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SEASONAL DIETS OF MINK AND MARTENS: EFFECTS OF SPATIAL AND TEMPORAL CHANGES IN RESOURCE ABUNDANCE

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

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Fairbanks, Alaska

May 1996

SEASONAL DIETS OF MINK AND MARTENS: EFFECTS OF SPATIAL AND TEMPORAL CHANGES IN RESOURCE ABUNDANCE

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Abstract

Seasonal changes in food availability and feeding habits of mink (*Mustela vison*) and martens (*Martes americana*) on Chichagof Island, Southeast Alaska, were studied through the analysis of natural abundance of stable isotopes. Dependence of the two species on marine-derived nutrients, carried to the terrestrial system via the upstream migration of spawning Pacific salmon (*Onchorhynchus* sp.), was investigated. Twenty-four mink and 75 martens were live-trapped repeatedly in early summer (prior to salmon runs), early autumn (post salmon runs), late winter, and in spring (during the mating season). A blood sample was obtained from each individual. In addition, 25 mink and 165 marten carcasses were obtained from trappers during late autumn 1991 - 1994. Concurrently, prey availability was monitored, and tissues from prey were collected. The abundance of stable isotopes in prey tissues and blood samples were compared, indicating that riverine mink depended on salmon (carcasses and fry), with little seasonal or individual variation, whereas coastal mink relied on intertidal organisms in spring and summer, but fed on salmon carcasses when they became available in autumn. In addition, analysis of blood progesterone revealed that timing of reproduction in female mink appear to be shifted, so that lactation coincided with the availability of salmon carcasses. In contrast, martens showed individual variation in their diets, with some individuals feeding exclusively on terrestrial organisms, while the diets of others include salmon carcasses. Incorporation of salmon in the diet depended largely on availability of small rodents and location of the martens home range on the landscape. Although salmon carcasses are not a preferred food item for martens, they act as a suitable alternative to maintain body condition and allow successful reproduction even in years when preferred food is not readily available.

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Preface

Spawning Pacific salmon (*Onchorhynchus* sp.) carry marine-derived nutrients into streams and rivers and fertilize those systems through decomposition and the effects of predation on their carcasses (Richey et al., 1975; Cederholm et al., 1989; Kline et al., 1989; Kline et al., 1993; Piorkowski, 1995). The annual arrival of salmon into streams in Southeast Alaska creates a seasonal pulse in food availability for mink (*Mustela vison*) and martens (*Martes americana*). For example, an annual average of 600,000 adult spawning pink (*O. gorbuscha*), chum (*O. keta*), and coho salmon (*O. kisutch*), enter the Kadashan River, on Chichagof Island, Southeast Alaska, where I conducted my research (M. D. Bryant, Pers. Comm.). Optimal foraging theory predicts that animals will select foods that result in energy returns equal to or greater than the energy expended on locating, capturing, and consuming that food (Pyke et al., 1977). Therefore, a pulse of such a readily available resource provided by carcasses of spawning Pacific salmon, is likely to influence the seasonal composition of diets of mink and martens. In this study, I investigated those changes in diets of mink and martens using stable isotope analysis.

Carbon and nitrogen are key elements in ecosystem processes, each existing in two stable isotopes $^{13}C/^{12}C$ and $^{15}N/^{14}N$ (Ehleringer and Rundel 1988). The natural abundance of the heavier stable isotopes are much lower than those of the lighter ones and are expressed (by convention) in parts per thousand (per mil) deviation (δ) from a recognized isotopic standard:

$$\delta X = (R_{sample} - R_{standard} / R_{standard}) \times 1000$$

Where $X = {}^{13}C$ or ^{15}N, and $R = {}^{13}C/{}^{12}C$ or $^{15}N/^{14}N$. Values of ^{13}C are expressed relative to PDB limestone, and ^{15}N relative to atmospheric N_2 (Ehleringer and Rundel 1988).

Recent investigations of food webs have demonstrated that stable isotopes of carbon and nitrogen are correlated with trophic level and can provide dietary information when tissues of consumer and food are compared (i.e., fractionation values) (Fry and Sherr, 1988; Gearing, 1991; Hobson, 1991; Schell et al., 1988; Schoeninger and DeNiro, 1984). The stable isotopic composition of the whole body of animals appears to be enriched in ^{13}C relative to the diet by about 1‰ and ^{15}N by about 3-4‰ (Hobson, 1991). Moreover, $\delta^{13}C$ and $\delta^{15}N$ in marine-derived nutrients are more enriched than those in terrestrial or freshwater-derived nutrients (Bunn et al., 1989; Kline et al., 1989), producing a natural marker to the incorporation of marine nutrients into the terrestrial systems (Kline et al., 1989). Further, this technique can utilize blood cells as samples, which allows multiple sampling of the same individual, and creates the possibility of monitoring dietary changes of individuals through time (Hobson, 1991).

Generalist predators tend to switch to alternative prey when the relative abundance of their primary prey changes (Taylor, 1984). Such short-term functional response can affect the predators reproductive output, and reduce the long-term numerical decline in predator populations that usually follows shortages in availability of preferred-food (Taylor, 1984). Reproductive success of females in solitary species is dependent on the amount of resources they are able to allocate to reproduction. This includes resource allocation to production of young as well as raising the young to age of dispersal (Horn and Rubenstein, 1984; Sandell, 1989). The dramatic seasonality of food availability produced by carcasses of spawning Pacific salmon to mink and martens, is likely to determine several aspects of their reproductive biology. In this study, I investigated timing of reproduction of mink, and reproductive performance of martens in relation to seasonal changes in their diet composition.

This thesis has been written in the form of manuscripts for publication, and therefore each chapter is an independent unit. This results in repetition in the description of the study area and some of the methods in the different chapters.

Chapter 1 describes the role of spawning salmon in seasonal changes in diets of coastal and riverine mink in Southeast Alaska. Chapter 2 explores timing of reproduction in wild mink in relation to timing of upstream migration of spawning salmon. Chapter 3 describes seasonal and annual changes in diets of martens in relation to food availability, and Chapter 4 explores reproductive performance of martens in relation to their diet composition. Each chapter has been submitted to a suitable technical journal, and therefore the format of the chapters is not uniform.

Although this work is my creation, I could not have done it without the collaboration of many individuals and agencies. Dr. D. R. Klein and Dr. T. A. Hanley initiated this project. Mr. R. W. Flynn (M. Sc.) shared and exchanged valuable data on martens. Dr. D. M. Schell supplied the laboratory for the stable isotope analyses and valuable discussions on the technique and the meaning of the results. Drs. J. E. Blake, R. T. Bowyer, and M. W. Oswood provided useful advise throughout the project as well as valuable comments on earlier drafts of the manuscripts. Funding for the project was provided by the USDA Forest Service, Pacific Northwest Station - Juneau, the Alaska Cooperative Fish and Wildlife Research Unit, and the Water Research Center, University of Alaska Fairbanks. Many volunteers, technicians, and friends have helped in different stages of the data gathering and processing. The contribution of these individuals, and agencies is acknowledged in three forms: co-authorship on the different manuscripts following guidelines of the Wildlife Society, listing in acknowledgments in each chapter, and more personally in the following acknowledgment section.

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Acknowledgments

In undertaking this process I have unintentionally followed the advice in the address of Dr. Robert May to the Forth International Behavioral Ecology Congress. He called us to integrate the study of individuals with the study of populations and ecosystem processes. Looking at this product I now realized that I have done just so. But I could not have done it alone. I had to learn new concepts, new methodologies, and new approaches. I needed guiding hands, challenging minds, and supporting souls to light the way. I owe thanks to many who have done that for me. Dr. Dave Klein of the Alaska Cooperative Fish and Wildlife research Unit, and Dr. Tom Hanley from the USDA - Forest Service, Pacific Northwest Station (USFS), initiated this study and offered it to me. Funding for the project was provided by the Alaska Dept. of Fish and Game; USDA Forest Service, Pacific Northwest Station - Juneau; Alaska Cooperative Fish and Wildlife Research Unit Water Research Center, and the Graduate School of the University of Alaska Fairbanks.

Dr. Dave Klein never lost his confidence in me even during times that I nearly lost it myself. All my committee members Drs. John Blake, Terry Bowyer, Tom Hanley, Mark Oswood, and Don Schell challenged me as a scientist, and field biologist. They also generously offered their assistance, and helpful comments whenever needed. Rod Flynn of the Alaska Dept. of Fish and Game (ADFG) became the living example of productive collaboration and a good friend as well. I've learned a lot from other faculty members who were always available to answer questions and engage in long discussions. Drs. Ron Barry, Pham Quang, Eric Rexstad, and Dana Thomas, assisted in the statistical analyses. Many graduate students inspired me, especially Karen Gerhart, Jay Gulledge, Brian Lance, Ellen Weintraub Lance, Steve Matsuoka, Doreen Parker, Dave Person, Bob Piorkowski, Eric Post, and Mitch Wagener. Norma Mosso had been more than helpful in solving the many financial tangles that are usually part of such a complicated endeavor. There are not enough words to thank ADFG technicians

complicated endeavor. There are not enough words to thank ADFG technicians Gail Blundell and Tom Schumacher, and my field assistants Molly Kemp, Steve Lewis, Nick Olmstad, Michael Rosing, Jeff Simonson, Bjorn Wissing, and Colleen Zank, for the long hours of hard work they have put into this project. I would still be struggling with obtaining blood samples from mink and martens if it wasn't for Chris Terzi's patience and craftsmanship in teaching me the procedures. My thanks are extended to all the students who assisted me in the lab, and to Norma Haubenstock and Bruce Barnette who performed the analyses of stable isotope ratios. The residents of Tenakee Springs opened their hearts and homes to me on my infrequent visits to "civilization". I have to admit that there is hardly anything better in the world than a good long soak in their wonderful spring. My family followed my adventures with pride and encouragement. And finally I need to thank all my many wonderful friends in Alaska, and elsewhere for sharing with me this period of my life. Thank you all!

Chapter 1 – Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon.

Merav Ben-David,Thomas A. Hanley, David R. Klein, and Donald M. Schell.

Summary

Feeding niches of riverine and coastal mink (*Mustela vison*) in Southeast Alaska, during spring and summer, differ in pery abundance, and medium density and viscosity, and so requires specialization in foraging strategies. In autumn, however, spawning Pacific salmon (*Oncorhynchus* sp.) carry marine-derived nutrients into streams and rivers along the Pacific Northwest coast, and create a pulse of food availability for mink. We studied seasonal changes in the diet of individual mink on Chichagof Island, Southeast Alaska, using analysis of stable isotopes (^{13}C, ^{15}N). Given the different foraging constraints mink encounter in coastal and riverine environments, we hypothesized that their diets, and therefore stable isotope ratios, would significantly differ during periods in which salmon were absent. We also hypothesized that salmon carcasses will constitute a large portion of the diet of both coastal and riverine mink during the salmon spawning season, and therefore their stable isotope ratios would not differ significantly, at that time. We live captured 24 mink repeatedly, from mid-March to late-November in 1992 and 1993. We also obtained 25 mink carcasses from trappers during late autumn in 1992 and 1993. Stable isotope analysis of clotted blood cells and muscle tissue were used to indicate diets for individual mink. These isotopic values were then compared with stable isotope ratios of prey collected in spring, summer, and autumn 1992 and 1993, using a multi-source mixing model. Our results indicare that riverine mink relied heavily on salmon carcasses in summer and autumn, and on small salmonids in spring, thereby obtaining marine-derived nutrients in this season as well. Mink living in coastal environments make use of several intertidal organisms in all seasons, but mainly

consume intertidal fish in spring and summer. In autumn, salmon carcasses were incorporated into diets of coastal mink. Thus, although diets of coastal and riverine mink, in Southeast Alaska, differed significantly in spring and summer, they contained large proportions of salmon carcasses in autumn. This outcome suggests that salmon is an important food resource for both riverine and coastal mink.

