high and competition for resources intense, efficient use of energy is favoured (K characteristics). On the other hand, in populations experiencing unpredictable, or variable fluctuations in environmental resources, and reduced competition due to density levels below the environmental carrying capacity, less efficient high rates of resource use are favoured (r characteristics). Pianka (1970) extended MacArthur and Wilson's (1967) theory to describe specific biological traits of r and K selected species (Table 1). Efficient resource use is accompanied by large body size, slow growth rates and higher investment in competitive ability (K-selected species), whereas species with small body size, rapid growth and high fecundity are considered to be r-selected. Pianka's interpretation of the r-K model has

TABLE 1: Biological predictions of r - K theory (from Krebs, 1985).

	r selection	K selection
CLIMATE	variable, unpredictable	stable, predictable
GROWTH	rapid	slower
PRODUCTION	many, small young	fewer, larger young
BODY SIZE	small	large
CONSEQUENCE	productivity	efficiency

been supported by studies on plants; for example McNaughton's (1975) experiments on cattail (Typha sp.) showed that allocation to somatic and reproductive tissues was r-selected in northern populations and K-selected in southern populations. Analysis of clutch/litter size variation with latitude for birds (Cody 1966) and mammals (Lord 1960, Spencer and Steinhoff 1968) has also supported the predictions of r-K theory, if northern environments are assumed to be more variable and less predictable.

Problems with the r-K theory are two-fold. First, the initial theory (ie. MacArthur and Wilson 1967) does not preclude an r-strategist from placing resources into somatic growth instead of reproduction, as long as a high rate of energy exchange or productivity (eg: high growth rates), rather than efficiency is selected. Since an increase in the rate of energy expenditure is associated with a concomitant decrease in efficiency (Smith 1976), high growth rates or high rates of reproduction imply a loss of efficiency. Hence, small body size need not be an expected characteristic of r-selected species as stated by Pianka (1970). Second, climatic predictability and variability need not covary as implied by Pianka's scheme. Zammuto and Millar (1985a) found higher elevations had more predictable and less variable temperature and precipitation patterns than lower altitudes. This is contrary to the predictions of

Pianka (1976) who assumed higher elevations would have less predictable and more variable climatic patterns. Therefore, quantification of climatic variables is necessary prior to making comparisons of life-history strategies. Stearns (1977) found that only 18 of 35 studies supported the biological predictions of r-K theory. More recently, Zammuto and Millar's (1985a) study on ground squirrels (_Spermophilus columbianus_) found K-selected characters at higher altitudes, which is contrary to that usually assumed by r-K theory.

Charnov and Schaeffer (1973) and Stearns (1976) presented bet-hedging theory as an alternative to r-K theory. Bet-hedging theory incorporates age-specific survivorship, such that the life-history strategy adopted by a population depends upon the variance of juvenile survival or the ratio of juvenile to adult survival. This, in turn, is determined by environmental predictability and variability. Bet-hedging theory predicts that when juvenile survival is less variable than adult survival or if parental survival is less predictable, r-selection will operate. Alternately, if juvenile survival is more variable or unpredictable, or the ratio of juvenile to adult survival is low, then K-characteristics will be favoured. An intraspecific comparison of life-history traits of 13 populations of the mussel _Anodonta piscinalis_ showed results consistent with the predictions of bet-hedging theory (Haukioja and Hakala (1978). In a stable environment where the variation in juvenile survival was low, the mussel populations exhibited short lifespans, high reproductive effort and rapid growth (r- characters). Those results conflict with the predictions of r-K theory which would predict that in such an environment the mussels should display K-type characters. Studies on other invertebrates have also supported bet-hedging predictions (Barclay and Gregory, 1981). However, Zammuto and Millar (1985b) found that the life history strategies adopted by Columbian ground squirrels (<u>Spermophilus</u> <u>columbianus</u>) at different elevations did not follow the predictions of bet-hedging theory.

Since different latitudes present environmental conditions which may differ in their predictability/ variability, patterns of life-history may be expected to vary under the influence of latitudinal seasonality. In this study I consider the r-K and bet-hedging models by examining patterns of covariation in several life-history traits: body size, litter size, survival, and growth between a northern and a southern population of the muskrat <u>Ondatra</u> <u>zibethicus</u>. Questions addressed include: 1) Are northern latitudes more variable /less predictable than southern latitudes as assumed by Pianka (1970) and Cody (1966)?; 2) Do muskrat life history tactics covary between northern and southern populations as predicted by r-K theory or by bet-hedging?; and 3) Do differences in life history tactics observed between the two populations studied indicate trends that are consistent over the muskrat's geographic range?

The muskrat is a semi-aquatic rodent which is widely distributed throughout North America. The muskrat is particularly suitable for the study of life history strategies owing to its distribution and variable habitat requirements. Boyce (1979) noted that muskrats in northern environments produce fewer, larger litters than muskrats at southern latitudes, but no detailed comparison of life-history traits at different latitudes has been made.

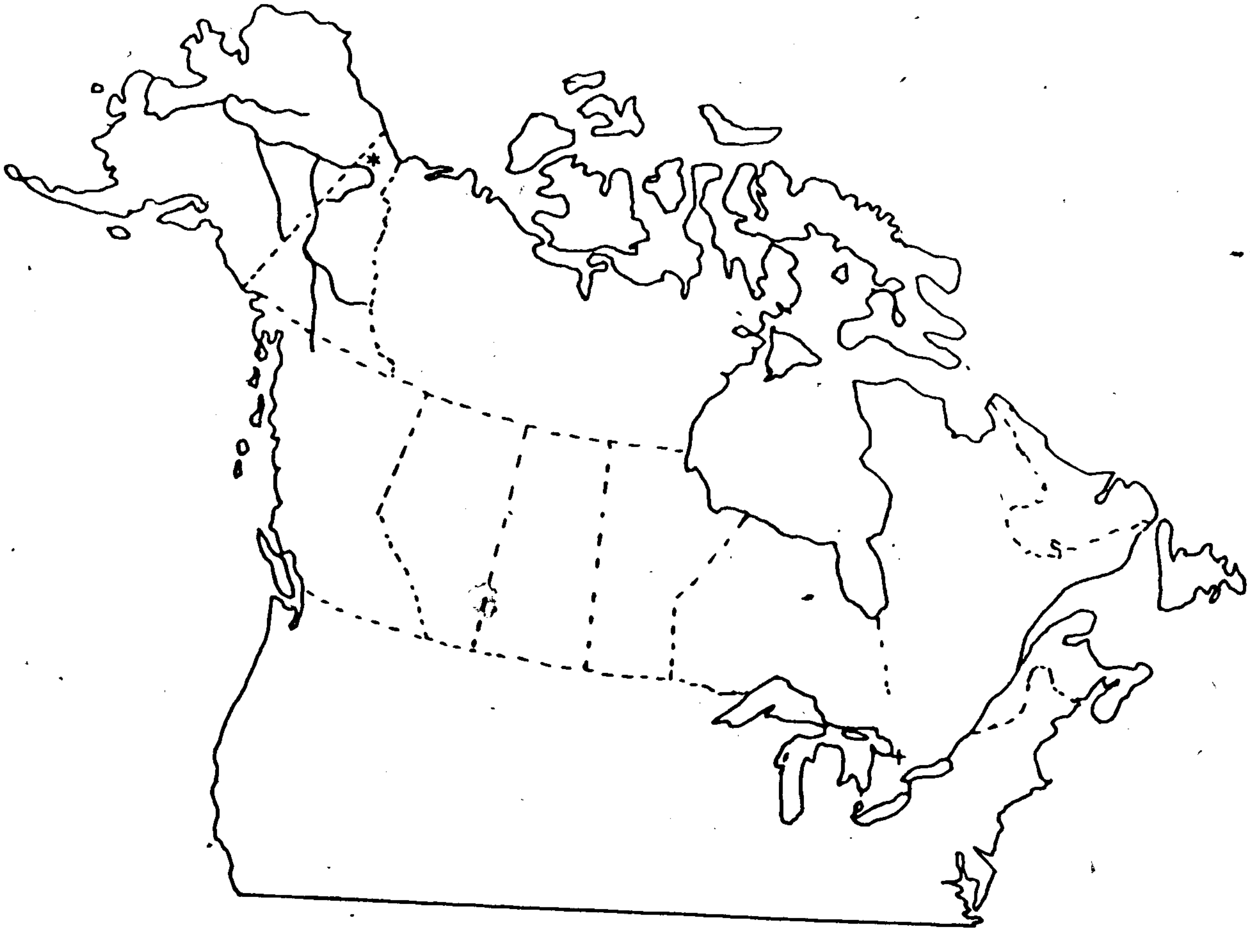
STUDY AREAS

Two study areas were selected, Old Crow flats in the Yukon Territory at the northern limit of the muskrats' range, and Tiny Marsh, Ontario (Figure 1). Selection of these sites was made to ensure that habitats with different environmental characteristics were studied.

Old Crow Flats (68 05'N, 140 05'W) is a 518,000 ha lacustrine basin with approximately 389,000 ha of small thermokarst lakes. Abundant submergent vegetation dominated by Potomogeton spp. and Myriophyllum spp. makes these lakes suitable muskrat habitat. Emergent vegetation is absent.

Tiny Marsh (44 35'N, 79 52'W), Ontario, is a 600 ha wetland with controlled water levels. Cattail (Typha spp.) which dominates the emergent vegetation, and bulrushes (Scirpus spp.) provide a rich habitat (Errington 1963) for muskrats. Cattail is used as a food source as well as construction material for muskrat lodges.

Figure 1. Geographic location of the two study sites, Old Crow flats, Yukon Territory(*) and Tiny Marsh, Ontario(+).



CHAPTER 1: ENVIRONMENTAL PREDICTABILITY AND VARIABILITY

Introduction

Many life history theories assume that habitats can be classified as either variable or stable and predictable or unpredictable (Stearns 1981). All temperate environments are relatively variable, and seasonal fluctuations in temperature are the most noticeable (Fretwell 1972). However, variability need not imply unpredictability since temperate environments can be predictable in the periodicity of their seasonal fluctuations. To date, there has been no concensus as to how predictable or variable environments should be defined. Stearns (1981) advocates deriving measures of predictability/variability independent of the organism being studied. This viewpoint is opposed by Dobson and Murie (1987). Indeed, differences will exist in the predictability/variability of habitats used, for example, by hibernating and nonhibernating mammals during the winter periods in the same area. The climatic variability of an insulated, subterranean burrow will be quite different from the variability of an exposed surface location. Therefore, any discussion of life history strategies should be initiated by identification of climatic parameters of relevance to the organism(s) under study.

For the muskrat, I will classify the predictability and variability of habitats on the basis of daily precipitation, presence or absence of snow and ice cover, and daily temperature. Many studies have acknowledged the importance of stable water levels for muskrat populations (Bellrose and Low 1943, Errington 1937, 1939, McDonnell 1979, Proulx 1981). Proulx (1981) found that production of muskrats was closely related to the water depth associated with the lodge. Errington (1963) also presents anecdotal evidence of the adverse effects of drought upon reproduction and survival of muskrats in Iowa. Therefore, the importance of precipitation during the vegetative growing season, as the primary factor in water level regulation, to muskrat reproduction and survival should be evident. Another important aspect of precipitation is the amount of snow fall. Snow is critical in determining the insulative value of pushups and lodges which minimize the energetic costs of thermoregulation in muskrats (MacArthur 1979). In addition, the amount of snowfall may affect overwinter survival by influencing the degree of freezing which occurs in the pushup plunge hole. The importance of snow cover is not based solely on the predictability of snow cover, but also upon the amount of snow.