Introduction

Previous investigators described two groups of mink (*Mustela vison*) in the Pacific Northwest: mink living along the coast, and mink inhabiting inland riparian habitats (Harbo 1958; Hatler, 1976; Johnson, 1985). Although mink forage under water and hunt while diving, the relatively small surface of their feet, their anterior propulsion, and their low storage capacity for O_2 make the mink an inefficient swimmer compared with other diving mammals (Dunstone and O'Connor 1979*a*; 1979*b*; Stephenson et al. 1988; Williams 1983; 1989; Williams and Kooyman 1985). Those limitations on swimming and diving efficiency affect the duration and depth of dives especially in sea water, which has higher density and viscosity than does fresh water (Vogel 1981). Although diving in riverine environments poses less difficulty than diving in coastal environments, the intertidal zone in Southeast Alaska offers high availability of prey species and prey biomass to the foraging mink (Feder and Jewett, 1986; Johnson, 1985; O'Clair and Zimmerman, 1986; Rogers et al., 1986). Many species of prey occur in shallow waters and are slow moving (Feder and Jewett, 1986; Johnson, 1985; O'Clair and Zimmerman, 1986; Rogers et al., 1986). Additionally, intertidal beaches and shallow rock-pools provide extensive feeding sites for mink during low tides (Ben-David et al., 1996; Hatler, 1976; Johnson, 1985). In comparison, the rivers in Southeast Alaska are fast flowing throughout the year, and their prey is limited to few species of fast moving fish, mostly juvenile salmonids (Bryant, 1984; Crone and Bond 1976; Murphy et al., 1988). Therefore, the feeding niches of riverine and coastal mink in Southeast Alaska differ substantially. This, in turn, can lead to specialization in foraging strategies and fidelity to a feeding niche by the foraging mink.

From late summer through autumn, spawning Pacific salmon (*Oncorhynchus* sp.) carry marine-derived nutrients into lakes and rivers along the Pacific Northwest and subsequently fertilize those systems through decomposition and consumption by predators (Cederholm et al., 1989; Kline et al., 1989; Kline et al.,

1993; Piorkowski, 1995; Richey et al., 1975). Cederholm et al. (1989) reported that <4% of all salmon carcasses were washed down stream, and most were retained within the riparian zone. Several studies in Idaho (Melquist et al., 1981) and on the Olympic Peninsula, Washington (Cederholm et al., 1989) indicated that during the spawning season mink relied heavily on salmon carcasses for food. Therefore, the arrival of salmon into streams in Southeast Alaska creates a pulse in food availability for mink living in riparian environments.

Although investigators agreed on the importance of intertidal organisms in the diets of coastal mink, they differed in opinion as to use of salmon by these mustelids (Harbo 1958; Hatler, 1976; Johnson, 1985). Although the cost of locating salmon carcasses is presumably higher for coastal mink than for riverine mink, the high energy and protein returns from salmon could out-weigh these costs. Harbo (1958) suggested that coastal mink would move upstream during the spawning season to take advantage of this resource.

We investigated seasonal changes in diet of individual mink on Chichagof Island, Southeast Alaska, using analysis of stable isotope ratios (^{13}C, ^{15}N). Analysis of food webs using natural abundance of stable isotope ratios compares the ^{13}C and ^{15}N values of predator and prey tissues. Values of ^{13}C differ between terrestrial and marine food sources, due to differential assimilation of ^{13}C by primary producers in these ecosystems, and enablethe tracing of food webs (Ehleringer and Rundel, 1988; Fry and Sherr, 1988; Tieszen and Button, 1988). The values of ^{15}N increase with consumption and, therefore, reflect both diet and trophic level (DeNiro and Epstein, 1981). The specific combination of values of ^{13}C and ^{15}N result from the dietary interaction of species or individuals (Ambrose and DeNiro, 1986; Gearing, 1991; Hobson, 1991; Schell et al., 1988; Schoninger and DeNiro, 1984). Given the different foraging constraints mink encounter in coastal and riverine environments, we hypothesized that their diets, and therefore stable isotope ratios, would differ significantly during periods in which salmon were absent. We also hypothesized that both coastal and riverine mink would consume

salmon carcasses to a large extent during the spawning season, and therefore their stable isotope ratios would not differ significantly at that time.

Methods

Study area

The study area was located on Chichagof Island in Southeast Alaska, USA (Tenakee Springs at 57° 52' N 135° 18' W; Figure 1). The region has a maritime climate; summers are cool and wet and winters are characterized by deep snow (2,360 mm annual precipitation). The snow-free period extends from early May to early November at lower elevations. Vegetation at higher elevations is typified by alpine tundra, and at lower elevations by coastal, old-growth forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with well-developed understory (mainly *Oplopanax horridus*, *Vaccinium* sp., *Menziesia ferruginea*, and *Rubus* sp.). The study area encompassed six streams that supported an annual run of three species of spawning Pacific salmon: pink salmon (*Oncorhynchus gorbuscha*), chum salmon (*O. keta*), and coho salmon (*O. kisutch*). Pink and chum salmon migrated upstream and spawn from early July to late September (Heard, 1991; Salo, 1991), whereas coho salmon entered the streams from early September to late November (Sandercock, 1991). Adult Dolly varden (*Salvelinus malma*), and adult steelhead trout (*O. gairdnerii*) entered the stream in late May. Adult Dolly varden remained in the streams until the end of November. Pink and chum salmon hatchlings emerged from the gravel in late March, and migrated down stream to the sea by early June (Murphy et al., 1988; Table 1). Juvenile coho salmon emerged from the gravel from early May to mid-July and remain in freshwater for up to 2 years (Crone and Bond 1976; Bryant, 1984; Table 1). Similarly, juvenile Dolly varden and steelhead remain in fresh-water ≤ 2 years (Armstrong, 1970; Table 1). Two additional fish species are common in the fresh water systems of the island: Coast-range sculpin (*Cottus aleutcus*), and Three-spined stickleback (*Gasterosteus aculeatus*) (Table 1). The intertidal zone supports a large variety of intertidal fish (Table 2), and intertidal invertebrates (Table 3). The nonvolant mammalian fauna of the island includes: Keen's deer-mice (*Peromyscus keeni;* also known as *P. sitkensis* [see Hogan et al.,

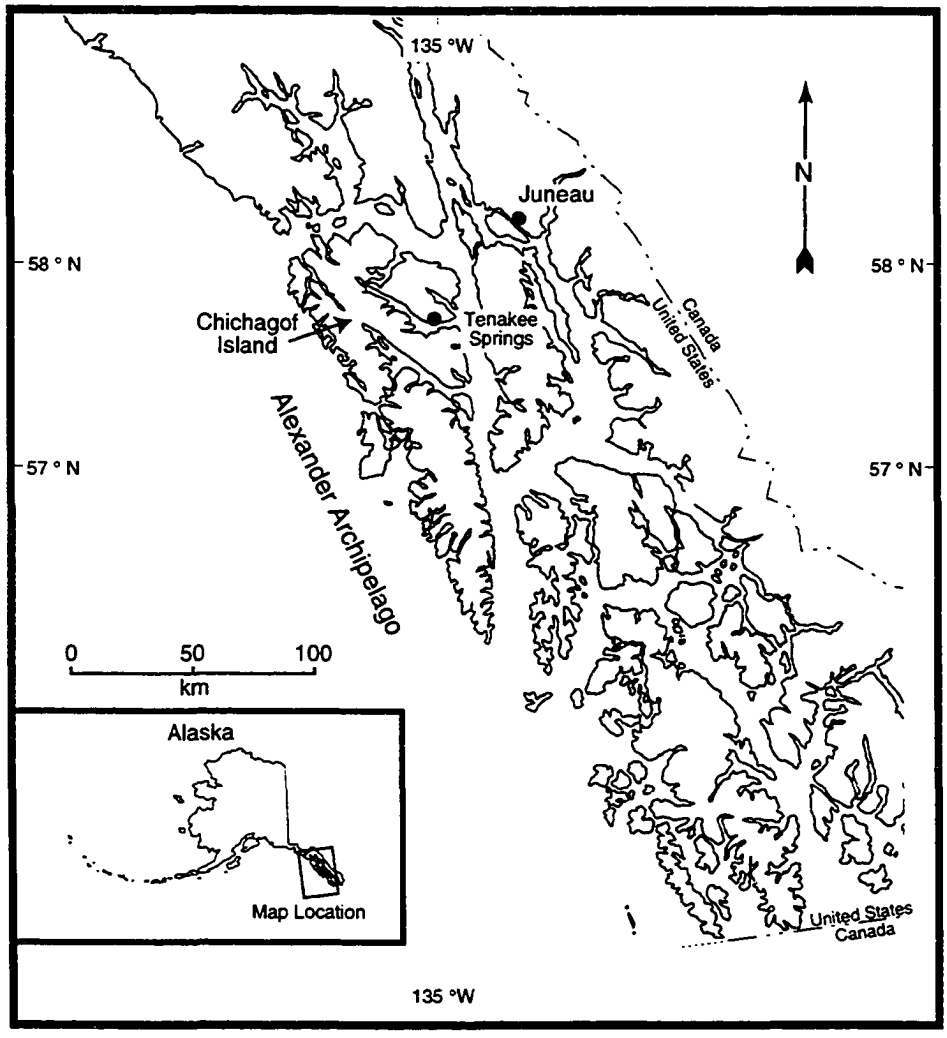

Figure 1. Location of study area (shaded) on Chichagof Island, Southeast Alaska, USA.

1993]), long-tailed voles (*Microtus longicaudas*), tundra voles (*Microtus oecnomus*), red squirrels (*Tamiasciurus hudsonicus*), common shrews (*Sorex cinereus*), Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), martens (*Martes americana*), river-otters (*Lutra canadensis*), and brown bears (*Ursus arctos*). Song birds such as dark-eye junco (*Junco hyemalis*), robin (*Turdus migratorius*), varied thrush (*Ixoreus naevius*), hermit thrush (*Catharus guttatus*), and Swainson's thrush (*Catharus ustulatus*), arrive on the island for the breeding season in early May and depart during the month of September.

Sampling mink

We trapped mink during 3 seasons: summer (late May to early August), autumn (early October to late-November), and spring (mid-March to early May) in 1992 and 1993. Twenty-four adult mink (10 females and 14 males; Table 4) were live-captured repeatedly using Tomahawk live traps (model 203; Tomahawk Live Trap Co., Tomahawk, WI). After immobilization with an injection of ketamine hydrochloride (15 mg/kg body weight; Aveco, Fort Dodge, IW), each individual was measured, weighed, and marked subcutaneously with a passive integrated transponder (PIT) tag (Biosonics, Seattle, Washington). Age was estimated for each individual by noting tooth replacement and wear, by measuring minimum width between the temporal muscles, and noting the size of the sagital crest (Magoun et al., 1988). A blood sample of 2 cc was drawn from the jugular vein once a season from each individual mink, and stored in a glass or plastic vial. Animals were released at the site of capture. Blood was spun at 3,000 rpm for 5 min. using a manual centrifuge within 2 hours after collection, and serum was siphoned into a separate vial. Both serum and samples of clotted blood-cells were frozen (-18°c) until analysis. All methods used in this study were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks.

Additionally, 25 carcasses of mink were obtained from trappers in late autumn of 1992 and 1993. Date and location of capture were recorded for each mink carcass. We determined age, sex, body measurements, and weight of each carcass before a muscle sample of 5 to 10 g was excised from the hind leg for stable isotope analysis.

Sampling prey

Seven to 13 trapping grids, each containing 25 Sherman live traps in 20 by 20m arrangement, were set on 3 consecutive nights in all 3 seasons (summer, autumn, and spring). The trapping grids were set within 50 m from stream bank or mean high tide, and traps were baited with rolled oats and peanut butter. All Keen's deer mice and long-tailed voles, that we live captured, were marked with paint and released; a subsample of 2 individuals per species per grid were randomly selected and euthanized with Halothene (Halocarbon, River Edge, NJ). A muscle sample was collected from each euthenized individual for stable isotope analysis. Additional samples were obtained from rodents collected in companion studies by T. A. Hanley (USFS, Pacific Northwest Research Station), and R. A. Flynn (Alaska Department of Fish and Game). The remainder of each carcass was prepared as a museum specimen (including frozen tissues) and archived at the University of Alaska Museum.

Concurrently, at each trapping site, 5 minnow traps were set at 5-m intervals in the stream or along the coast below mean low tide. Minnow traps were baited with salmon eggs in the river and with bait herring in the intertidal zone. Fish and marine invertebrates, captured in traps, were identified to the level of genus or species (Trautman, 1973; Tables 1 - 3), counted, and a random sample of 2 individuals per species per trap was collected for stable isotope analysis. Juvenile coho salmon were assigned an age class (0+, 1+, 2+ years) according to their fork length (Murphy et al., 1988; Table 1). Similarly, for further analysis, other freshwater fish species were grouped by the same criteria of fork length adopted

Table 1. Common and scientific names, and mean weight in grams (± SE) of freshwater fish, collected on Chichagof Island, Southeast Alaska, during 1992 and 1993.

Common name	Scientific name	Summer			Autumn			Spring		
		n	Weight	SE	n	Weight	SE	n	Weight	SE
Pink salmon	*Oncorhynchus kisutch*									
Age 0+ (< 50mm)								12	0.16	0.01
Chum salmon	*Oncorhynchus kisutch*									
Age 0+ (< 50mm)								9	0.32	0.03
Coho salmon	*Oncorhynchus kisutch*									
Age 0+ (< 50mm)		13	0.4	0.07	23	0.92	0.06	3	0.61	0.22
Age 1+ (50 - 80mm)		49	2.69	0.13	33	2.82	0.26	25	2.31	0.20
Age 2+ (> 80mm)		7	6.85	1.15	19	10.01	0.86	13	7.01	1.07
Dolly varden	*Salvelinus malma*									
(< 50mm)					2	1.1	0.11			
(50 - 80mm)		13	2.99	0.33	11	1.9	0.2	5	1.90	0.26
(> 80mm)		30	11.22	1.27	19	12.82	1.64	17	10.25	1.22
Coast-range sculpin	*Cottus aleutcus*									
(50 - 80mm)		6	3.41	0.36	6	3.98	0.75	6	3.57	0.53
(> 80mm)		19	8.87	0.56	12	11.22	1.09	7	6.82	0.83
Three-spined stickleback	*Gasterosteus aculeatus*	10	1.37	0.13	10	1.38	0.17	14	1.16	0.17

Table 2. Common and scientific names, and mean weight in grams (± SE) of intertidal fish, collected on Chichagof Island, Southeast Alaska, during 1992 and 1993.

Common name	Scientific name	Summer			Autumn			Spring		
		n	Weight	SE	n	Weight	SE	n	Weight	SE
Sculpins		35	9.83	1.15	12	7.05	1.52	14	5.30	1.27
Tidepool sculpin	*Oligocottus maculosus*									
Northern sculpin	*Icelinus borealis*									
Pacific staghorn sculpin	*Leptocottus armatus*									
Gunnels		31	7.15	0.67						
Crescent Gunnel	*Pholis laeta*									
Other Fish		10	10.51	4.32	4	15.34	4.03	1	14.64	
Arctic shanty	*Stichanes punctatus*									
Searcher	*Bathymaster signatus*									
Daubed shanny	*Lumpenus maculatus*									
Black prickleback	*Xiphister atropurpureus*									
Rock prickleback	*Xiphister muscosus*									
Walleye pollock	*Theragra chaleogramma*									
Pacific sandlance	*Ammodytes hexapterus*									

Table 3. Common and scientific names, and mean weight in grams (± SE) of intertidal invertebrates, collected on Chichagof Island, Southeast Alaska, during 1992 and 1993.

Common name	Scientific name	Summer			Autumn			Spring		
		n	Weight	SE	n	Weight	SE	n	Weight	SE
Blue mussels										
Bay blue mussel	*Mylitus trossulus*									
Amphipods					19	0.22	0.03	25	0.36	0.04
Amphipod	*Anonyx sp.*									
Hermit crabs		20	0.58	0.01	22	0.69	0.14	15	0.61	0.09
Hermit crab	*Pagurus sp.*									
Crabs		19	3.90	2.35	20	0.67	0.11	5	1.66	0.46
Helmet crab	*Telmessus cheirogonous* *Hemigrapsus oregonensis* *Hemigrapsus nudus* *Pugetia gracilis*									
Shrimps		6	3.28	0.60	11	4.31	0.78	6	3.64	0.95
	Pandalus platyceros *Pandalus danae* Hippolytidae									

for juvenile coho (Table 1). Numbers of captured fish and invertebrates are presented as the total number captured per season corrected for differences in trapping efforts (i.e., divided by the total number of trap nights in each season).

In addition to the trapping grids, 10 transects, each 50-m long, were walked along the beach at low tide in each season. Additional samples of intertidal fish, crab, and blue-mussel (*Mytilus trossulus*) were collected from tidal pools for stable isotope analysis. Tissue samples from adult Dolly varden, and pink, chum, and coho salmon were obtained from individuals captured in dip-nets or from carcasses that were encountered while monitoring trap-lines for mink along streams from late May to late November 1992 and 1993. Tissue samples of mallards (*Anas platyrhynchos*), buffleheads (*Bucephala albeola*), and mergansers (*Mergus merganser*) were obtained from hunters in November.

Analysis of Stable Isotope Ratios

Tissues (clotted blood-cell, muscle samples, and whole fish and invertebrates) were kept frozen between collection and preparation for determination of stable isotope ratios. Samples were dried at 60° to 70° C for 48 hours and then ground to fine powder using a Wig-L-Bug grinder. Samples of intertidal invertebrates were than dissolved in 95% HCl solution to remove calcium carbonates and re-dried. Subsequently, a subsample of 1-1.5 mg was weighed into a miniature tin cup (4 by 6 mm) for combustion. We used a Europa C/N continuous flow mass-spectrometer to obtain the stable isotope ratios. Each sample was analyzed in duplicate and results were accepted only if the variance between duplicates did not exceed that of the peptone standard (CV = 0.1). For further analysis we determined the diet source based on the combined values of ^{13}C and ^{15}N. We used the dual-isotope, multiple-source mixing model (see chapter 3; Ben-David et al., in review), to estimate of the relative contribution of each prey to the diet of individual mink. The mixing model requires that all types of prey will be significantly different from each other in both ^{13}C and ^{15}N. This model assumes

that each predator consumes all possible types of prey, and therefore will tend to overestimate the proportion of prey that are rarely consumed and underestimate prey that are commonly consumed. Consequently, we have used the results as an index of prey consumption rather than as an estimate of actual diet composition.

We used fractionation values of 2 ‰ for carbon when mammalian and avian prey were consumed and 1‰ when fish or invertebrates were consumed (Appendix A; S. Farley and C. Robbins, Pers. Comm.). For nitrogen we used fractionation values of 3 ‰ when mammalian prey, avian prey and invertebrates were consumed and 2 ‰ when fish was consumed (Appendix A). We introduced to the model only prey items that were captured in the trap grids and transects as well as avian prey that was observed on the study area, assuming that our censusing was indicative of the availability of such prey to mink.

Statistical Analysis

We employed K nearest-neighbor randomization test (Appendix C; Schilling, 1986; Rosing et al., in review) to investigate whether stable isotope ratios of all possible prey items sampled were significantly different from each other. In this test values of ^{13}C and ^{15}N are treated as spatial data because the unit of measurement in both variables is equal and stable. This test uses a Bonferroni correction when evaluating the differences between all possible prey (Appendix C; Rosing et al., in review). We used Pearson's χ^2 test to investigate differences in abundance of prey between seasons (BMDP; Dixon 1990) and the Kruskal-Wallis test with multiple comparisons or Mann-Whitney test (Zar, 1984) to compare differences in the proportions of the different prey in the diet of mink between seasons.

Results

Trapping mink

We trapped mink repeatedly (some individuals up to 5 times/ day) during spring and summer (Table 4), but were unable to capture more than one mink from late-July to late-November, although we observed mink along our trap lines regularly during that period. We captured one individual female (4 times) during the last 2 weeks of November, 1993, on the coast. Individuals originally captured on the coast during summer 1992 and 1993 were trapped repeatedly within that same habitat, and individuals originally trapped along rivers were captured repeatedly along rivers throughout summer (Table 4). During the mating season in spring we captured 6 male mink that were long distances (3 – 7 km) from their original capture point and in both habitats (Table 4).

Abundance and stable isotope ratios of riverine prey

Juvenile pink and chum salmon were trapped only during spring (late-March to early May; Figure 2). Juvenile coho salmon of age class 0+ first appeared in early May and were present through the summer. The numbers of Age 0+ of all species in our traps were probably low because of the ability of these small fish to exit the traps more easily than larger fish (Bloom, 1976). Numbers of juvenile coho salmon differed between summer and autumn and between autumn and spring (χ^2 test, $df = 2$, $P < 0.05$; Figure 2). This was more likely a result of an increase in the size of coho from age group 0+ than in actual increase in total abundance of juvenile salmonids in the river. Numbers of captured individuals did not differ between seasons for any of the other species (χ^2 test, $df = 2$, $P > 0.05$; Figure 2). The size group of 50 - 80 mm for coho, Dolly varden, and coast-range sculpin had the highest representation in our traps (Figure 3).

No significant difference occurred between the stable isotope ratios of juvenile coho salmon and those of juvenile pink and chum salmon of the age 0+ in spring

Table 4: Mean number of captures (± SD)of male and female mink on Chichagof Island, Southeast Alaska, during each season from summer 1992 through autumn 1993. Two riverine male mink were caught along the coast, and 4 coastal male mink were captured along streams in spring 1993.

	Summer 1992			Autumn 1992			Spring 1993			Summer 1993			Autumn 1993		
	n	Captures	SE	n	Captures	SE	n	Captures	SE	n	Captures	SE	n	Captures	SE
Males															
River	3	9.0	6.1				10	3.5	3.2	4	3.8	4.6			
Coast							5	2.0	1.2	3	1.5	1.0			
Females															
River	2	2.5	2.1							4	1.0	0.0			
Coast	1	4.0					1	4.0		2	3.5	2.1	1	4.0	

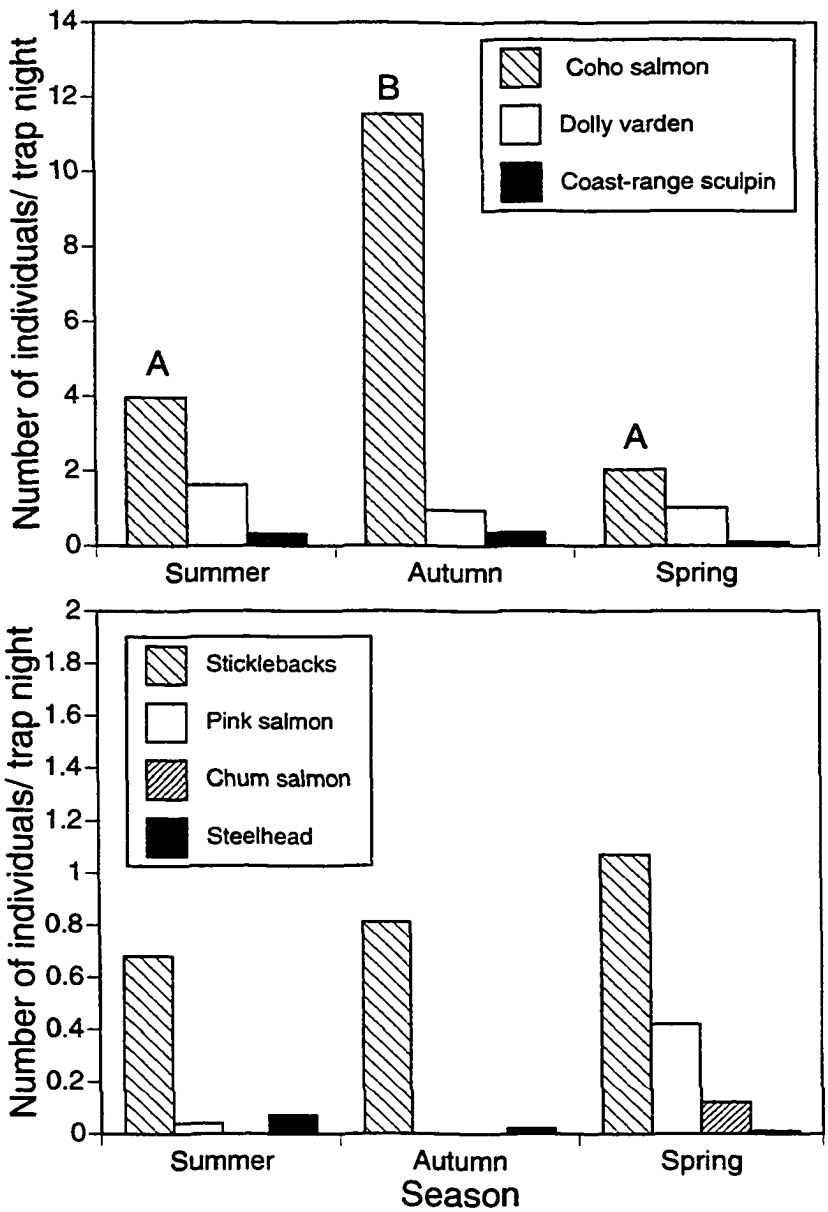

Figure 2. Seasonal abundance (number of individuals/ trap night) of freshwater fish captured in streams on Chichagof Island, Southeast Alaska in 1992 and 1993. Letters represent significant difference between seasons at $\alpha = 0.05$ (χ^2 test). Trapping effort: summer - 300 trap nights; autumn - 315 trap nights; spring - 195 trap nights.