Since growth and breeding of muskrats in northern environments are confined to the open water season (Perry 1982), the predictability and variability of growing season length could be critical to production and survival of muskrats. Erickson (1963), using livetrapping data, indicated that snow, ice conditions, and temperature were important factors affecting spring dispersal. Predictability and variability of ice break-up is a function of a number of factors. First, the thickness of the ice is a negative function of the amount of snowfall and temperature (Jelinski 1984). Temperature also determines the rate of ice-melt in the spring.

Temperature has also been considered to influence muskrat reproduction and survival. Olsen (1959) determined that high temperatures combined with light rainfall triggered the onset of breeding on Delta Marsh, Manitoba. Similarly, Danell (1978) observed a relationship between the onset of breeding and air temperature in muskrat populations of northern Sweden. Temperature also influenced spring dispersal of muskrats in New York State (Erickson 1963). Temperature may also be considered important for survival, especially during the growing season, when juvenile muskrats are small and susceptible to hypothermia (MacArthur 1979). An environmental parameter which is directly related to muskrat energetic expenditure and survival is the number of days in which the environmental temperature, during the growing season, lies outside the muskrats thermoneutral zone. For adult <u>O. zibethicus</u>, the thermoneutral zone is 10^{o} to 32^{o} (McEwan et al. 1974).

The purpose of this chapter is to assess the variability and predictability of those environmental variables that are likely relevant to the survival and production of muskrats. The results of this analysis will permit me to predict the life history traits expected, on the basis of r-K selection and bet-hedging, in northern and southern populations of muskrats.

Methods

Climatic data for a five year period (1981-1985) were obtained from climatic stations (Monthly Atmospheric Record, Canadian Climate Normals) at the Old Crow airport (67 35′N, 139 50′W) and at Midland, Ontario (44 45′N, 79 54′W). The climatic stations were 60km and 35km respectively from the Old Crow and Tiny Marsh study sites. Powell and MacIver (1977) found 3-7 years of climatic data was adequate to describe the normal, 30 year temperature and precipitation patterns of the forested areas of the prairie provinces. Daily mean temperature and precipitation were used to classify the predictability and variability of the study sites. At both areas consistent records were not maintained on diurnal variation in temperature or precipitation to allow a finer scale analysis. Study of these variables on a mean monthly basis did not allow the use of powerful statistical tests due to sample size problems.

The mean number of frost-free days per season at each site was used as an approximation of the vegetative growing season and the ice-free period. Predictability and variability of temperature and precipitation at both sites were analyzed within the frost-free period. Snowfall patterns were compared throughout the winter season.

Predictability was defined as the degree of relationship between the amount and pattern of year to year values for daily temperature and precipitation. This was analyzed by doing pair-wise comparisons of the climatic parameters of successive years using Spearman Rank Correlation tests of association (Daniel 1978). The Spearman Rank Correlation test measures the degree to which two ranked arrays are similarly ordered. At each site, a multiple comparison of correlation coefficients test (X^2 with k-1 df, Zar 1984) was used to determine if predictability was significantly different between years. If there was no significant difference in the correlation coefficients at a site, a pooled Spearman Rank correlation coefficient was derived. Pooled Spearman Rank correlation coefficients were compared to test for differences in predictability between sites using a Chi-squared test (Zar 1984).

Environmental variability was defined as the statistical variance in weather parameters, from daily measurements, over the vegetative growing season (Zammuto and Millar 1985a). Differences in the variance between sites were tested using an F-max test for equality of variance (Sokal and Rohlf 1981).

The mean and variance of the number of days in which daily environmental temperature was outside the thermoneutral zone (10^{o} to 32^{o}; McEwan et al., 1974) were compared between the northern and southern sites for 1981-1985.

All means are reported +/- one standard deviation unless otherwise noted. In all statistical tests the 0.05 significance level was used.

Results

The length of the growing season (number of days in which temperature> 0^{o}C) for 1981-1985 was significantly greater for Tiny Marsh ($X=174$ +/- 17.9 days) than Old Crow ($X=72.6$ +/- 5.68days; $t=12.063$, $p<0.001$).

Predictability

There was no significant difference between years in the timing or relative amount of snowfall at either site (Tiny: $X^2=0.0092$, Old Crow: $X^2=0.330$; $p>0.05$). Pooled Spearman Rank correlation coefficients for Tiny Marsh and Old Crow were 0.734 and 0.478 respectively, and were not significantly different ($X^2=0.148$; $p>0.05$).

Spearman Rank Correlation coefficients for precipitation between years (Table 1.1), were not significantly different for either Old Crow ($X^2 = 9.658$, $0.25> p >0.05$; pooled $r=0.287$), or Tiny Marsh ($X^2 = 9.3399$, $0.25> p >0.05$; pooled $r=0.048$). The pooled

Table 1.1: Spearman Rank Correlation coefficient matrices of year to year association of daily precipitation at Old Crow and Tiny Marsh.

OLD CROW

	1981	1982	1983	1984
1982	0.365	--	--	--
1983	0.215	0.237	--	--
1984	0.479	0.327	0.305	--
1985	0.271	0.301	0.205	0.127

TINY MARSH

	1981	1982	1983	1984
1982	-0.003	--	--	--
1983	0.080	0.073	--	--
1984	-0.022	0.025	0.110	--
1985	0.022	-0.131	-0.096	0.011

correlation coefficients for precipitation were significantly (X^2 =4.94 0.05<P<0.025) different between sites indicating precipitation was more predictable at Old Crow than at Tiny Marsh.

There was no significant difference in predictability between years for Old Crow temperature (X^2 =14.5291, 0.10>P>0.05; pooled coefficient=0.724; Table 1.2). However, there was a significant difference between years for temperature at Tiny Marsh (X^2 = 17.5681,0.05>P>0.025. A Tukey-type test (Zar 1984) was used to make pair-wise comparisons between the Spearman Rank correlation coefficients for Tiny Marsh, as well as making the comparison with the pooled Spearman Correlation coefficient for Old Crow (Table 1.3). Old Crow was significantly more predictable than Tiny Marsh for 8 of the 11 comparisons made.

To summarize, predictability of precipitation and temperature was greater at Old Crow than at Tiny Marsh. There was no significant difference in the predictability of snowfall patterns between the two sites.

<u>Variability</u>

Variance in length of growing season was significantly greater for Tiny Marsh than for Old Crow (F=9.938, p<0.025). The coefficients of variation for growing season length were 10.29% and 7.82% for Tiny Marsh and Old Crow flats respectively. Significantly

Table 1.2: Spearman Rank Correlation coefficient matrices of year to year association of daily temperature at Old Crow and Tiny Marsh.

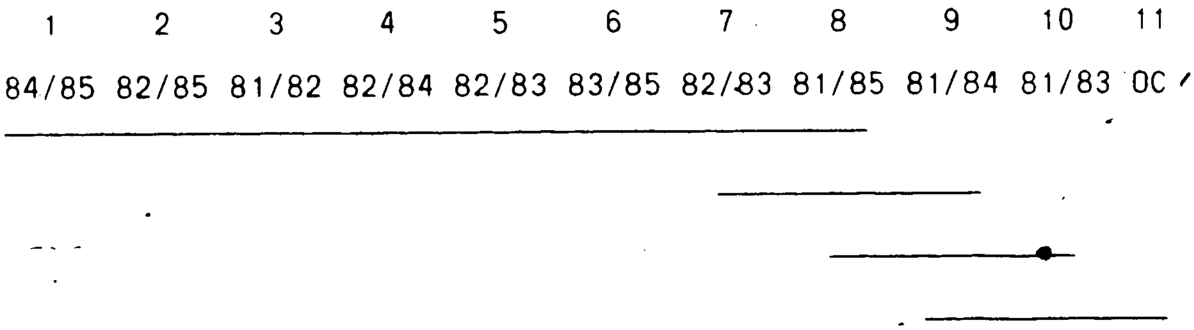
OLD CROW

	1981	1982	1983	1984
1982	0.754	--	--	--
1983	0.783	0.769	--	--
1984	0.760	0.666	0.781	--
1985	0.629	0.733	0.723	0.588

TINY MARSH

	1981	1982	1983	1984
1982	0.508	--	--	--
1983	0.663	0.522	--	--
1984	0.643	0.511	0.567	
1985	0.536	0.452	0.527	0.448

Table 1.3: Similarities (P>0.05) are indicated with a solid line, Tiny Marsh correlation coefficients, taken from Table 1.2, are ranked from smallest to largest. Coefficient 11 is the pooled correlation coefficient for Old Crow.



1	2	3	4	5	6	7	8	9	10	11
84/85	82/85	81/82	82/84	82/83	83/85	82/83	81/85	81/84	81/83	OC

more snow fell on Tiny Marsh (X= 26.4 +/- 4.4cm) than on Old Crow flats (X= 8.98 +/- 4.24cm; t= 2.84, p= 0.005). Variability in snow fall was lower at Tiny Marsh than at Old Crow (F= 1.09, p<0.05), as indicated by the coefficients of variation for Tiny Marsh (16.7%) and Old Crow (47.22%) respectively.

Precipitation and temperature were more variable for the growing season at Tiny Marsh than at Old Crow (Precip.: F=4.341, p< 0.01; Temp.: F= 1.04, p<0.01). There was no significant difference between sites in the number of days in which minimum temperature, during the reproductive season, was outside the thermoneutral zone of muskrats (X = 63.2+/-15.1days at Tiny, X = 55.2+/-4.62days at Old Crow;t=1.01, p<0.17). A test for equality of variance indicated that Tiny Marsh was more variable (F=10.68, p<0.05) than Old Crow in the number of days outside the muskrats thermoneutral zone. Coefficients of variation for Old Crow and Tiny Marsh were 8.37% and 23.89% respectively.

Variability was greater at Tiny Marsh when compared to Old Crow for 3 of 4 environmental parameters. Old Crow was less variable in temperature, precipitation and in the number of days the ambient temperature was outside the muskrats thermoneutral zone. Tiny Marsh was less variable in snowfall pattern than Old Crow.

Discussion

Pianka (1970) and Cody (1966) assumed that northern latitudes and higher altitudes were more variable and less predictable in climatic pattern than southern latitudes or low altitudes. However, Zammuto and Millar (1985a) demonstrated that higher altitudes were more predictable and less variable in temperature and precipitation than lower altitudes. Similarly, variability of daily precipitation and temperature were greater at the southern site than at the northern site in this study. Predictability of precipitation and temperature patterns was greater at the northern site than at the southern site. Predictability of snowfall was not significantly different between the two sites.

Attempts to quantify environmental predictability and variability in life history studies have been rare and there seems to be no agreement on how to measure these factors (Stearns 1981). Investigators have often relied on anecdotal evidence to make generalized statements, which has probably helped perpetuate the misconception that northern and high altitude environments are more variable and less predictable than their southern or low altitude counterparts. Zammuto and Millar (1985a) outlined a methodology by which these aspects of environmental variation could be measured. Unfortunately, their approach to measuring predictability does little to alleviate the problem. Zammuto and Millar

(1985a) used 18 equations from information theory, parametric and nonparametric statistics. From a practical standpoint, it is simpler and easier to interpret the results by using a single estimate of predictability such as that used in this study until a general concensus is reached on the "best" method to measure variation and predictability.