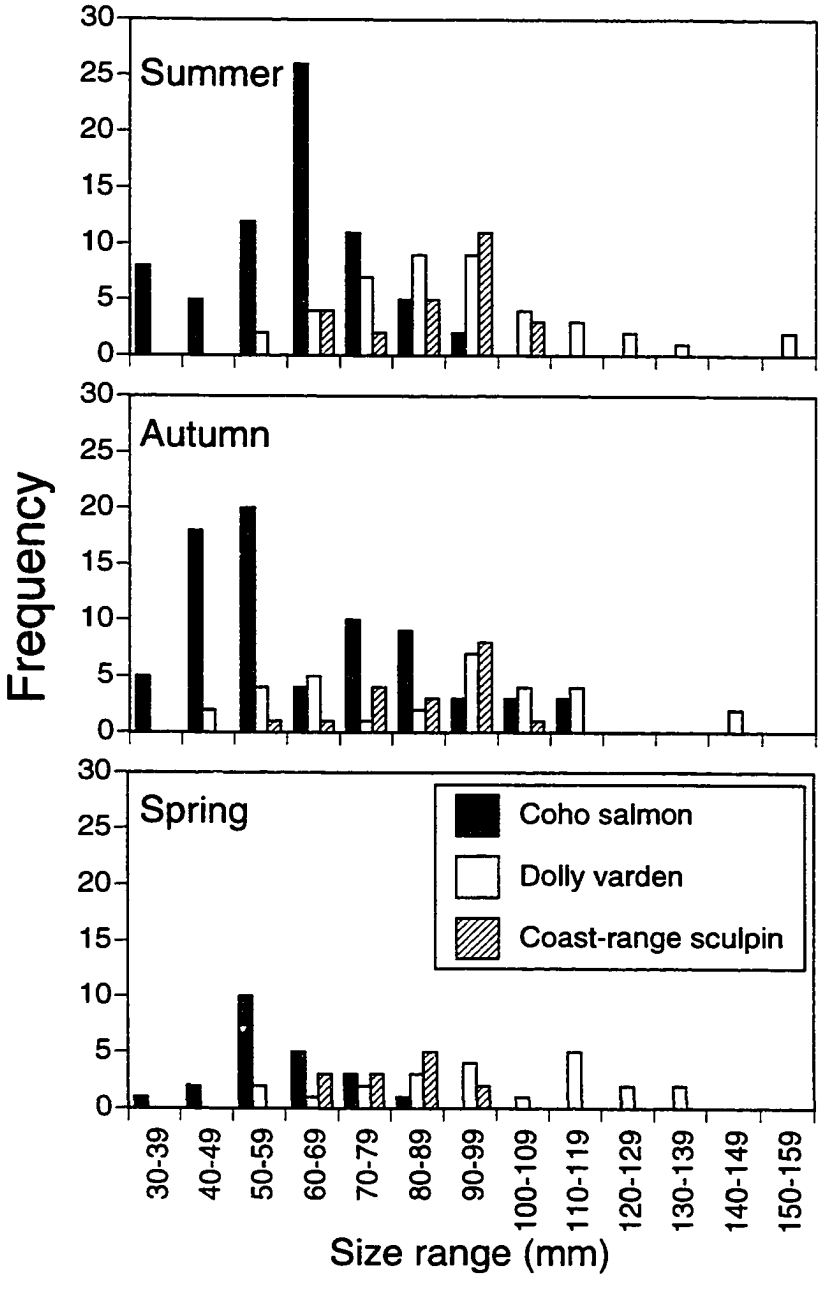

Figure 3. Size distribution of juvenile coho salmon, juvenile Dolly varden, and Coast-range sculpin trapped in streams on Chichagof Island, Southeast Alaska in 1992 and 1993.

and summer (K nearest-neighbor randomization test; $P = 0.3614$). Therefore, we termed this group small fish.

Stable isotope ratios of juvenile coho salmon of age 1+, and 2+ did not differ significantly within each season (K nearest-neighbor randomization test ; $P = 0.5327$, summer; $P = 0.9443$, autumn; $P = 0.9625$, spring). Similarly, there was no significant difference in the isotopic ratios of coho salmon for these age groups and juvenile Dolly varden or Coast-range sculpins of the same fork lengths ($P = 0.747$). Therefore, we were unable to differentiate between the different species and size groups of these fish and regarded them as one diet group termed large fish.

Numbers of small rodents changed significantly between seasons (χ^2 test, $df = 4$, $P < 0.001$) in 1992 and 1993. This difference wasmpst pronounced between summer 1992 and autumn 1992 and between summer 93 and autumn 1993. Apostiriori comparisons indicated that no significant difference occurred between autumn 1992 and spring 1993 or spring 1993 and summer 1993 (Figure 4).

Isotopic ratios of deer mice did not differ significantly from those of voles ($P = 0.2606$). Therefore, we were unable to differentiate between them and regarded them as one diet group termed small rodents.

There was no significant difference in the stable isotope ratios of ducks and large fish in all seasons (K nearest-neighbor randomization test; $P = 0.7684$). Therefore we were unable to determine the relative contribution of ducks to the diet of riverine mink.

Our final classification of prey types for riverine mink consisted of sticklebacks, small fish, large fish, adult salmon (including adult Dolly varden), and small rodents. The K nearest-neighbor randomization test revealed that all these types of prey were significantly different from each other in each season (Figures 5 - 7; $P < 0.05$), except for small and large fish in autumn ($P = 0.5634$). Additionally, there was a significant difference in the stable isotope ratios of small

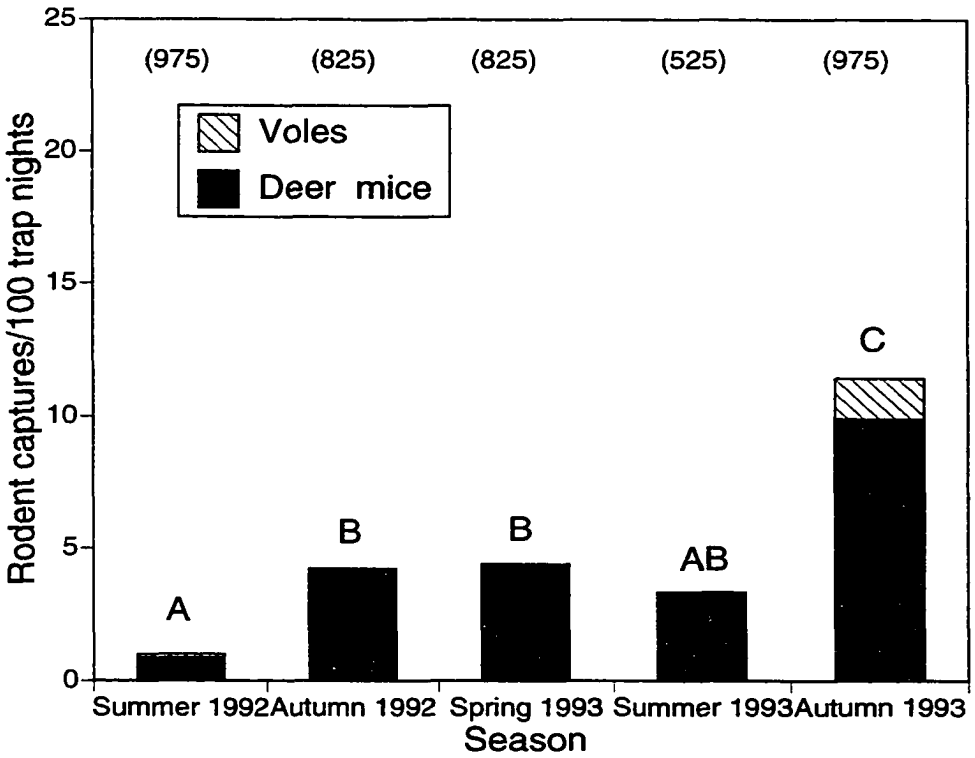

Figure 4. Number of small rodent (captures/ 100 trap nights) captured in summer 1992 through autumn 1993 on Chichagof Island, Southeast Alaska. Letters represent significant difference at $\alpha = 0.05$ (χ^2 test). Numbers in parentheses are total number of trap nights per season.

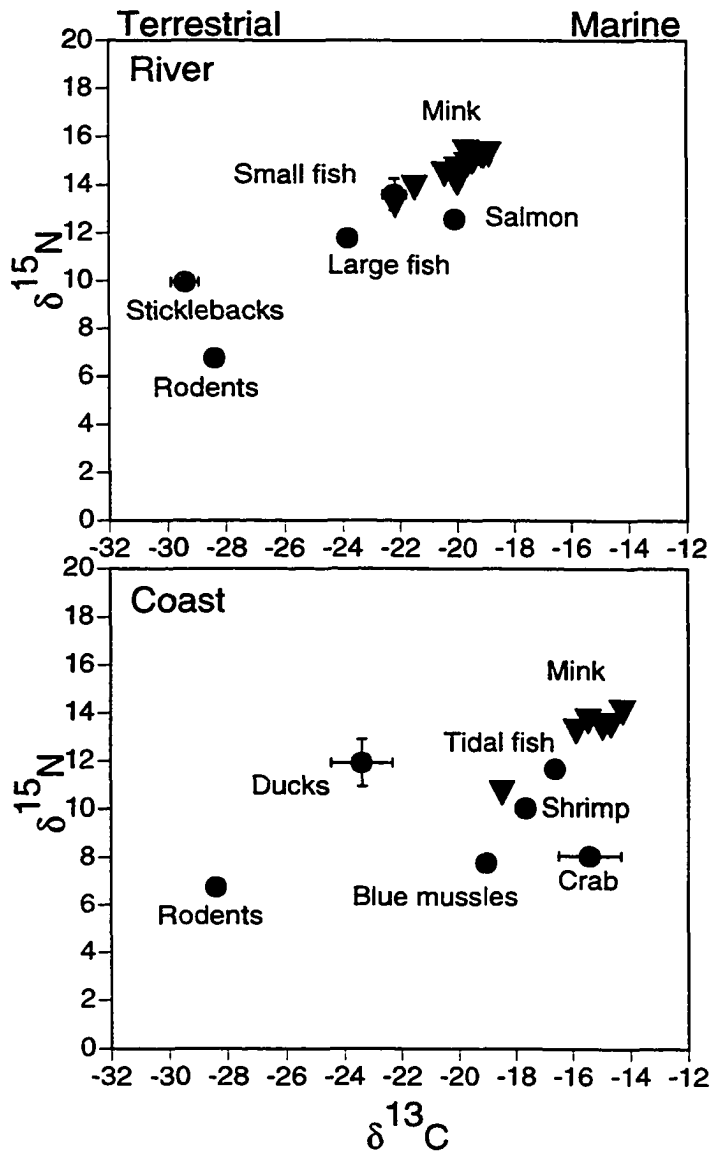

Figure 5. Values of ^{13}C and ^{15}N for mink captured along streams (n = 13; top), and along the coast (n = 6; bottom) in summer 1992 and 1993 on Chichagof Island, Southeast Alaska. Mean values ± SD are given for small fish (n = 13), large fish (n = 124), sticklebacks (n = 10), adult salmon (n = 46), small rodents (n = 60), ducks (n = 6), intertidal fish (n = 76), Blue mussels (n = 19), crabs (n = 39), and shrimp (n =6).

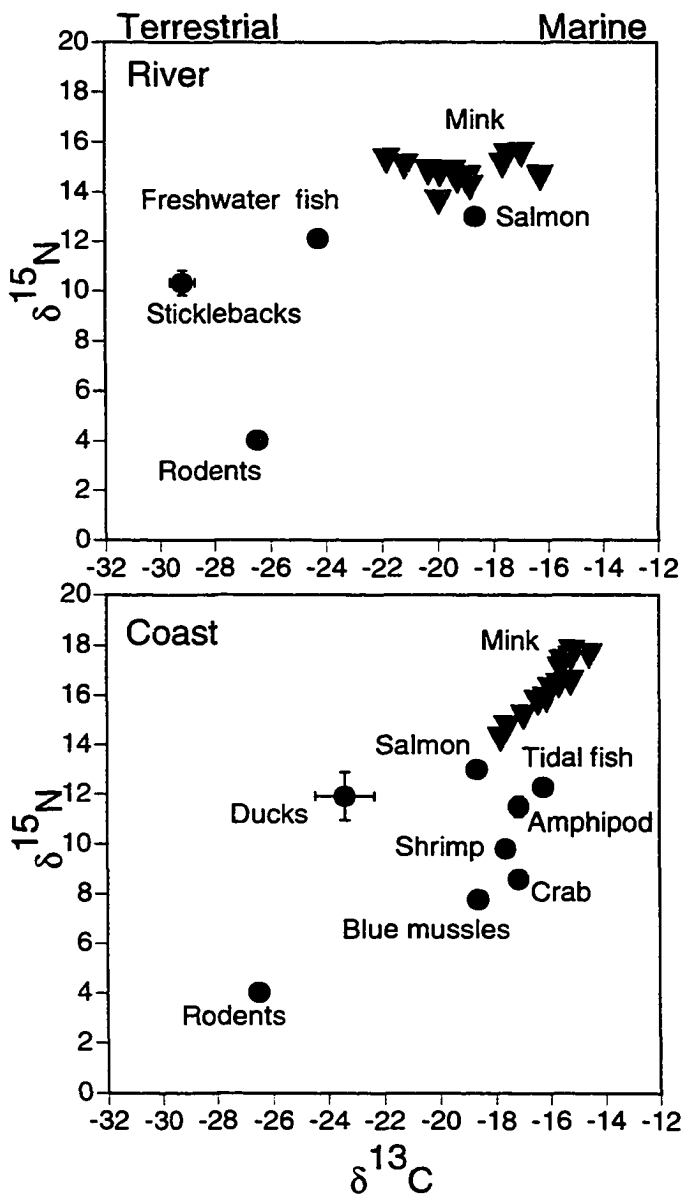

Figure 6. Values of ^{13}C and ^{15}N for mink captured along streams (n = 13; top), and along the coast (n = 13; bottom) in autumn 1992 and 1993 on Chichagof Island, Southeast Alaska. Mean values ± SD are given for fresh water fish (n = 125), sticklebacks (n = 10), adult salmon (n = 18), small rodents (n = 49), ducks (n = 6), intertidal fish (n = 16), Blue mussels (n = 15), crabs (n = 42), shrimp (n = 11), and amphipods (n = 19).

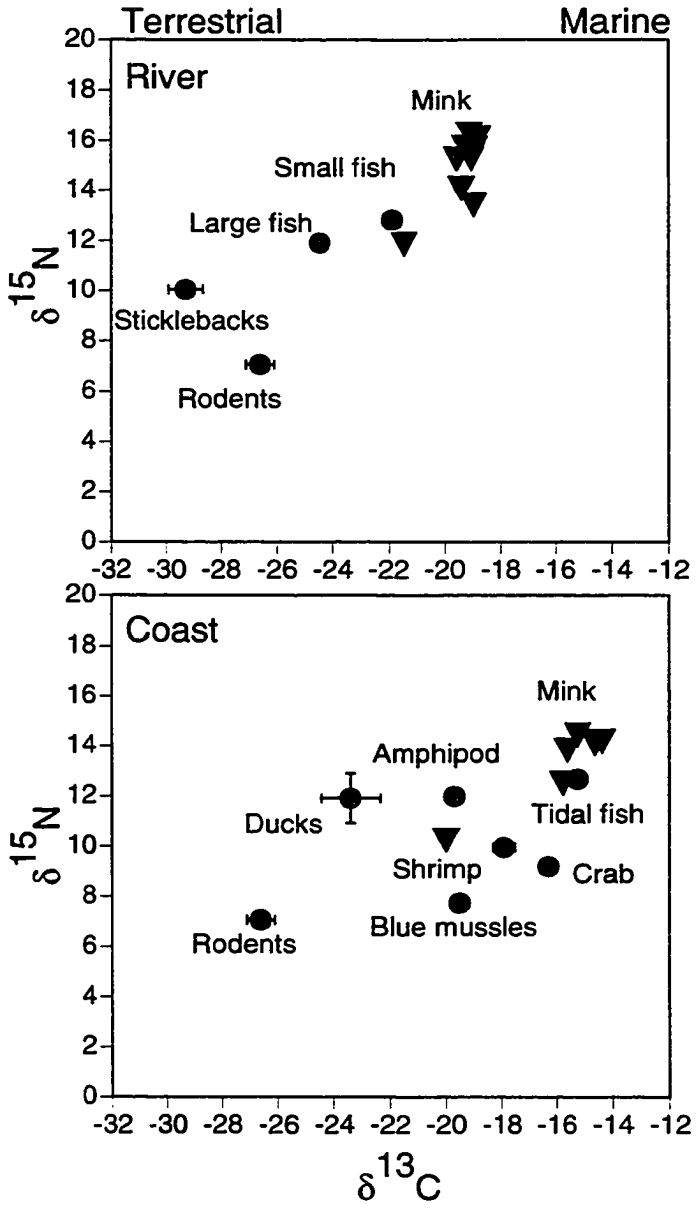

Figure 7. Values of ^{13}C and ^{15}N for live mink captured along streams (n = 10; top), and along the coast (n = 6; bottom) in spring 1992 and 1993 on Chichagof Island, Southeast Alaska. Mean values ± SD are given for small fish (n = 24), large fish (n = 36), sticklebacks (n = 14), small rodents (n = 18), ducks (n = 6), intertidal fish (n = 15), Blue mussels (n = 11), crabs (n = 20), shrimp (n = 6), and amphipods (n = 25).

fish between summer and autumn and between spring and autumn ($P < 0.001$). Although the stable isotope ratio of small fish significantly differed from those of adult salmon (K nearest-neighbor randomization test, $P < 0.001$), the small fish in spring (mainly pink and chum; Table 1; Figure 2) had isotopic signature characteristic of a marine environment. The values of ^{13}C of salmon roe are usually depleted compared with the values of salmon muscle (Kline et al., 1989; Kline et al., 1993).

Diet of riverine mink

Stable isotope ratios obtained from riverine mink (Figures 5 – 7) did not differ significantly between summer and autumn (K nearest-neighbor randomization test, $P = 0.93$), between spring and autumn (K nearest-neighbor randomization test, $P = 0.381$), or between spring and summer (K nearest-neighbor randomization test, $P = 0.315$). Results from the multi-source mixing model (Table 5) indicate that summer and autumn diets of mink consisted largely of salmon (49% ± 4.6 (Mean ± SE) in summer; 57% ± 6.1 in autumn). Nonetheless, because salmon carcasses were unavailable to mink in spring this food was not introduced to the mixing model in that season. The mixing model identified small fish as the main prey in diets of riverine mink in spring (51% ± 2.6). Introducing salmon as a potential prey to the mixing model in spring results in 35% ± 2.7 (mean ± SE) salmon, and 32% ± 1.5 small fish, in the diet of mink, which is still a substantial percent. The relative contribution of small fish to the diet of mink in summer and autumn was significantly lower than in spring (Table 5; Kruskal-Wallis, $P < 0.05$), and probably resulted from the availability of adult salmon.

Large fish, sticklebacks and small rodents had relatively low contribution to the diet (Table 5), although these prey were available to mink throughout the year (Figures 2 – 4). Although the relative contribution of large fish did not differ significantly between spring and summer (Mann-Whitney test, $P < 0.05$; Table 5), their contribution to the diet in autumn could not be determined independently

Table 5. Relative contribution (mean ± SE) of prey item to the diet of coastal and riverine mink (n), captured on Chichagof Island, Southeast Alaska, during 1992 and 1993. Percentages were calculated using the multi-source mixing model (Ben-David et al., in review). Letters represent significant difference in percent between seasons at $\alpha = 0.05$ (Kruskal-Wallis test with multiple comparisons).

Prey Item	Percentages in mink diet					
	Summer		Autumn		Spring	
	%	SE	%	SE	%	SE
Riverine	n = 13		n = 13		n = 10	
Small freshwater fish	24^a	1.5	24^a	4.1	51^b	2.6
Large freshwater fish	17^a	3.5			23^a	0.1
Sticklebacks	5^a	0.3	9^b	1.2	11^b	0.4
Rodents	5^a	0.4	9^b	1.1	15^c	1.2
Salmon	49^a	4.6	57^a	6.1		
Coastal	n = 6		n = 13		n = 6	
Intertidal fish	44^a	9.3	17^b	1.7	30^a	8.3
Blue mussels	17^a	9.5	7^a	0.3	12^a	4.5
Crabs	12^a	2.3	9^a	0.4	21^b	5.3
Shrimp	18^a	3.0	12^a	0.4	17^a	2.2
Rodents	3^a	0.5	3^a	0.6	5^a	1.4
Amphipods			21^a	1.0	9^b	0.9
Ducks	5^a	0.8	7^a	0.4	6^a	1.7
Salmon			23	3.0		

of that of small fish. This relatively low contribution of freshwater fish in autumn diets of mink was most likely a result of the high degree of consumption of salmon during that season, because the number of trapped freshwater fish was higher in autumn than in spring or summer. Similarly, sticklebacks and small rodents composed relatively small portion of diets for riverine mink. The significant increase in the relative contribution of these two prey in autumn and spring is likely a result of the fewer number of items introduced to the mixing

model in those seasons, and might not represent a true increase in consumption. The significant increase in the percentage of small rodents between autumn and spring, can not be attributed to an increase in small rodent availability, as small rodent numbers did not increase between autumn and spring (Figure 4).

Abundance and stable isotope ratios of coastal prey

Crescent gunnels were captured only during summer, whereas no amphipods were captured during that season (Figure 8). No significant difference in number of individuals caught per trap occurred between seasons (χ^2 test, $df = 2$, $P < 0.05$; Figure 8) except for hermit crabs which were caught in large numbers in autumn (χ^2 test, $df = 2$, $P > 0.1$; Figure 8).

Stable isotope ratios of intertidal fish of different species and sizes (Table 2) did not differ significantly within each season (K nearest-neighbor randomization test; $P = 0.0801$). Therefore, we were unable to differentiate between them and regarded them as one dietary group that we termed intertidal fish. Similarly, no significant difference was detected between the different species of crabs and hermit crabs (Table 3) in each of the seasons (K nearest-neighbor randomization test ; $P = 0.4412$), and they were treated as a single group.

Our final classification of prey types for coastal mink consisted of intertidal fish, crabs, shrimp, amphipods, blue mussels, adult salmon, ducks, and small rodents (Figures 5 – 7). The K nearest-neighbor randomization test revealed that all these prey types were significantly different from each other in all seasons ($P < 0.05$).