The direct effect of climatic seasonality is to create temporal variation in resource availability (Fretwell 1972). Most significant to an organism existing in a seasonal environment is variation in the availability of food and nutrients (Karr 1976). This variation may have major impact on productivity if experienced during the period favourable for breeding and reproduction, and hence can be important in the formation of life history strategies.

Populations are expected to exhibit a set of traits that are adapted to local variation in length of growing season and other climatic parameters (Zammuto and Millar 1985a, Dobson and Kjelgaard 1985). Life-history models allow the prediction of the biological traits based on an evaluation of climatic variables affecting a population's habitat. According to Pianka (1970), less variable/more predictable habitats such as Old Crow (less variable in growing season length, precipitation and temperature) should exhibit the K-characteristics of larger body size, conservative reproduction, and low growth rates (Intro:Table 1). The combination of these characters results in efficiency of resource utilization as opposed to productivity. Individuals in more variable environments such as Tiny Marsh are expected to employ more productive life history traits such as smaller body size, higher growth rates and higher reproductive effort than the Old Crow population.

Bet-hedging theory predicts the K-characteristics of conservative reproduction and large body size if the observed environmental variation results in variable juvenile survival. On the basis of greater variation in the number of days of energetic stress on muskrats at Tiny Marsh, I would predict greater variation in juvenile survival. Therefore, muskrats at Tiny Marsh, in a more variable environment, will be expected to be more K-selected than muskrats in more stable environments, eg. Old Crow, if juvenile survival does in fact vary in the predicted direction in response to environmental variation.

CHAPTER 2: COMPARISON OF LIFE HISTORY STRATEGIES BETWEEN NORTHERN AND SOUTHERN POPULATIONS OF MUSKRATS.

Introduction

Detailed intraspecific comparisons of life-history strategies between populations of mammals are at present confined to studies of ground squirrel life-history strategies over elevational gradients (Bronson 1979, Dobson and Kjelgaard 1985, Murie 1985, Zammuto amd Millar 1985a). Zammuto and Millar (1985a) characterized higher elevations as more stable and more predictable than lower altitudes, contrary to the predictions of Pianka (1970) and Cody (1966). They found that litter size was smaller, annual adult survival greater, and age of reproduction was delayed at higher elevations, when compared to lower altitudes, supporting the r-K life-history model (Zammuto and Millar 1985a, Dobson and Kjelgaard 1985) for traits expected in stable and predictable environments.

Currently, there is no comparable study of mammalian life-history strategies on a latitudinal scale. The purpose of this study was to examine the life-history characteristics of two geographically distant populations of muskrats (see chapter 1). Specifically, I compared reproductive effort, growth rates, survival, and body weight between a northern and a southern population of muskrats. From r-K theory I would expect the southern population to exhibit more r-selected characteristics of higher reproductive effort and growth rates. According to bet-hedging theory, if the greater climatic variation in the southern population results in lower or more variable juvenile survival, then we would predict the K-type characteristics of conservative reproduction and large body size.

Methods

Livetrapping

Northern Population:Old Crow

Four study sites were selected on the Old Crow flats. All areas were located within a 10km radius. To enumerate the muskrat population at each site, each area was livetrapped using Tomahawk livetraps (18 X 18 X 50cm) baited with apple. Two areas were trapped simultaneously at any one time. Trapping was initiated in April and early May, continued until June 15 of 1985 and 1986, resumed in late July, and continued until September. Trapping sessions varied from 5-11 days, and ended when at least 70% of the animals previously trapped were recaptured. Traps were then moved to a new site. Each study site was trapped for at least two sessions during both the spring and fall periods. During the ice-free period (June-Sept.), traps were placed on feeding sites along the shore of the lakes and in the vicinity of burrow openings. During the periods of ice cover (April and May) traps were placed on the feeding sites within pushups (see Slough 1982 for description) and then covered with snow (Stevens 1953). Traps were checked every eight hours, and remained set for twenty-fours each day. The sex of captured animals was determined and each animal was marked with a numbered ear tag, and weighed with a spring scale. Age was determined by pelage characteristics; the adult pelage is a characteristic brown color with long guard hairs, whereas juveniles have a gray brown pelt (Schwartz and Schwartz 1959). Reproductive condition was assessed in females by the presence/absence of conspicuous teats, and the condition of the vagina (perforate/non-perforate), and in males by the position of the testes (scrotal/abdominal). Animals were released at the capture site. Carcasses obtained from native trappers in the spring of each year were used to obtain embryo counts to determine litter size. I removed all trappable female adults in September 1986 on all areas to obtain counts of placental scars to determine annual production.

Southern Population: Tiny Marsh

At Tiny Marsh, muskrats were live-trapped in three separate areas of the marsh using National live-traps (18 X 18 X 50cm). Traps were placed on muskrat lodges and feeding platforms, baited with apple, and covered with vegetation. Traps were set in early evening and checked the following morning. Trapping occurred from April to

September in 1985 and 1986. Upon capture muskrats were handled as described above. Muskrat lodges were also opened during May-August to capture unweaned litters in their nests to determine litter size. Each litter was toe clipped with a unique combination to allow future identification. In 1985, sixty-four adult females were removed to obtain counts of placental scars for determining annual production. Placental scars in muskrats are known to be visible until commencement of the next breeding season (Proulx 1984; Parker and Maxwell 1984), and therefore indicate the number of offspring produced during the year.

Growth and Survival

For both populations, growth rates were calculated assuming a linear model (Case 1978, Millar 1977), where growth rate was the difference in mass divided by the number of days between two successive trapping sessions.

Mass at weaning was approximated as weight of first capture of juveniles in both populations. This was used to calculate two measures of reproductive investment for each litter:

Reproductive Index(RI)= weight of 1 offspring/weight of female

Reproductive Effort(RE)= mean annual production x RI

Litters, and maternal association were defined from the livetrapping data, at both sites, by analyzing the location and timing of capture. If only one female was associated at a trap site, and that trap site also had juveniles emerging for the first time within a three to four day period, the female was then associated with that litter. The juveniles also had to be of similar weight (+/-25g) to qualify as members of the same litter. Olsen (1959) found that at weaning, weights of all siblings were within 10g of each other.

Minimum values of overwinter survival were calculated by comparing the proportion of ear tagged individuals captured in 1985 that were retrapped in 1986. This is a minimum estimate since it does not account for individuals that may have lost their tags, dispersed from the site, or escaped further capture. Data were analyzed by age and sex. Variance in overwinter survival was calculated at each site by comparing between four trapping grids at Old Crow and three grids at Tiny Marsh.

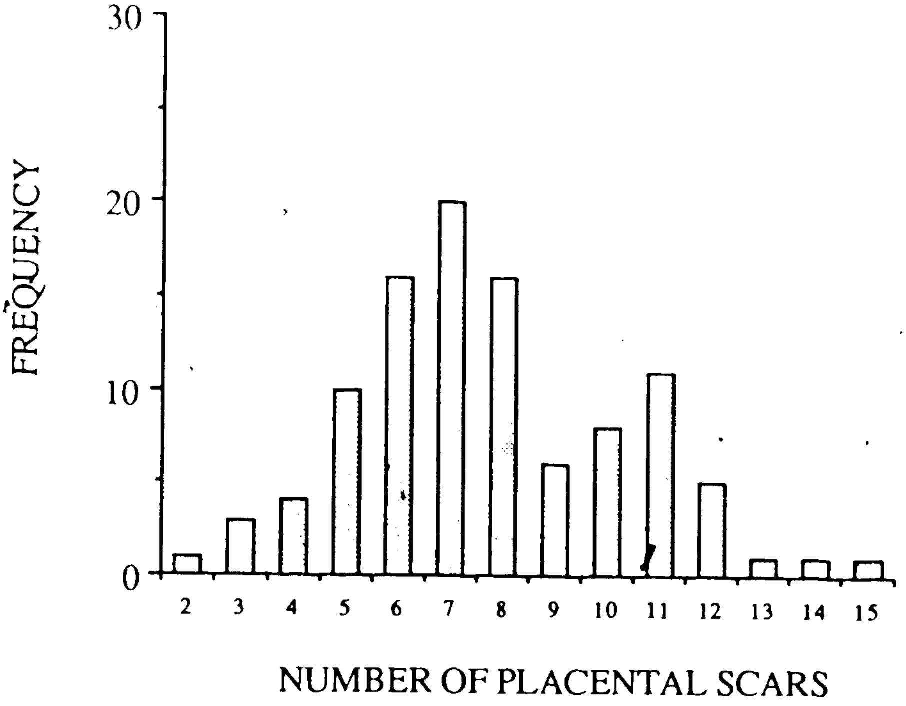
Unless otherwise noted, means are reported +/- one standard deviation.

Results

Reproduction

Mean number of offspring produced per female in Old Crow, as indicated from placental scars, was 7.75 +/- 2.6 in both 1985 (n=59) and 1986 (n=44)(Figure 2.1). There was no significant difference between years in the mean (t=0.0083, p=0.50), or in the variance (F=1.03,

FIGURE 2.1: Frequency distribution of the number of placental scars of female muskrats removed on Old Crow Flats. Data for 1985 and 1986 are combined.


30
20
10
0
FREQUENCY
2
3
4
5
6
7
8
9
10
11
12
13
14
15
NUMBER OF PLACENTAL SCARS

$p<0.05$). Litter size at Old Crow, as indicated by embryo counts collected in 1985, was 7.86 +/- 0.64 (n=8). Juvenile muskrats were first captured on 11 August 1985 and 7 August 1986 indicating that only one litter per year was produced in this area. As well, division of the annual production (placental scars) by litter size (from embryo counts) indicated females on average produced one litter per year.

Mean size of complete litters enumerated in their nests at Tiny Marsh was 7.15 +/- 1.57 (n=99). The mean number of placental scars, counted in 1985 in 68 females, was 14.3 +/- 4.38 (Figure 2.2). Three peak periods of reproduction are indicated at Tiny Marsh by the occurrence of litters in nests (Figure 2.3). However, when the annual production (mean number of placental scars) is divided by the mean litter size, it suggests 1.98 litters are produced on average. There was no significant difference in litter size between the two populations (t=1.79 p=0.09). However there was a significant difference in annual production (t=8.98, $P<0.001$) when placental scar counts were compared.

The reproductive index associated with juvenile weight at first capture was 0.308 +/- 0.06 (n=14) and 0.232+/-0.014 (n=21) for Old Crow and Tiny Marsh respectively. RE values were 2.609 and 4.98 for Old Crow and Tiny Marsh respectively.

FIGURE 2.2: Frequency of Placental scars counted in female muskrats trapped on Tiny Marsh in 1985.