Diet of coastal mink

Stable isotope ratios of coastal mink (Figures 5 – 7) differed significantly between summer and autumn (K nearest-neighbor randomization test, $P < 0.001$) and spring and autumn ($P < 0.001$), but not between spring and summer (K nearest-neighbor randomization test, $P = 0.961$). Results from the multi-source mixing model (Table 5) indicate that diets of coastal mink from spring and

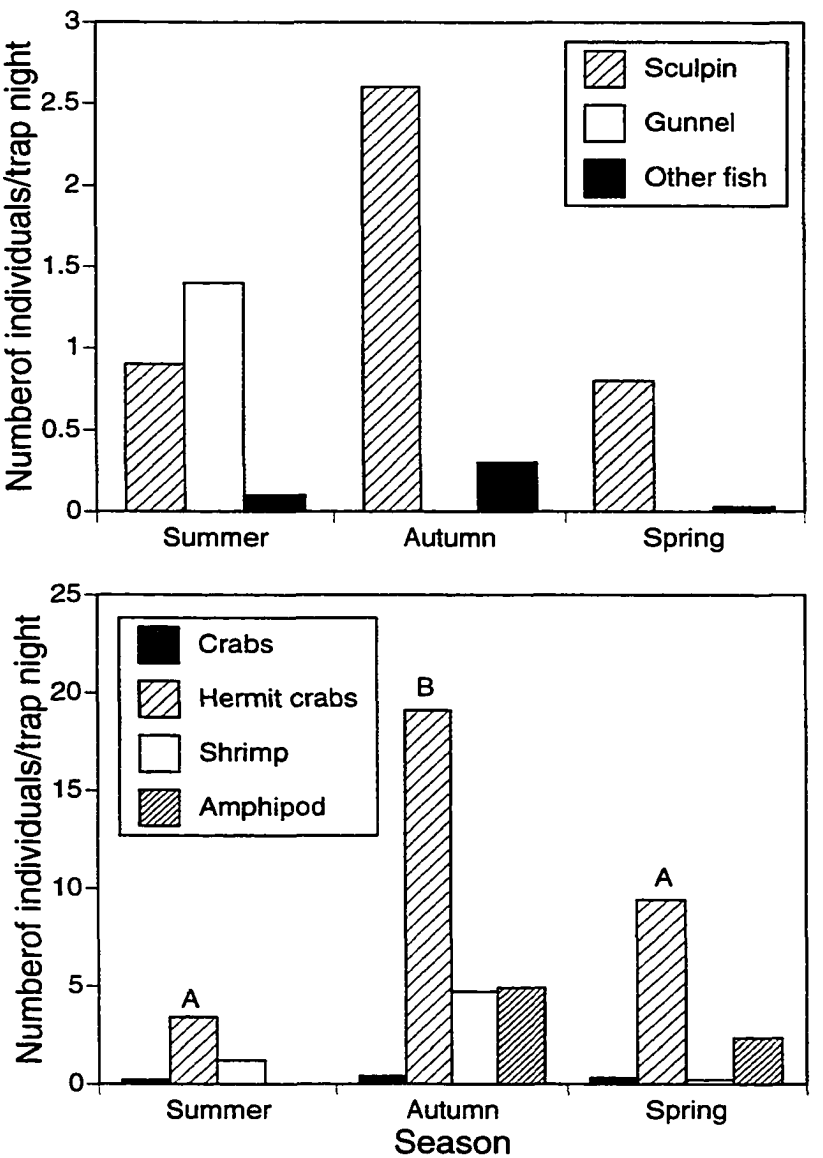

Figure 8. Seasonal abundance (number of individuals/ trap night) of intertidal fish and invertebrates captured along the coast on Chichagof Island ,Southeast Alaska in 1992 and 1993. Letters represent significant difference between seasons at $\alpha = 0.05$ (χ^2 test). Trapping effort: summer - 240 trap nights; autumn - 270 trap nights; spring - 135 trap nights.

summer consisted largely of intertidal fish (44% ± 9.3 (Mean ± SE), summer; 30% ± 8.3, spring; Table 5). In autumn, percent of intertidal fish decreased significantly (Kruskal-Wallis, $P < 0.05$), although the numbers of sculpins did not significantly differ between seasons (χ^2 test, $df = 2$, $P < 0.05$; Figure 8). This change in isotopic ratios of coastal mink in autumn was likely a result of the incorporation of salmon in their diet (Figure 6; Table 5). The relative contribution of intertidal organisms other than fish was comparatively low and did not show significant differences among seasons (Table 5), except crabs that increased in mink diets during spring. The relative contribution of small rodents and ducks to the diet of coastal mink was low and did not change with season (Table 5).

The stable isotope ratios of coastal and riverine mink differed significantly in spring and summer (K nearest-neighbor randomization test, $P < 0.001$). Similarly, stable isotope ratios of coastal mink in autumn significantly differed from those of riverine mink in that season (K nearest-neighbor randomization test, $P < 0.001$), and is probably a result of the incorporation of other different prey in the diet of individuals from the two environments.

Discussion

Marine-derived nutrients (C and N) play a major role in the diet of riverine mink on Chichagof Island, Southeast Alaska, throughout the year. Mink consumed adult Dolly varden in early summer, spawning pink, chum, and coho salmon in summer and autumn, and emerging juvenile salmonids in spring.

Although emerging juvenile salmonids are small (Table 1), mink are efficient at catching small sized fish, that occur in loose schools (Poole and Dunstone, 1976). In addition, large numbers of juvenile coho salmon and Dolly varden, mostly of age class 0+, are commonly trapped in shallow off-channel pools following floods (up to 600 individuals per pool; M. N. Rosing, pers. comm.). Such off-channel pools offered little cover and left the fish were highly exposed to predation by mink, river-otters and mergansers (M. N. Rosing, pers. comm.).

An alternative explanation to the marine signature of mink in spring could be consumption of salmon carcasses cached in autumn. We observed several mink (n = 5) carrying carcasses away from the stream bank in summer and autumn, and located frozen salmon carcasses (n = 13) in root cavities of large spruce trees as well as under rock overhangs. We were unable, however, to quantify the availability of such carcasses. Introducing salmon as a potential prey to the mixing model in spring reduced the relative contribution of small fish to the diet of mink to 32% ± 1.5. Nonetheless, this value indicates that the role of small fish in spring diet of mink would still be substantial.

The comparatively low percent of other freshwater fish in the diet of mink is comparable to those reported in other studies on mink in North America, and Europe (where the mink is feral) (Gerell, 1967; Chanin and Linn, 1980; Wise et al., 1981; Dunstone, 1993). Other studies, however, reported higher percentages for large freshwater fish (Melquist et al., 1981). This difference could result from the ample cover provided for fish in the streams of Southeast Alaska (Bisson et al., 1987; Bryant, 1984; 1990; Sullivan et al., 1987). Dunstone and O'Connor (1979*a*)

have shown that available cover for prey was the most important factor affecting predatory success of diving mink.

Mammals played a lesser role in the diet of mink in our study area than in diets of mink elsewhere (Gerell, 1967; Melquist et al., 1981; Dunstone, 1993). We offer three possible explanations: our study area was especially rich in marine resources; populations of small rodents in our study area were at low densities in 1992 and 1993 (Figure 4) and few other possible mammalian prey were available on Chichagof Island; and differences in techniques used in the different studies to evaluate diets of mink. Gerell (1967), Chanin and Linn (1980), Melquist et al. (1981), and Dunstone, (1993) used fecal or gastrointestinal analyses, which tend to overestimate the occurrence of prey items with large amounts of indigestible, readily recognizable tissues such as fur, small bones, teeth and jaws. Stable isotope analysis, on the other hand, assesses assimilation of nutrients derived from prey, and therefore, is not influenced by such factors.

Unfortunately, we were unable to determine the relative contribution of ducks to the diet of riverine mink because we could not differentiate them from large freshwater fish. Avian prey usually constitute a small portion of mink diet (Gerell, 1967; Chanin and Linn, 1980; Melquist et al., 1981; Wise et al., 1981; Dunstone, 1993), although waterfowl may be important when locally abundant (Eberhardt and Sargeant, 1977). Ducks were not especially abundant in riverine habitats in our study area. We were able to evaluate the relative contribution of ducks to the diets of coastal mink, which was comparatively low.

Diets of coastal mink in our study area were comprised largely of intertidal fish in summer and spring, which is consistent with results of other studies of the feeding ecology of coastal mink (Hatler, 1976; Cuthbert, 1979; Johnson, 1985; Dunstone and Birks, 1987). The combined percentages of invertebrates composed the other major portion of the diet. Our analysis indicates, however, that crabs did not constitute a large portion of the diet of mink, in contradiction to reports for most other populations of coastal mink (Hatler, 1976; Cuthbert, 1979; Johnson,

1985; Dunstone and Birks, 1987). The discrepancy could be a result of either difference in techniques used (crab shells are indigestible, readily identified, and usually overestimated in fecal and gastrointestinal analyses; Bowyer et al., 1994; Johnson, 1985), or differences between study areas, or both. The relative contribution of crabs increased significantly in spring (21%). This could be a result of a seasonal change in the behavior of crabs; we did not observe an increase in their numbers in that season. Several studies of intertidal organisms reported changes in behavior in relation to season or tidal level (Feder and Jewett,1986; Feder and Bryson-Schwafel, 1988).

Our estimates of the proportions of shrimp and amphipods in diets of mink were higher from those reported by Hatler (1976), and Johnson (1985) or Dunstone and Birks (1987). The abundance of these prey was higher in our study area than that reported in other studies, although, the difference in estimation of abundance between the studies prevents accurate comparison of the results. Alternatively, this difference in the relative contribution of shrimp and amphipods could be a result of higher assimilation of more digestible food (Johnson, 1985), in comparison to the remains such food leaves in the feces.

The low proportions of mammals in the diet of coastal mink in our study area is comparable to that reported by Hatler (1976) and Johnson (1985). Dunstone and Birks (1987), however, reported high consumption of rabbits (*Oryctolagus cuniculus*), in coastal South Scotland, where this prey was abundant. No such prey is available on Chichagof Island, and during 1992 and 1993 abundance of small rodents was low.

Adult salmon carcasses played a major role in autumn diets of coastal mink in our study area. Johnson (1985) reported similar results for mink on Prince of Wales Island, Southeast Alaska. Coastal mink could obtain salmon carcasses in estuaries, however, if less than 4% of salmon carcasses are washed from rivers to the estuaries (as reported by Cederholm et al., 1989), then coastal mink are likely to move upstream in search for this resource. Johnson (1985) did not observe such

movements among his radio-tracked mink, and our mark-recapture records (Table 4) also indicated strong fidelity to habitat. Nonetheless, we had great difficulty trapping mink in autumn (presumably because of the high abundance of salmon), and our data provide no insight into movements of mink in that season. We did, however, capture male mink long distances (3 - 7 km) from their original capture site and across both habitats in spring. Although these movements were most likely associated with breeding rather than feeding, they suggest that mink are capable of long movements in search for an important resource.

Our results from stable isotope analysis indicate that the diets of coastal and riverine mink differed significantly in spring and summer, supporting our expectation that the two groups would occupy two different feeding niches. The feeding niches converged in autumn as adult salmon became an important food for both coastal and riverine mink. Nevertheless, stable isotope ratios of coastal mink in autumn significantly differed from those of riverine mink in that season, reflecting the differences in food resources in these two habitats.

In conclusion, our results suggest that although coastal and riverine mink in Southeast Alaska differ in their diets in spring and summer, both groups rely heavily on the abundant salmon carcasses during autumn. This significant seasonal pulse of resources is likely to determine several aspects of mink ecology in Southeast Alaska, such as timing of reproduction (see chapter 2; Ben-David, in review), and dispersal patterns, and merits further investigation.

Acknowledgment

We wish to thank J. Simonson, C. Zank, M. Kemp, N. Olmstad, M. Rosing, B. Wissing, and S. Lewis for valubale assistance in the field. We also are grateful to the trappers of Chichagof Island for providing us with mink carcasses Dr. W. E. Barber assisted in identifying the intertidal fish, and T. Rucker assisted with

identifying the intertidal invertebrates. N. Haubenstock and B. Barnette performed the stable isotope ratio analysis. Drs. R. T. Bowyer, M. Oswood, and J. A. Blake provided helpful comments on earlier versions of the manuscript. Funding for the project was provided by the USDA Forest Service, Pacific Northwest Research Station, Juneau; Alaska Department of Fish and Game; Alaska Cooperative Fish and Wildlife Research Unit; and Water Research Center, University of Alaska Fairbanks.

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Chapter 2–Timing of reproduction in free-ranging wild mink: evidence from blood-progesterone levels

Merav Ben-David

Summary

In many species of seasonally breeding mammals, reproduction occurs later at higher latitudes. Records of timing of reproduction in free-ranging American mink (*Mustela vison*) in North America and in Europe, suggest a similar trend for this species. Observations on mink in Southeast Alaska, however, revealed a deviation from this pattern, suggesting that factors other than latitude and associated day length may affect timing of breeding. I investigated timing of reproduction and body condition of wild, free-ranging mink on Chichagof Island, Southeast Alaska and hypothesized that seasonal food availability, especially abundant carcasses of spawning Pacific salmon (*Onchorhynchus* sp.) would determine timing of breeding in this population of mink. Levels of blood progesterone, body condition, and testicle lengths were recorded for 24 adult mink, live-trapped repeatedly from mid-March to late-July 1992 and 1993. Results suggest that these free-ranging mink mate during the later part of April to early May, and parturition occurs in late June to early July. Although male mink seemed to respond to photoperiodism in initiating reproduction, timing of reproduction in female mink was shifted so that lactation coincided with the availability of carcasses of Pacific salmon.