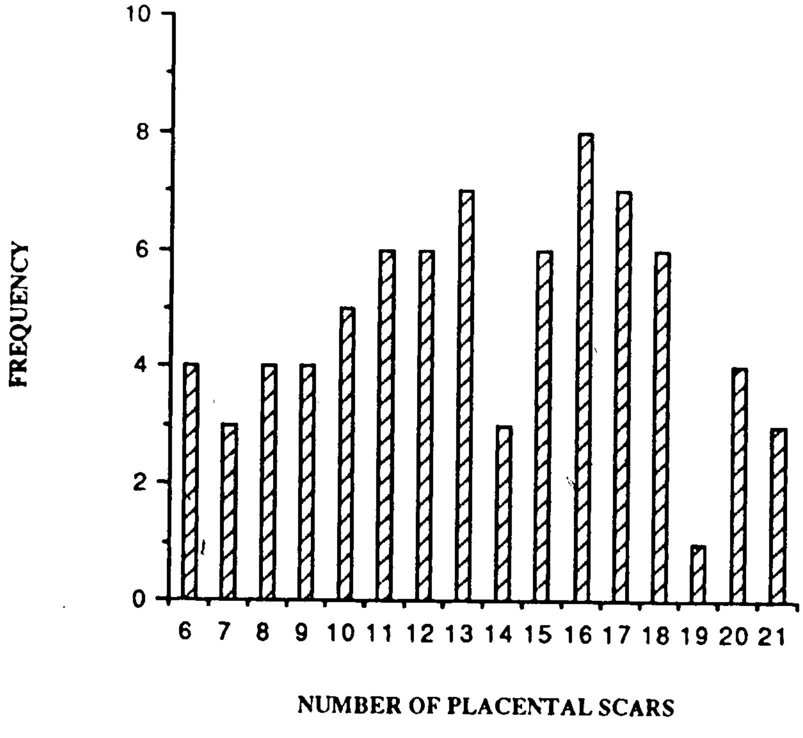
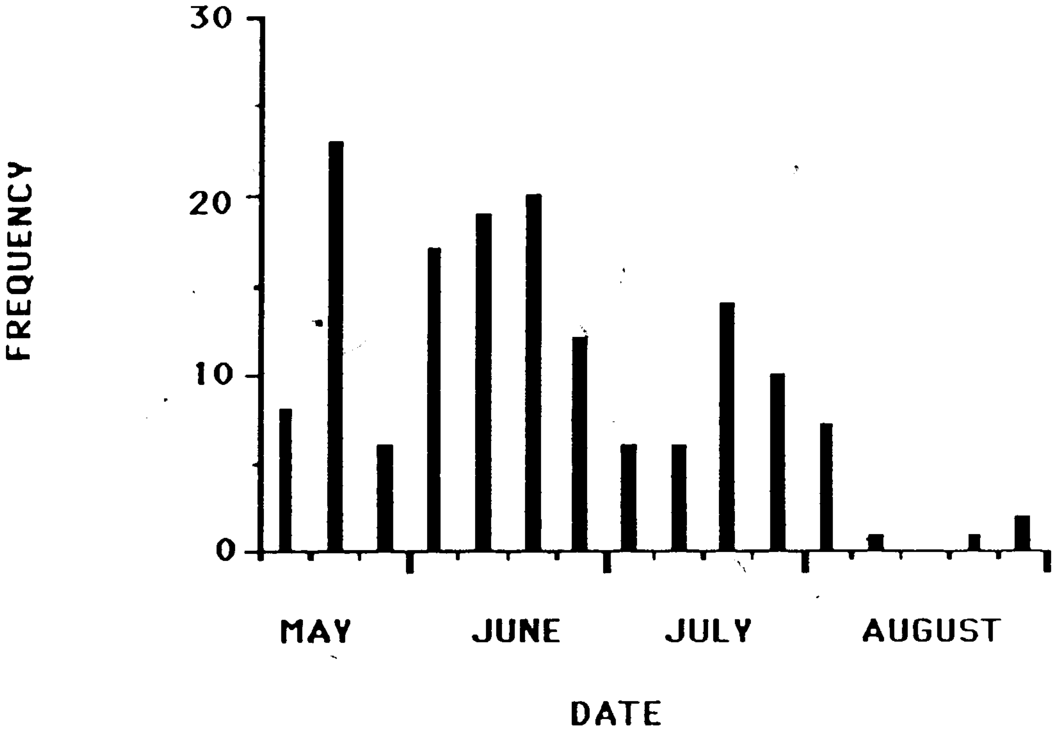

FREQUENCY
10
8
6
4
2
0
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
NUMBER OF PLACENTAL SCARS

FIGURE 2.3: Frequency of litters censused in nests on Tiny Marsh from May 12 to August 31, 1985.


30
20
10
0
FREQUENCY
MAY
JUNE
JULY
AUGUST
DATE

Growth Rates

Calculations were made between trapping sessions, rather than within sessions, to avoid problems with weight loss associated with repeated captures over short time periods. Weight loss of individuals within trapping sessions varied from 10 to 100g/day. There was no significant relationship between weight loss within a trapping session and number of captures within a session for the Old Crow population (F=1.24 , p=0.14).

Mean growth rates were analyzed by sex and age groups with an analysis of variance. There was no significant effect of sex on juvenile growth rates for the Old Crow population (F=0.28; P=0.596; X=4.04 g/day and X=3.78 g/day for males (n=33) and females (n=30) respectively). Similarily, there were no significant differences between growth rates of male (n=72) and female (n=105) juveniles at Tiny Marsh(X = 7.10 g/day, X = 8.84 g/day respectively; F=2.30, p=0.127). At Old Crow, adult muskrats had a lower growth rate (X=3.98, n=50) than juveniles (X=4.11) (F=9.54; P=0.003). Growth rates on Old Crow and Tiny Marsh were not significantly affected by the time of year at which juvenile or adult muskrats were captured.

Comparison of growth rates between Old Crow and Tiny Marsh indicated that rate of growth was significantly greater for juveniles at Tiny Marsh (X=8.56, n=168) than at Old Crow (X=4.12, n=100; t= 4.82, p<0.01). Adult growth rates at Tiny Marsh (X=8.37) were significantly greater than adult growth rates at Old Crow (X=3.98: F=7.57, P=0.008). A nested ANOVA (Table 2.1) on juvenile growth rates, with sex nested within location indicated location accounted for a greater proportion (20.5%) of the variance component than did sex (3.2%).

Body Weight

Adult muskrats on Tiny Marsh were significantly heavier than Old Crow adults in both the spring (Figure 2.4a,b) and fall (Figure 2.5a,b). In the spring of 1985, the weight difference was due to a significant difference in female weight (t=4.18, p=0.001). There was no significant difference in male adult weight (p=0.922). Both sexes were significantly heavier in the fall on Tiny Marsh (t=11.29, p=0.001; t=14.127, p=0.001 for 1985 and 1986 respectively).

Male and female juvenile muskrats, caught as free ranging kits in the fall, were significantly heavier on Tiny Marsh than on Old Crow flats (t=12.02 for males, t=16.836 for females, P<0.0001 Figure 2.6). On Old Crow flats, the fall weight of juvenile muskrats was less than 50-60 percent of the fall adult weight (Figure 2.7a,b). At Tiny Marsh however, fall captured juveniles weighed 10-110 percent of the mean fall adult weight (Figure

Table 2.1: Results of a nested ANOVA on juvenile growth rates. Location(Old Crow and Tiny Marsh) was used as the major grouping, sex was used as a subgrouping.

ANOVA TABLE

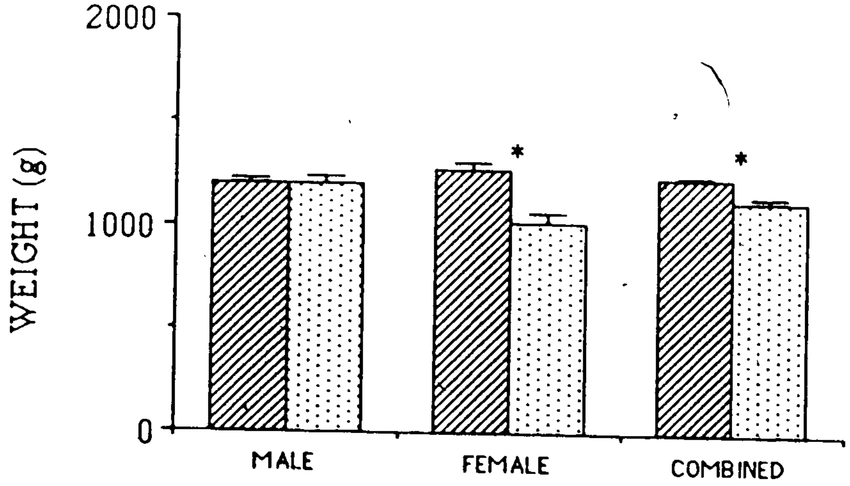
LEVEL	SS	DF	MS	FS
LOCATION	1326.5657	1.	1326.56600	9.6908 0.005>p>0.001
SEX	273.7786	2.	136.88930	3.7672 0.025>p>0.01
TOTAL	9484.0586	261.	36.33739	

VARIANCE COMPONENTS

LEVEL	VAR.COMP.	PERCENT
LOCATION	9.75484	20.4786
SEX	1.54204	3.2373
TOTAL	36.33739	76.2841

Figure 2.4: Comparison of spring body weight between adult muskrats captured at Tiny Marsh (▨) and Old Crow (░) during 1985 (a) and 1986 (b). Sexes are presented separately and then combined. An asterisk indicates significant differences at the 0.05 level of significance. Error bars indicate 1 standard error of the mean.

1985


2000
1000
0
WEIGHT (g)
*
*
MALE
FEMALE
COMBINED

1986

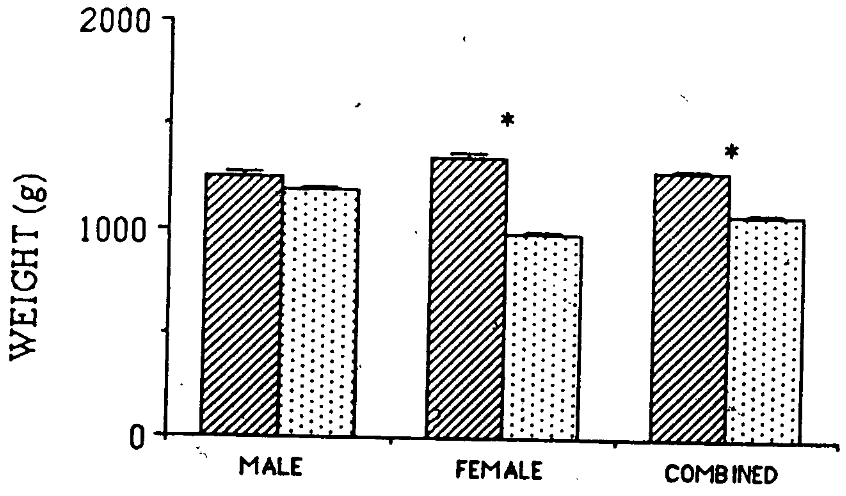
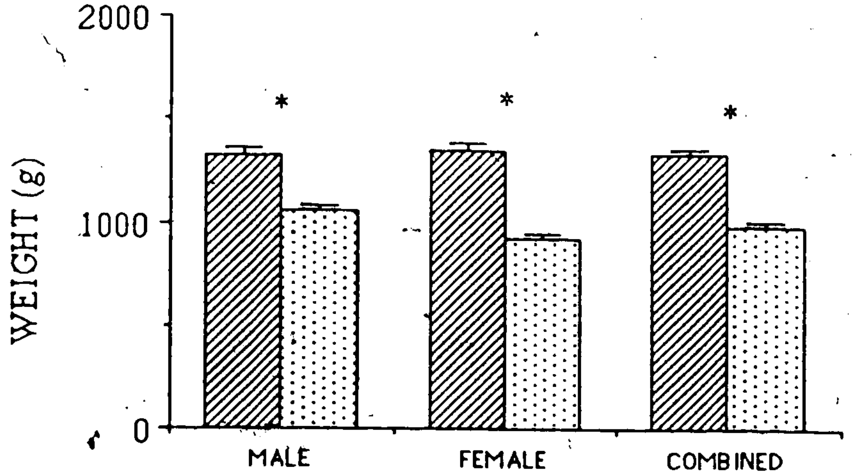

2000
1000
0
WEIGHT (g)
*
*
MALE
FEMALE
COMBINED

Figure 2.5: Comparison of fall body weight between adult muskrats captured at Tiny Marsh (▨) and Old Crow ░ during 1985 (a) and 1986 (b). Sexes are presented separately and then combined. An asterisk indicates significant differences at the 0.05 level of significance. Error bars indicate 1 standard error of the mean.