Introduction

In many species of seasonally breeding mammals, reproduction occurs later at higher latitudes (Hamilton and Eadie, 1964; Conaway et al., 1974; Lauhachinda, 1978; Bunnell, 1982; Humphrey and Zinn, 1982; King and Moody, 1982; Budde, 1983; Verme and Ozoga, 1987; Bubenik et al., 1990). Timing of reproduction in free-ranging American mink (*Mustela vison*) in North America as well as in Europe (where the species is feral), suggests a similar trend for this mustelid. Humphrey and Zinn (1982) reported mink mating during late autumn in Florida. In the southern part of the Britain, mating occurred as early as mid-February to early March, with parturition occurring in late April to the first week of May (Dunstone, 1993). In Ireland, Smal (1991) reported mink mating in March and all births occurred before the end of May. In Sweden, Gerell (1970) obsereved mating in March and parturition in May, whereas in Interior Alaska, Harbo (1958) noted mating from middle to late April and parturition during the middle of June. In Southeast Alaska, however, Johnson (1985) reported mink mating in mid-May and parturition in mid-July (Johnson, 1985). In addition, Hatler (1976) documented mating in late May and parturition in the end of July for mink on Vancouver Island, British Columbia. These observations imply that factors other than latitude and associated day length may affect timing of breeding of mink along the coast in the Pacific Northwest. I investigated timing of reproduction and body condition of wild, free-ranging mink on Chichagof Island, Southeast Alaska, and hypothesized that seasonal availability of food, especially abundant carcasses of Pacific salmon (*Onchorhynchus* sp.) would determine timing of breeding in this mink population.

Methods

Study area

The study area is located on Chichagof Island in Southeast Alaska, USA (Figure 1; Tenakee Springs at 57° 52' N 135° 18' W). The island is one of the three large northern islands of the Alexander Archipelago and is part of the Tongass National Forest. The archipelago has a maritime climate; summers are cool and wet and winters are characterized by deep snow (236 cm annual precipitation). The snow-free period extends from early May to early November at lower elevations. Vegetation at higher elevations is typified by alpine tundra, and at lower elevations by coastal, old-growth rainforest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with well-developed understory (mainly *Oplopanax horridus*, *Vaccinium* sp.,*Menziesia ferruginea*, and*Rubus* sp.). The study area encompassed six streams that support an annual run of spawning Pacific salmon (*Onchorhynchus gorbuscha*, *O. keta*, and *O. kisutch*), from late summer to late autumn. The mammalian fauna of the island includes: Keen's deer mice (*Peromyscus keeni*), long-tailed voles (*Microtus longicaudas*), tundra voles (*Microtus oeconomus*), red squirrels (*Tamiasciurus hudsonicus*), common shrews (*Sorex cinereus*), martens (*Martes americana*), river-otters (*Lutra canadensis*), brown bears (*Ursus arctos*), and Sitka black-tailed deer (*Odocoileus hemionus sitkensis*). Song birds such as winter wren (*Troglodytes troglodytes*), dark-eye junco (*Junco hyemalis*), robin (*Turdus migratorius*), varied thrush (*Ixoreus naevius*), hermit thrush (*Catharus guttatus*), and Swainson's thrush (*Catharus ustulatus*), arrive on the island for the breeding season in early May and depart in September.

Sampling

Twenty-four adult mink (10 females and 14 males; > 1-year old) were live-captured repeatedly from mid-March to late-July in 1992 and 1993, using Tomahawk live traps. After immobilization with an injection of Ketamine Hydrochloride (15 mg/kg body weight; Aveco, Fort Dodge, IW), each individual

was measured, weighed, and marked subcutaneously with a passive integrated transponder (PIT) tag (Biosonics, Seattle, Washington). Age was estimated for each individual by noting tooth replacement, and wear, and by measuring minimum width between the temporal muscles, and examining the size of the sagital crest (Magoun et al., 1988). For each adult mink, a blood sample of 2 cc was drawn from the jugular vein and stored in a glass or plastic vial. Upon recovery from sedation, animals were released at the site of capture. Blood was spun at 3,000 rpm for 5 min. using a manual centrifuge within 2 hours after collection, and serum was siphoned into a separate vial. Both samples of serum and clotted blood-cells were frozen (-18°C) until analysis. All methods used in this study were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks.

Progesterone Assays

Progesterone assays were done using Diagnostic Products iodinated solid-phase RIA kit (by Dr. R. A. Mead, University of Idaho, Moscow, Idaho). Intra- and inter-sample variation were 4.5 ±0.3 and 8.5 ± 1.8 (mean ± SE; n = 38), respectively. I used levels of blood progesterone from captive female mink that were either mated or unmated (Ben-David and Blake, unpublished), as well as levels reported in the literature (Allais and Martinet, 1978) as a standard to determine reproductive status for the free-ranging mink (Table 6).

Measurements of morphological characters and external reproductive organs

Body weights for all mink I handled were determined using a spring scale (± 5 g). Body length was measured as the distance between the tip of the snout to the base of the tail, while the animal was positioned on its sternum. Because body condition is, in part, dependent on body size (Farley and Robbins, 1994), body weight was divided by body length to represent an index of body condition (Duffy et al., 1993). Testicle length was measured for each adult male at each handling using museum calipers (± 1 mm). Because of small sample sizes, data on

Table 6. Progesterone levels (ng/ml) and reproductive status of female mink. Data from Ben-David and Blake (unpublished) [1], and Allais and Martinet (1978) [2].

Reproductive status	Progesterone level (ng/ml)	Source
Non-reproductive	0.1 – 7.7	1
Pre-implantation		
(all values)	13.1 – 56.1	1
(peak values)	40.0 – 160.0	2
Post-implantation	29.7 – 51.2	1
First week of lactation	2.7 – 9.3	1
Second week of lactation	0.1 – 3.4	1

testicle length and body condition for males were pooled by 2-week intervals for analysis. For females, the occurrence of mating scars were recorded at each handling. In addition, mammary glands, and vulva were examined, and abdominal palpitation was performed on each female at each handling.

Statistical analysis

A Kruskal-Wallis test with Tukey's multiple comparisons (Zar, 1984; BMDP - Dixon, 1990) was employed to investigate differences in testicle lengths and index of body weight for males. Similarly, Kruskal-Wallis test (Zar, 1984; BMDP - Dixon, 1990) was used to examine differences in the index of body weight of nonreproductive, implanting, pregnant, and lactating females.

Results

Females

Of the 10 female mink trapped in this study (one of which was captured twice), 5 were lactating, 2 appeared pregnant, 2 had fresh mating scars, and 2 appeared to be nonreproductive (Table 7). Levels of blood progesterone (Figure 9)

Table 7. Date of capture, weight (g), occurrence of mating scars, mammary glands condition, and the number of embryos recorded through abdominal palpation, for female mink live-trapped on Chichagof Island, Southeast Alaska during 1992 and 1993.

Animal ID	Date of capture	Weight (g)	Mating scars	Number of embryos	Milk production
MK04	June 20,1992	720	healing	none	yes
MK05	June 29,1992	800	healing	two	no
MK06	July 6, 1992	580	healing	none	yes
MK14	April 14, 1993	600	none	none	no
MK19	June 2, 1993	825	fresh	none	no
MK14	June 3, 1993	650	fres	none	no
MK20	June 26, 1993	925	healing	one	no
MK21	July 6, 1993	675	healing	none	yes
MK22	July 7, 1993	700	healing	none	yes
MK23	July 7, 1993	650	healing	none	yes
MK24	Nov. 17, 1993	625	none	none	no

suggest that in 1993, implantation occurred in early June. Values obtained for the 2 animals caught on the 2nd and 3rd of June were in the high range of pre-implantation values (Table 6). In addition, extrapolation from progesterone levels

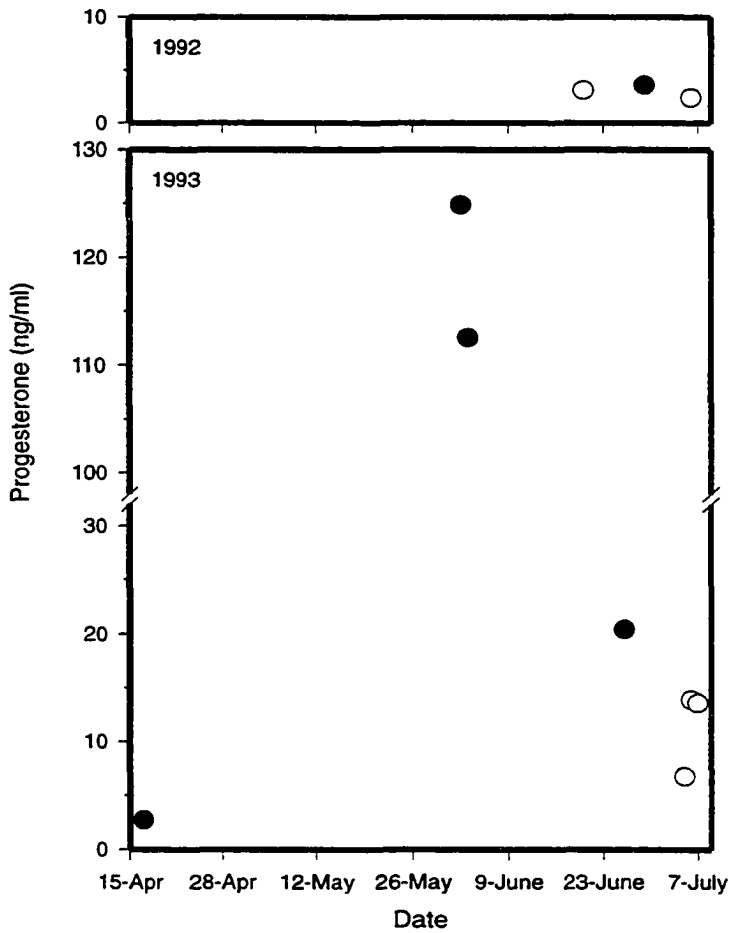

Figure 9. Blood progesterone levels (ng/ml) of female mink live-trapped, on Chichagof Island, Southeast Alaska, during the breeding season 1992 and 1993. (O) represent lactating and (●) nonlactating female.

of the pregnant female caught on 26 June (assuming 28-31 days of gestation; Enders, 1952), indicates implantation occurred during early June. Similarly, progesterone values for the three lactating females caught on the 6-7 July suggest that these mink gave birth during late-June to early-July, which in turn means they implanted during late-May or early-June. In 1992, two lactating females were caught on 20 June and 6 July (Table 7). The lower progesterone levels recorded for these females (Figure 9) suggest earlier parturition and therefore earlier implantation during 1992, although one female caught on 29 June was pregnant (Table 7). Progesterone levels recorded for that female were low for pregnant females (Table 7), but within the range for the first week of lactation, suggesting she might have been at or near the end of pregnancy. The female caught on 14 April did not show external signs of reproduction (Table 7), and had low levels of blood progesterone (Figure 9). When recaptured on the 3 June, this individual had fresh mating scars (Table 7) as well as progesterone levels suggesting implantation (Figure 9), implying that she had mated after 14 April.

Pregnant females and implanting females had a tendency to have higher values of body condition than did lactating or nonreproductive females, although these values were not significantly different, likely because of small sample size (Figure 10; Kruskal-Wallis, $P < 0.1$).

Males

Males had well developed testes when captured during the second half of March (Figure 11), and testicle size did not significantly change until the later part of May when testes began to decrease in size (Kruskal- Wallis, $P < 0.05$; Tukey Multiple comparisons, $\alpha = 0.05$). By the end of June testicle length declined to nonreproductive levels (Figure 11).

Body condition of males followed a similar trend with high values in early spring (Figure 12), declining towards the end of spring and early summer (Kruskal- Wallis, $P<0.05$; Tukey Multiple comparisons, $\alpha = 0.05$).