2000
1000
0
WEIGHT (g)
*
*
*
MALE
FEMALE
COMBINED

1985

1986

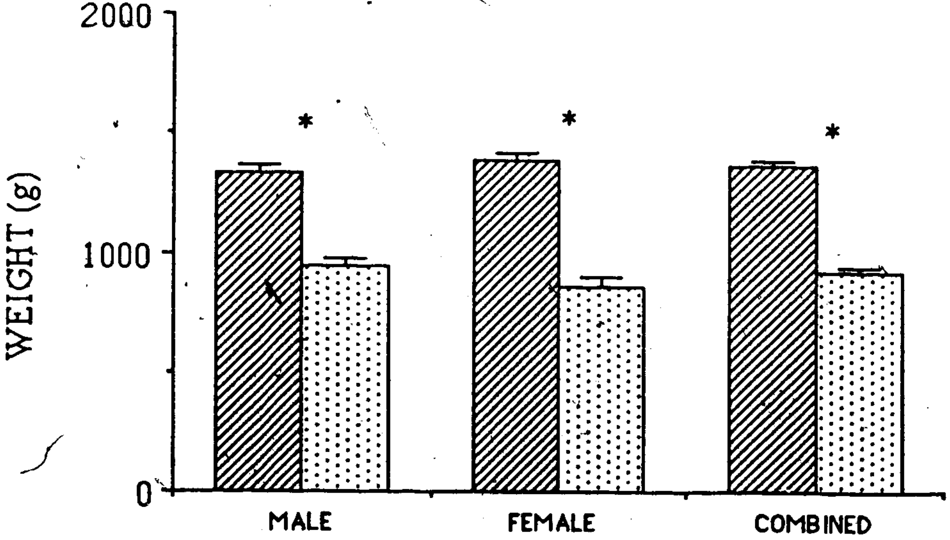
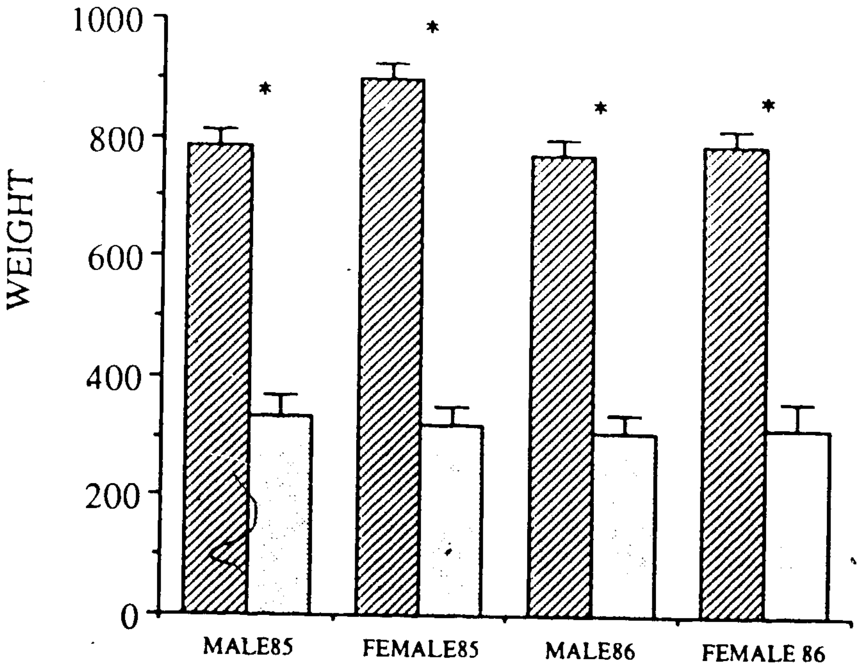

2000
1000
0
WEIGHT (g)
*
*
*
MALE
FEMALE
COMBINED

Figure 2.6: Comparison of fall body weight between male and female juvenile muskrats captured at Tiny Marsh (▨) and Old Crow ( ) during 1985 and 1986. Sexes are presented separately. An asterisk indicates significant differences at the 0.05 level of significance. Error bars indicate 1 standard error of the mean.


1000
800
600
400
200
0
WEIGHT
*
*
*
*
MALE85
FEMALE85
MALE86
FEMALE 86

2.7a,b).

Survival

Minimum estimates of overwinter survival (Table 2.2) indicated that juvenile survival was greater for the northern (X=35.9%), than for the southern population, (X=19.1%). Overwinter survival for Old Crow adults was 21.2%, which was not significantly different from that on Tiny Marsh (12.6%). The ratio of adult to juvenile survival was 0.59 and 0.66 for Old Crow and Tiny Marsh respectively. Coefficients of variation for juvenile overwinter survival, calculated using each trapping grid separately, were 59.4% and 69.1 for Old Crow and Tiny Marsh respectively. For adult survival the coefficients were 69.0% and 109% respectively.

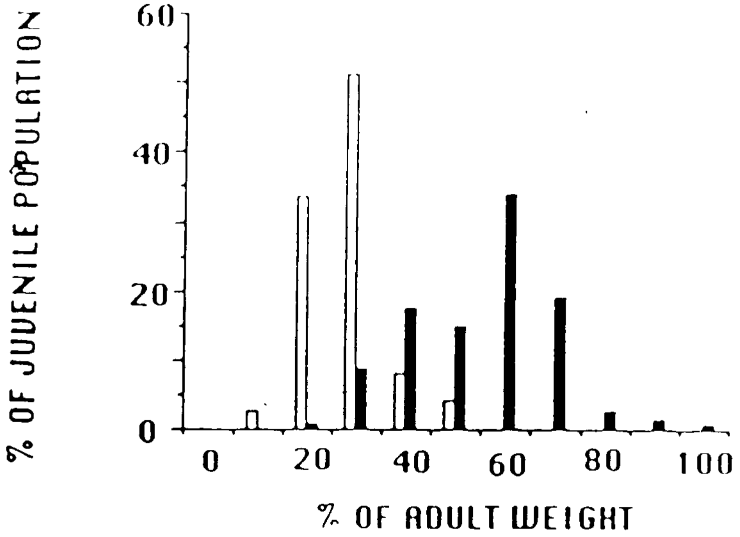
A summary of the differences in life-history parameters studied between Tiny Marsh and Old Crow is presented in Table 2.3.

Discussion

The bet-hedging model of life-history selection predicts that in an environment that is relatively more stable and predictable, and in which juvenile survival a) is greater or b) less variable or where c) there is a higher ratio of juvenile/adult survival, a life-history strategy of higher production of offspring should be observed when compared to a population with opposite traits (Horn 1978). To test the bet-hedging model, I

Figure 2.7: Comparison of fall body weight of juvenile muskrats captured at Old Crow and Tiny Marsh ● during 1985 and 1986. Juvenile weight is represented as a percent of the mean adult weight at each site during the same time period.

1985


% OF JUVENILE POPULATION
60
40
20
0
0
20
40
60
80
100
% OF ADULT WEIGHT

1986

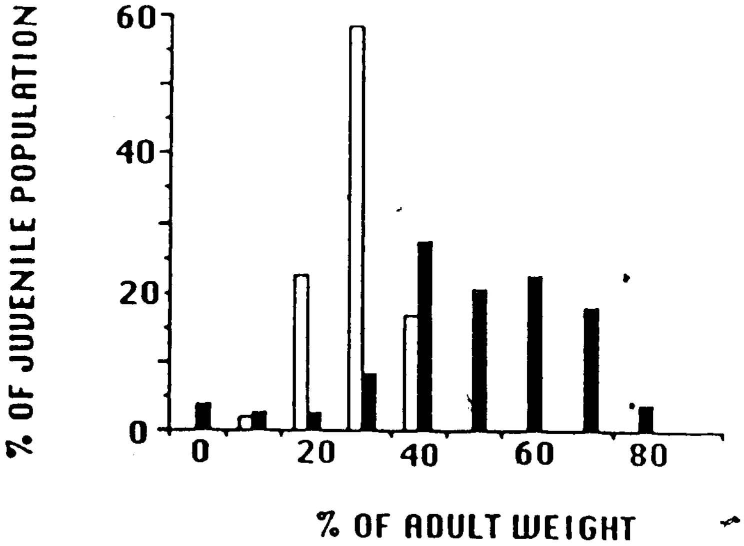

% OF JUVENILE POPULATION
60
40
20
0
0
20
40
60
80
% OF ADULT WEIGHT

Table 2.2: Comparison of the proportion of juveniles and adults surviving overwinter at Tiny Marsh and Old Crow.

	SITE	#ALIVE	#DEAD	%SURVIVING
Juveniles	Old Crow	76	136	35.6
	Tiny Marsh	104	441	19.1

G(Williams) = 22.39
G = 22.48
P < 0.001

	SITE	#ALIVE	#DEAD	%SURVIVING
Adults	Old Crow	24	89	21.2
	Tiny Marsh	20	139	12.6

G(Williams) = 3.558
G = 3.602

0.1 < P < 0.05

Table 2.3:- Summary of the life-history parameters exhibited by two wild populations of muskrats. Values presented are averages calculated with both sexes combined.

	OLD CROW		TINY MARSH
Fall body weight	950g	<	1348g
Spring Body weight	1100g	<	1260g
Juvenile survival	35.9%	>	19.1%
Adult survival	21.2%	=	12.6%
Litter size	7.75	=	7.15
Number of litters	1	<	1-3 (2)
Growth Rate	3.9g/day	<	4.2g/day
Reproductive effort	2.61	<	4.98
Reproductive Index	0.31	>	0.23

compared absolute juvenile overwinter survival, juvenile/adult survival ratio, and within site variance in survival between my study populations. I could not measure between year variance in survival. At Tiny Marsh juvenile survival was both lower, and more variable than at Old Crow. As well, the ratio of juvenile to adult survival was lower on Tiny Marsh. Given these results the bet-hedging model would predict higher offspring production at Tiny Marsh. This is contrary to my findings. Therefore I rejected bet-hedging as a model to explain the pattern of life-history strategies in my two study populations. The observed pattern of variation in growth, reproductive effort, and survival at the northern and southern study sites, are best explained by the r-K model of life-history variation.

On Old Crow flats, less variation in environmental parameters of relevance to muskrats led to predictions, based on r-K theory, of slower growth, better survival of adults and juveniles, fewer larger young and larger body size when compared to the population in the more variable southern environment at Tiny Marsh (see Chapter 1). The observed pattern of life-history traits supports all but one of these predictions. Contrary to the predictions of r-K theory, spring and fall body weight of adults, and fall weight of juveniles were greater in the southern population than at the northern site.

Boyce (1979) suggested that large body size in homeotherms is an adaptation to survive extended periods of resource shortage which occur in temperate environments. Therefore, based on Boyces' seasonality-selection hypothesis northern muskrats should exhibit larger body size than their southern counterparts since the period of resource shortage is extended. However that is contrary to my findings. Downhower (1976), however, found that climatic variability, which implies resource variability, was selecting for large body size in Galapagos finches (<u>Geospiza</u> spp.). The relationship between climatic and body weight parameters studied here agree with the latter finding. However, since body weight is highly influenced by proximate factors such as resource adundance and quality it may be a trait which cannot be easily classified as r- or K- selected in intraspecific comparisons.

Errington (1941) observed that muskrat body size was related to the abundance and quality of forage available. Proulx (1981) found that muskrats in cattail habitats were heavier than muskrats from other vegetation types on Luther Marsh, Ontario. For muskrats, cattail (<u>Typha</u> <u>sp.</u>) is considered to be highly nutritious (Stearns and Goodwin 1941), and is a preferred food (Bellrose 1950). Larger body size on Tiny Marsh may therefore be the result of high densities of cattail stands providing a nutritious food supply. On Old Crow flats, the less nutritious Potomogeton and Myriophyllum spp. presumably result in a lower quality food resource, and therefore lower body weight.

The observed pattern of body weight in muskrats is also contrary to the thermoregulatory theory of Bergmann (1847, cited in McNab 1971). Bergmann's rule states that larger races of a species will be found in cooler regions of the species' distribution. However, for a species which lives in a "closed" environment for over half of the year, thermoregulatory costs may not be a major concern. In muskrats, behavioural responses rather than larger body size may accomplish the thermal adjustments necessary in cold weather. Indeed, muskrats undergo altered behavioural patterns in winter (MacArthur 1981), such as altering foraging time duration, resulting in the maintenance of a constant thermal regime.

Reproduction in muskrats is considered to be restricted by the length of growing season and climatic severity (Boyce 1979). Wilson (1954) reported that muskrats on tidal marshes of North Carolina produced litters throughout the year, except during unusually cold winters. Similarly, O'Neal (1949) and Lay (1945) observed year-round breeding in Louisiana and Texas marshes respectively. However, in northern areas, such as the Mackenzie Delta, NWT and Old Crow flats, YT, reproduction is limited to June-August (Stevens 1955; Ruttan 1974). Spencer and Steinhoff (1968) argued that shorter growing seasons at higher elevations/latitudes resulted in increased litter size. At lower latitudes, they argued that females will increase their probability of survival by producing more smaller litters. This provides an advantage over those females, at the same altitude/latitude, producing large litters and a concomitant reduction in their probability of survival. In a shorter growing season, females have fewer larger litters to achieve the same reproductive capacity as low latitude females, since the probability of extended survival is extremely low. Lord (1960) suggested that greater litter size in northern environments simply compensates for higher winter mortality. However, I did not observe either greater litter size in the northern environment or higher overwinter mortality. In fact the observed pattern of overwinter survival of muskrats in this study was higher survival in the northern environment, which would reject Lord's hypothesis.

One major assumption of life history theory is that increased reproductive effort results in lower female survival. The effort devoted to reproduction varied between the two populations. Effort per litter was greater at Old Crow than on Tiny Marsh. Adult survival was also greater on Old Crow flats, thus apparently rejecting the life history assumption that increased reproductive effort results in lower adult survival.

However, although litter size is usually used as the currency of reproductive effort, annual production should be used in polyestrous species such as the muskrat. Annual reproductive effort was greater in the southern population where 2-3 litters a year were produced and survival was significantly lower, thus supporting the assumption of a trade off between reproduction and survival.

Covariation in the life-history traits found in this study best supported the r-K model of selection. Lower reproductive effort at the northern site, accompanied with higher juvenile survival are opposite to the predictions of the bet-hedging model of life-history selection. In the more stable and predictable northern environment, muskrats exhibited conservative reproduction indicating that selection favours an energetically efficient life-history strategy. In more variable southern populations of muskrats, productivity is favoured by selection.

CHAPTER 3: GEOGRAPHIC VARIATION IN MUSKRAT REPRODUCTION: A LITERATURE REVIEW

Introduction

A number of interspecific analyses of mammalian life histories indicate that body size accounts for most of the covariation in life-history traits (Millar 1977, Tuomi 1980, Eisenberg 1981, Stearns 1983). For example, Armitage (1981) found offspring weight at weaning to be directly related to female weight. Similarly, litter size in small mammals was positively correlated with body size (Tuomi 1980). However, comparisons of this type are confounded by phylogeny and do not account for the effects of environmental influences. In intraspecific comparisons of populations, phylogenetic influences are considered less important (Dobson and Murie 1987) than in interspecific studies. Dobson and Kjelgaard (1985) considered food resources to be responsible for variable life histories among conspecific populations of Columbian ground squirrels (Spermophilus columbianus).

The objective of this chapter is to examine geographic trends in muskrat (Ondatra zibethicus) reproduction using data obtained from the literature. The analysis is designed to separate the effects of different environmental variables in the covariation of muskrat life history traits.

Methods

Life-history traits for 42 North American populations of muskrats were obtained from the literature (Appendix 1). European populations were not included since Danell (1978) observed trends in litter size which are opposite to those suspected in North America. Size and number of litters, and body weight, were recorded when available.

Environmental parameters used in the analysis were habitat type (marsh, pond/lake, or river), latitude, mean annual precipitation, and mean July temperature. Habitat types were defined on the basis of the dominant vegetation and drainage. Marsh habitats are dominated by emergent vegetation such as cattail (_Typha_ spp.) and bulrush (_Scirpus_ spp.), whereas pond/lake habitats are dominated by submergent vegetation. Precipitation and temperature values were derived from climatic maps (Espenshade and Morrison 1978). These climatic variables were assigned different class designations based upon the range presented on the maps (Table 3.1), since precise values could not be obtained for all sites. Latitude was used as an index of growing season length since it is a measure of season length (Pianka 1976), independent of other climatic parameters.

Interrelationships between different characteristics were analyzed by correlation and regression techniques. Regression residuals were used to remove the effect of one of two interacting parameters on a third variable

Table 3.1: Climatic categories assigned for temperature and precipitation.

Temperature: °C	
Class 1	-1 to 10
Class 2	10 to 21
Class 3	21 to 32
Class 4	over 32
Precipitation: cm	
Class 1	under 25 cm
Class 2	25 to 50 cm
Class 3	50 to 100 cm
Class 4	150 to 200 cm
Class 5	over 200 cm

(Atchley et al 1976).

Results

Latitude was significantly correlated with litter size (Figure 3.1, $p=0.012$, $R^2=0.15$, $n=39$), and inversely correlated with number of litters (Figure 3.2, $p=0.05$, $R^2=0.17$, $n=36$). A 2nd order polynomial regression did not explain significantly more of the variation about the regression line in either case (Comparison of correlation coefficients: $Z=1.299$ and $Z=0.574$ respectively; $0.25>P>0.1$; Zar 1984). However, analysis of subsets of the data indicated litter size and number of litters were asymptotic above 45° latitude (Figure 3.3, 3.4). The slope of the lines above 45° were not significantly different from the null hypothesis of $b=0$ for litter size ($t=-1.99$, $p=0.082$) or number of litters ($t=-0.91$, $p=0.389$). Number of litters was significantly correlated with litter size (Figure 3.5, $p=0.01$, $R^2=0.18$, $n=35$). There was no significant correlation between body weight and litter size (Figure 3.6, $p=0.364$, $R^2=0.24$, $n=16$) or between body weight and number of litters (Figure 3.7, $p=0.331$, $R^2=0.26$, $n=16$).

Temperature and precipitation were significantly correlated with litter size and the number of litters (Table 3.2). However, both climatic variables were also correlated with latitude (Table 3.3). When latitude was held constant, the effects of temperature and

Figure 3.1: Regression of muskrat litter size on latitude ($y=3.18 + 0.06x$).

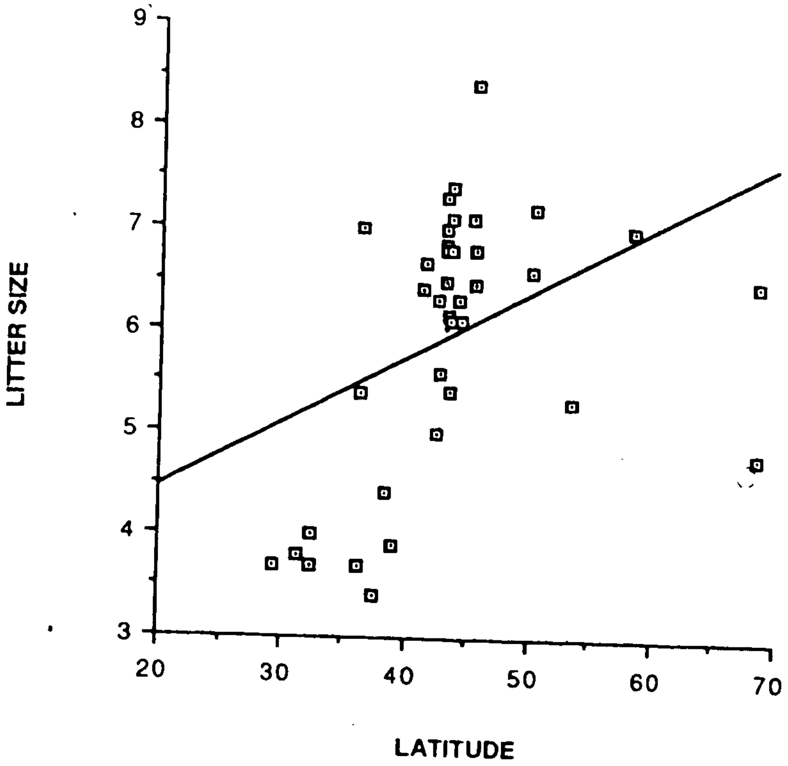
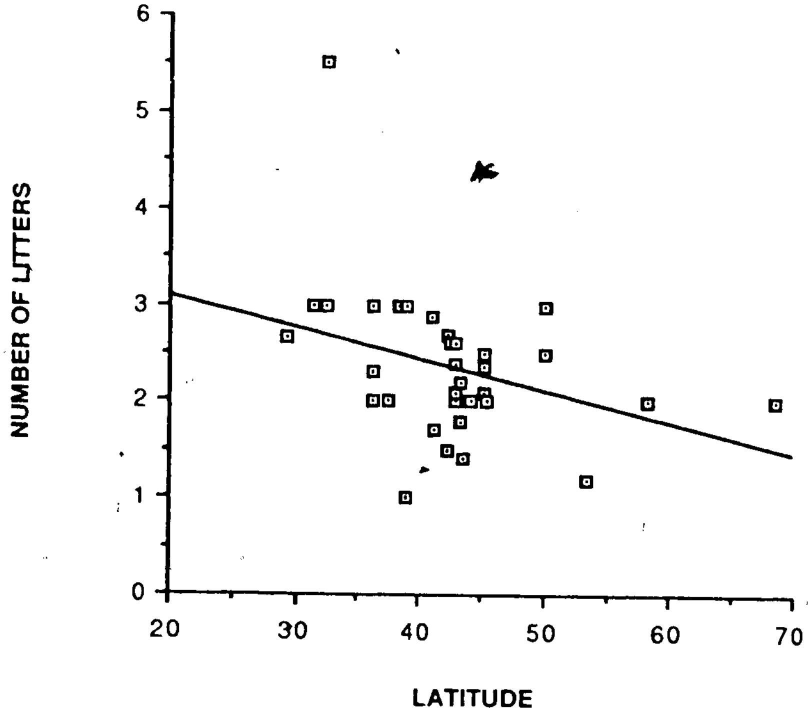

LITTER SIZE
9
8
7
6
5
4
3
20
30
40
50
60
70
LATITUDE

Figure 3.2: Regression of number of litters per reproductive season on latitude ($y=3.76 - 0.03x$).



NUMBER OF LITTERS
0
1
2
3
4
5
6
20
30
40
50
60
70
LATITUDE

Figure 3.3: Regression of muskrat litter size on latitude. Data has been partitioned at 45° of latitude to indicate the asyptotic nature of the relationship (A: $y=-3.51+0.23x$; B: $y=9.93-0.06x$)

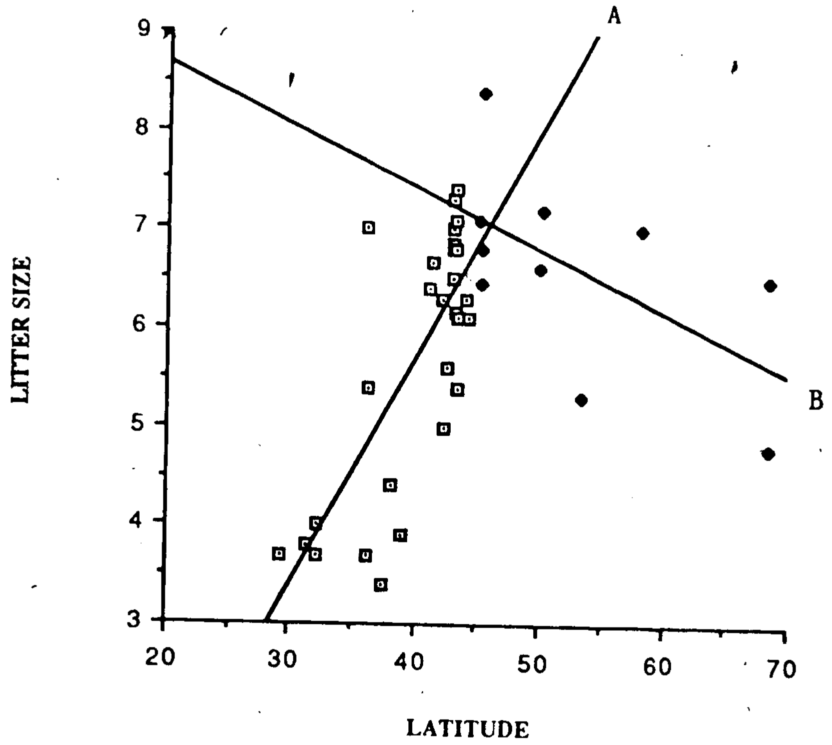

A
B
9
8
7
6
5
4
3
LITTER SIZE
20
30
40
50
60
70
LATITUDE

Figure 3.4: Regression of number of litters per reproductive season on latitude. Data has been partitioned at 45° of latitude (A: y=6.33-0.10; B:y=3.0-0.02)

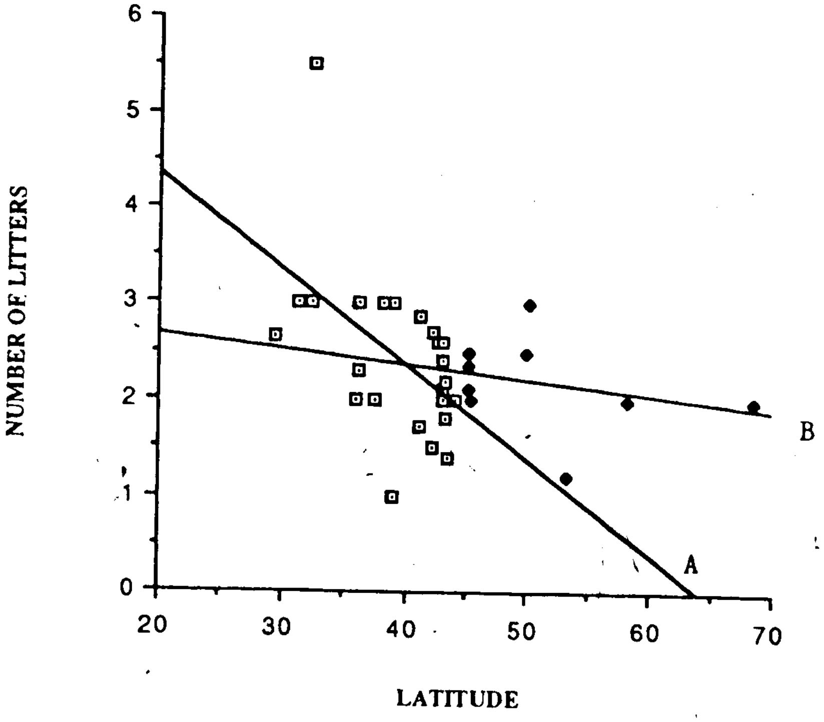

NUMBER OF LITTERS
6
5
4
3
2
1
0
20
30
40
50
60
70
LATITUDE
A
B

Figure 3.5: Regression of litter size on the number of litters per year by muskrat populations over a latitudinal gradient (y=3.75-0.24x)

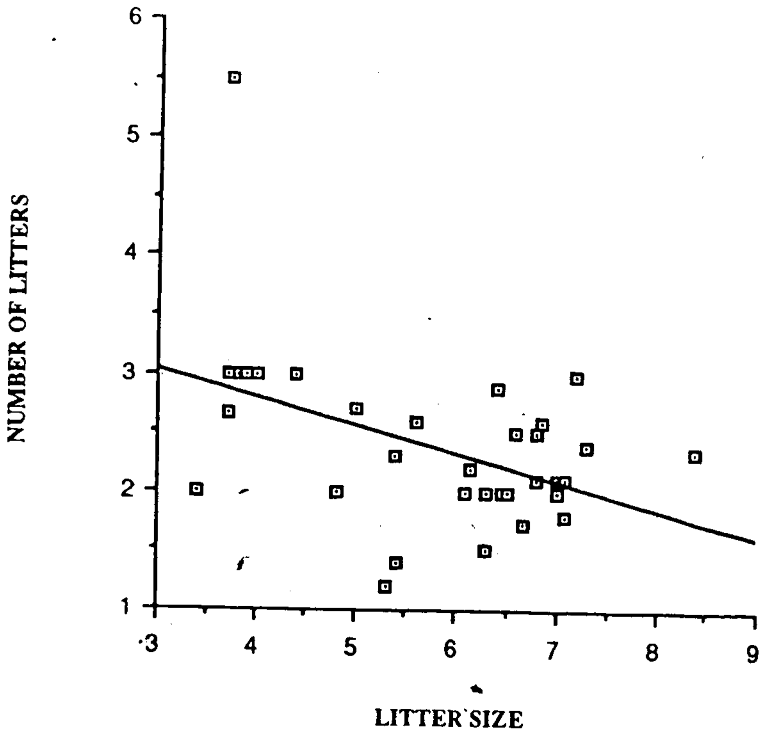
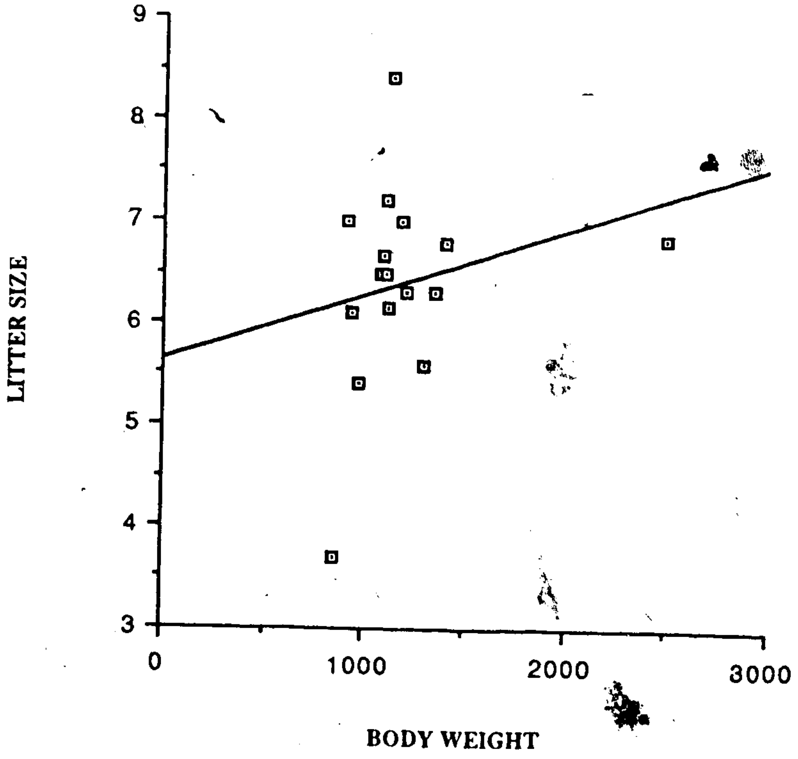

NUMBER OF LITTERS
6
5
4
3
2
1
3
4
5
6
7
8
9
LITTER SIZE

Figure 3.6: Regression of litter size on body weight.



9
8
7
6
5
4
3
0
1000
2000
3000
LITTER SIZE
BODY WEIGHT

Figure 3.7: Regression of number of litters produced per season on body weight.

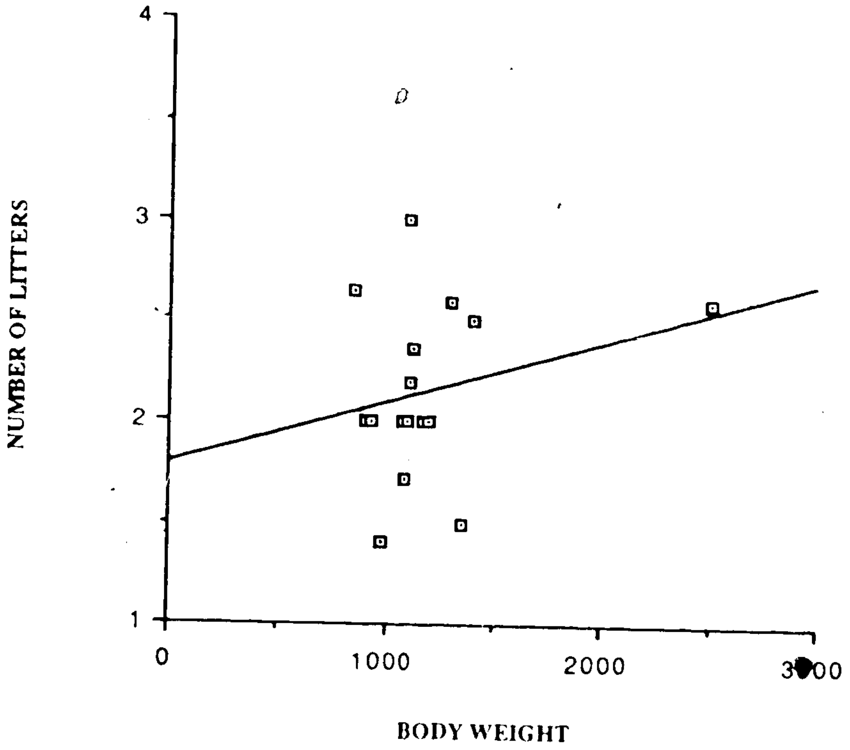

4
3
2
1
0
1000
2000
3000
NUMBER OF LITTERS
BODY WEIGHT

Table 3.2: Correlation coefficients of climatic variables with litter size and number of litters in muskrats.

	LITTER SIZE			NUMBER OF LITTERS		
	N	r	p	N	r	p
TEMPERATURE	36	-0.32	0.06	36	0.32	0.05
PRECIPITATION	36	-0.50	0.002	36	0.36	0.03
LATITUDE	39	0.40	0.012	36	- 0.32	0.05

Table 3.3: Correlation matrix indicating the intercorrelations of climatic variables (n= 38).

	Latitude	Temperature
Temperature	-0.901	---
Precipitation	-0.725	0.627

* all correlation coefficients are significant $p<0.001$.

precipitation on litter size were no longer significant (Temp:$p>0.25$, $R^2=0.016$; Precip. $p>0.25$, $R^2=0.24$). A one-way analysis of variance with each habitat type as a treatment indicated habitat type had no statistically significant effect upon litter size or number of litters ($F=2.00$, $P=0.157$).

Discussion

The observed trend in litter size and number of litters over the muskrat's geographic range support Spencer and Steinhoff's (1968) hypothesis of litter size variation. They argued that shorter growing seasons at higher latitudes would result in fewer larger litters in northern environments. That relationship however, is not supported by my findings in Chapter 2 where, though number of litters was lower at high latitude as predicted, litter size was not significantly different between the northern and southern populations. As well, there are indications that litter size may decrease or reach an asymptote at high latitudes (above 45°).

Interspecific studies of mammalian reproduction indicate that body size is a primary determinant of reproductive characteristics (Armitage 1981; Swihart 1984). Tuomi (1980) found that litter size and body weight were positively correlated in small mammals (less than 1kg). However, neither litter size, or the number of litters produced per year in muskrat populations were correlated with body weight in this review. The lack of a general relationship of reproductive characteristics in muskrats with body size is consistent with the findings of Krohne (1981) in a study of Microtus californicus. According to Stearns (1980), intraspecific comparisons such as this study and Krohnes', will not detect first-order (eg:body size) life-history trends exhibited in broad scale (mouse to elephant) interspecific studies due to the limited range (+/-300g in this study) in body size of an intraspecific study. Life-history strategies exhibited at the intraspecific level of study arise from interpopulation variation and are expected to have an ecological basis. Dobson and Kjelgaard (1985) found that, as weight increased, age at maturity decreased and reproductive effort increased in different populations of Columbian ground squirrels. This is opposite to the interspecific results found in ground-dwelling sciurids (Armitage 1981).

Litter size increased, and the number of litters per year decreased in muskrat populations as the length of growing season shortened. Swihart (1984) found growing season length to be an important second-order factor in determining reproductive characteristics of lagomorph species. Similarly, Spencer and Steinhoff (1968) argued that growing season length was a primary determinant of litter size variation in Peromyscus. However, since the regression of size and number of litters on latitude explains only 15 and 17 percent of the variation about the regression line respectively, other factors such as resource quality, or environmental predictability/variability may also influence reproductive output. Lackey (1976) found that in an unpredictable environment, where adult survival was low, increased litter size and number of litters were observed for Peromyscus leucopus. In chapter one, I demonstrated that climatic predictability and variability varied between northern and southern study areas. Therefore, variation about the litter size-latitude regression may be explained by the stability/predictability of forage availability in the habitat in which the muskrats were studied or by the quality and abundance of the forage (Errington et al. 1963).

Boyce (1979) suggested that the observed geographic variation in muskrat litter size and number of litters is a result of the pattern of juvenile survivorship and winter mortality. He assumed that northern populations of muskrats experienced higher overwinter mortality. Selection favoured those individuals which allocated their resources to reproduction and the production of large litters. However, Boyce (1979) did not test the assumption of higher winter mortality in northern muskrats. As indicated in chapter two of this study, overwinter mortality was significantly lower in the northern population than in the southern population. Therefore, Boyce's argument can be rejected as an explanation for the pattern of geographic variation in muskrat litter size and number.

Interspecific patterns of allometric scaling of reproductive characteristics were not found in a geographic comparison of muskrat populations. The primary factor identified as a determinant of litter size and number in muskrats was growing season length, as represented by latitude, thus supporting the hypothesis of Spencer and Steinhoff (1968).

GENERAL DISCUSSION

Life-history comparisons at the interspecific level are confounded by phylogeny and body size differences between species (Dobson and Murie 1987). Although the value of interspecific studies cannot be questionned, caution must be taken when interspecific patterns are applied to intraspecific comparisons. Interspecific studies of life-history strategies, such as those by Armitage (1981) and Tuomi (1980) indicate that body size is a primary determinant of litter size and reproduction in mammals. However intraspecific studies, which consider a narrower range of body sizes, find body size to be a poor predictor of life history patterns (Dobson and Murie 1987). Life-history strategies observed at the intraspecific level may be largely responses to environmental factors (Caswell 1983) such as food resource abundance (Dobson and Kjelgaard 1985), and climatic factors (Spencer and Steinhoff 1968; Swihart 1984; this study). In interspecific studies, environmental factors have been implicated as affecting life history patterns (Tuomi 1980), and may be responsible for some of the variation around the major factor, body size. Therefore, comparisons of life-history strategies, at both the intraspecific and interspecific levels, requires knowledge of the environmental factors which influence, directly or indirectly, life-history traits.

Although present life-history models like r-K and bet-hedging assume that interpopulation differences in life-history strategies have a genetic basis, the violation of this assumption does not detract from the use of these models as predictors of expected life history strategies given knowledge of a specific environment. Only when an evolutionary argument is made for the development of a life history strategy is knowledge of the genetic basis necessary to test life history models. In this study I found the r-K model to be a good predictor of the life history patterns observed between northern and southern populations of muskrats.

The basic concept underlying the r-K model is selection for efficiency in populations experiencing high densities and resource shortages and selection for productivity in resource-abundant environments (MacArthur and Wilson 1967). MacArthur and Wilson (1967) assumed that in seasonal climates, overwinter survivors will recolonize a resource-abundant environment each year where density-dependent effects are low, therefore r-selection will operate. However, this will occur only when overwinter mortality in more seasonal (eg:northern) areas is higher than in southern areas. If overwinter survival is greater in a northern location with a stable or predictable climate when compared to a southern population, as in muskrats, selection should favour efficiency (K-selection) of resource conversion.

Therefore, northern populations, should exhibit the K-characteristics of slow growth and conservative reproduction as seen in this study. A similar argument can be made for Zammuto and Millar's (1985a) altitudinal study of Columbian ground-squirrel life-history stategies.

In conclusion, life-history patterns in muskrats were associated with the predictability and variability of climatic and environmental factors of relevance to muskrat populations. Precipitation and growing season length were correlated with muskrat reproduction over a range of latitudes. Of the life-history models assessed, the r-K model best explained the pattern of muskrat life-history strategies.

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APPENDIX

AUTHOR	LATITUDE	LITTER SIZE	# OF LITTERS	HABITAT	PRECIPITATION	TEMPERATURE	BODY WEIGHT
1	29.3	3.7	2.65	1	5	4	850
2	31.3	3.8	3	1	5	5	
3	32.3	4	3	0	4	5	
4	32.3	3.7	5.5	1	5	5	
5	36.08	7	2	1	2	4	1170.3
6	36.15	3.7	3	1	4	5	
7	36.15	5.38	2.3	3	4	5	
8	37.42	3.4	2	0	3	4	
9	38.2	4.4	3	1	4	4	
10	39	3.9	3	1	4	4	
11	39		1	2	4	4	
12	40			2	3	4	1224.69
13	41.1	6.4	2.87	1	4	4	
14	41.25	6.66	1.72	1	3	4	1088.62
15	42.25	6.3	1.5	2	4	4	1350
16	42.3	5	2.7	1	4	4	
17	42.55	5.6	2.6	1	4	4	1289.9
18	43	7	2.1	1	3	4	
19	43	6.85	2.6	2	2	4	2500
20	43	6.5	2	2	3	4	1100
21	43	6.8	2.1	1	3	4	
22	43	7.3		0			
23	43	7.3	2.4	1	2	4	
24	43.26	6.15	2.2	1	3	4	1108
25	43.3	7.1	1.8	3	3	4	
26	43.3	7.4		0			
27	43.3	6.8		0	3	4	
28	43.46	5.4	1.4	4	4	3	976
29	43.48			0			1057.9
30	43.5	6.1		0			
31	44	6.3	2	1	3	4	1200
32	44.24	6.1	2	1	3	4	926.1
33	45.11	7.1	2.1	1	4	4	
34	45.3	8.4	2.36	1	3	3	1130
35	45.3	6.8	2.5	1	4	3	1400
36	45.38	6.45	2	3	3	4	
37	50	6.6	2.5	1	4	3	
38	50.11	7.2	3	1	3	3	1095
39	53.3	5.3	1.2	1	3	3	
40	58.2	7	2	2	2	3	910
41	68.44	4.8	2	2	1	1	
42	68.44	6.5	2	2	1	1	1079.6

APPENDIX 1
(LEGEND TO AUTHOR CODES)

1. Svihla and Svihla, 1931
2. Arthur, 1931
3. Beshears and Haugen, 1953
4. O'Neil, 1949
5. Sooter, 1946
6. Wilson, 1954
7. Schacher and Pelton, 1975
8. Arata, 1959
9. Smith, 1938
10. Harris, 1952
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12. Baumgartner and Bellrose, 1943
13. Smith and Jordan, 1976
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15. Erickson, 1963
16. Chamberlain, 1951.
17. Alexander 1951, 1955
18. Errington, 1951
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22. Mathiak, 1966
23. Reeves and Williams, 1956
24. Dorney and Rusch, 1953
25. Clay and Clark, 1985
26. Beer and Truax, 1950
27. Seamans, 1941
28. Clough, 1987
29. Buss, 1941
30. Wragg, 1953
31. Proulx, 1981
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32. McCann, 1944
33. Gashweiler, 1950
34. Parker and Maxwell, 1984
35. Parker and Maxwell, 1980
36. Stewart and Bider, 1974,
37. McKay, 1976
38. Olsen, 1959
39. Mcleod, 1948