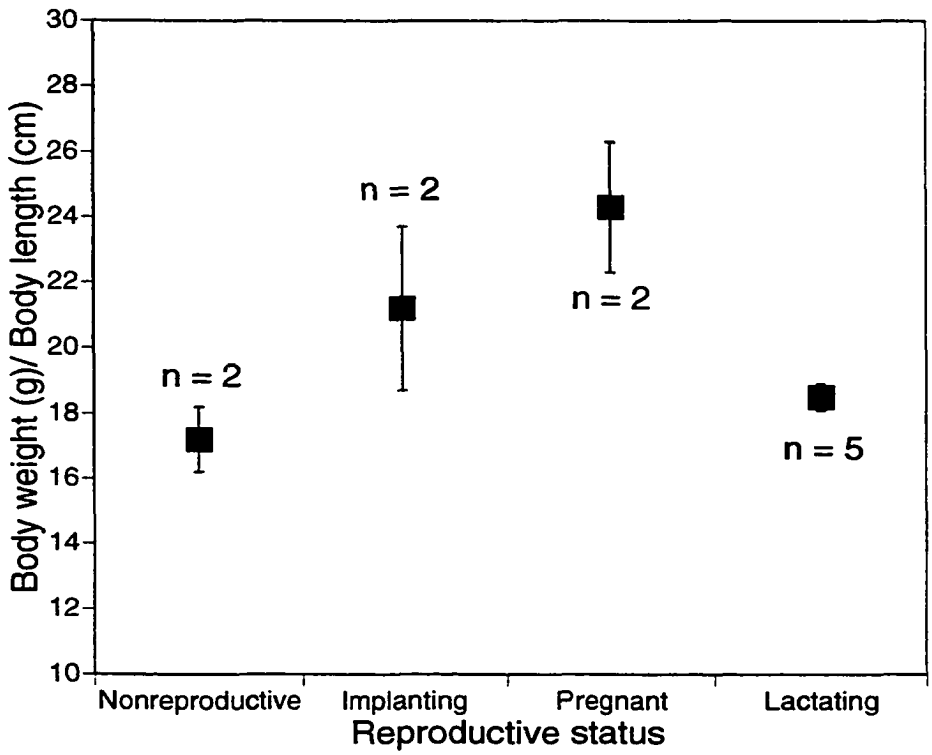

Figure 10. Body condition expressed as body weight (g)/body length (cm) ± SE of live-trapped female mink, in 1992 and 1993, on Chichagof Island, Southeast Alaska, in relation to reproductive status.

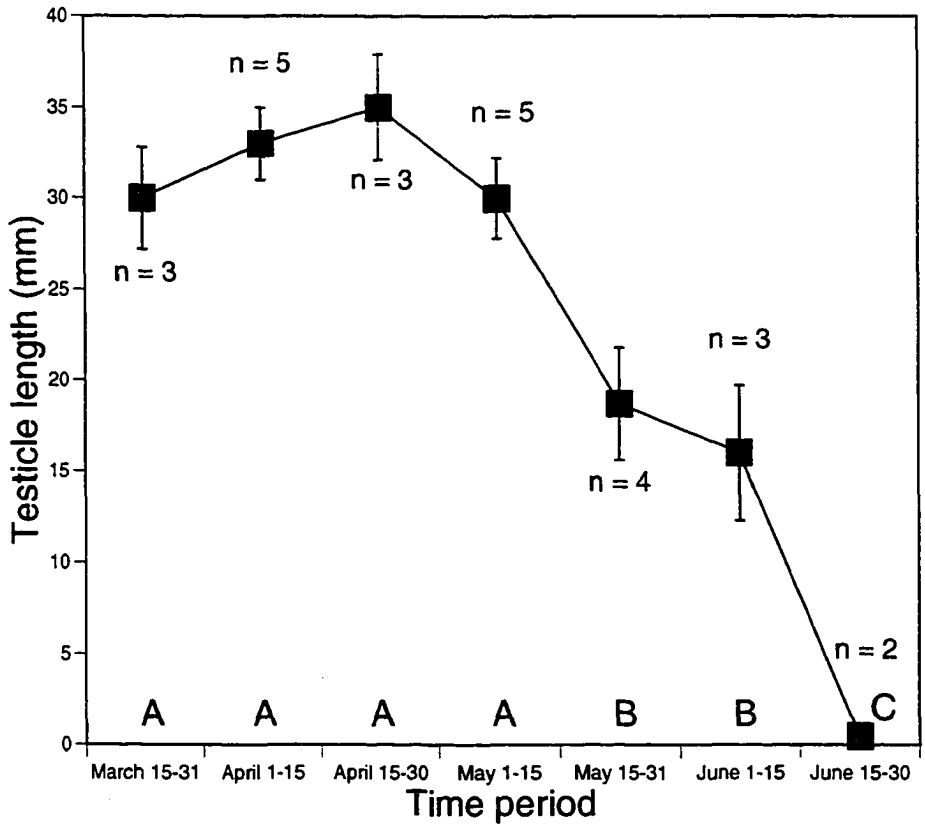

Figure 11. Testicle length (mm) ± SE recorded for live-trapped male mink, on Chichagof Island, Southeast Alaska, grouped in 2-week intervals during spring and summer 1992 and 1993. Letters represent significant differences (Tukey's multiple comparisons; $\alpha = 0.05$).

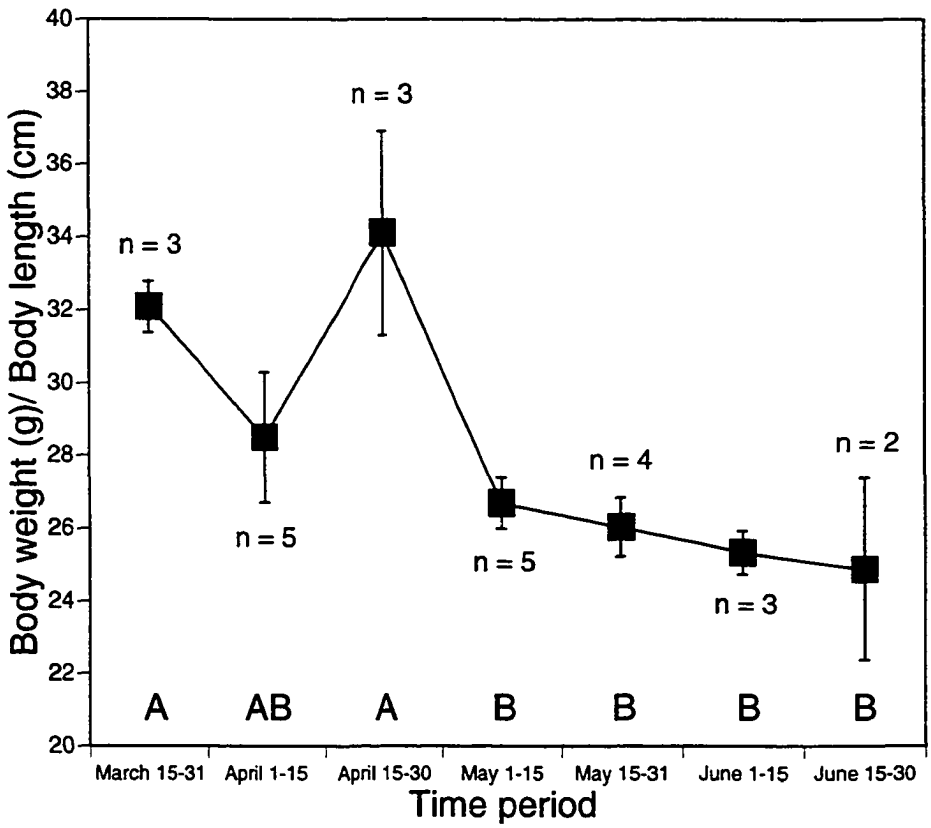

Figure 12. Body condition expressed as body weight (g)/body length (cm) ± SE of live-trapped male mink, on Chichagof Island, Southeast Alaska, grouped in 2-week intervals during spring and summer 1992 and 1993. Letters represent significant differences (Tukey's multiple comparisons; $\alpha = 0.05$).

Discussion

Data on blood progesterone, and occurrence of mating scars on female mink from Chichagof Island, suggest that these free-ranging mink mated during late of April and early May, and parturition occurred in late June and early July. This is further supported by decrease in body condition of males during the later part of April. This decline in body condition could be attributed to extended movements while searching for mates, and male-male competition for mates, as was shown for male mink in other studies (Gerell, 1970; Hatler, 1976; Dunstone, 1993). In addition, stable isotope ratios of carbon and nitrogen suggest that, during this period, male mink feed less than they do during other periods (See chapter 1; Ben-David et al., in review *a*). Although, this timing of reproduction is later than that reported for Interior Alaska mink (latitude 67° N; Harbo, 1958), mink on Prince of Wales Island in Southeast Alaska (latitude 54° N) mate in mid-May and parturition occurrs in mid-July (Johnson, 1985). Similarly, Hatler (1976) reproted mating in late May and parturition in the end of July for mink on Vancouver Island, British Columbia (latitude 49° N). Conversely, a female mink captured in Prince William Sound, in Southcentral Alaska (latitude 61° N; Ben-David et al., 1996) was lactating on 8 June 1991. These reports seem to indicate that timing of reproduction in mink in the coastal Pacific Northwest, follows an opposite trend to that expected from increasing latitude, as mink seem to breed later with decreasing latitude (Figure 13).

Studies on captive mink have shown the importance of photoperiodism in controlling the development of male sex organs (Boissin-Agasse and Boissin, 1985; Martinet and Allain, 1985; Martinet et al., 1992), and length of the delay in blastocyst implantation in the female (Allais and Martinet, 1978; Martinet et al., 1983; Lagerkvist et al., 1992). Photoperiodism as a cue is the plausible explanation for delayed reproduction with increasing latitudes and associated day length, however, it fails to fully explain the observed trend of mink reproduction along the coast of the Pacific Northwest (Figure 13). Whereas photoperiodism is an

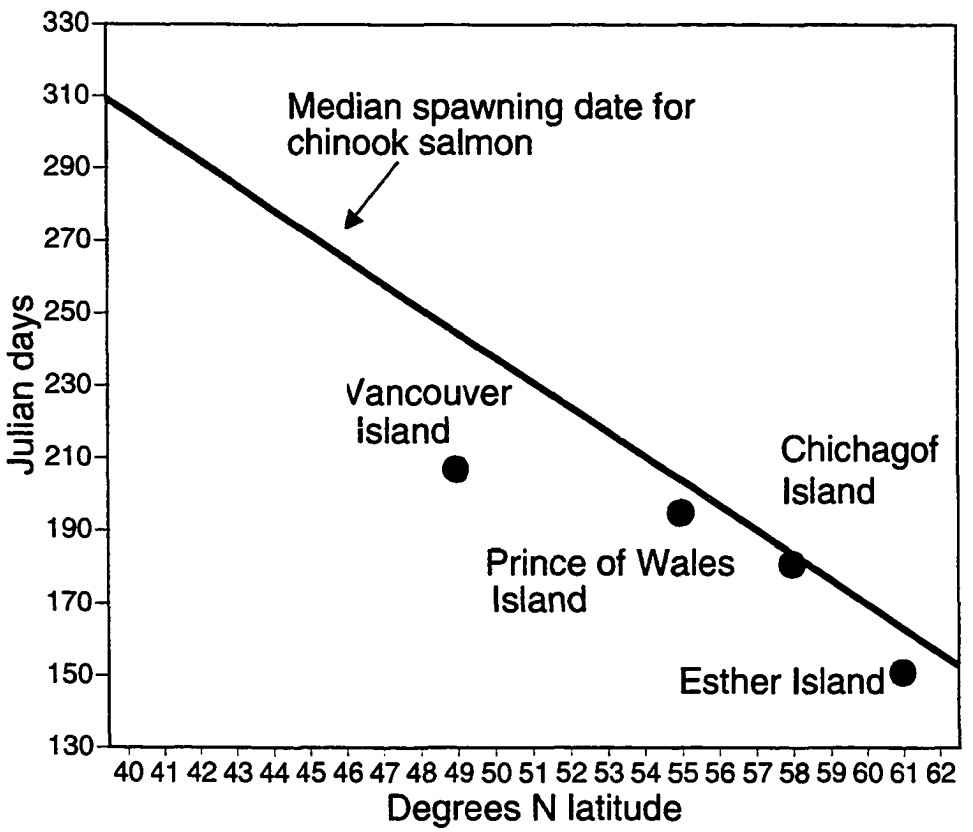

Figure 13. Mean dates of mink parturition in relation to latitude (Chichagof Island - this study; others adopted from Ben-David et al., 1996 - Esther Island, Johnson, 1985 - Prince of Wales Island, and Hatler, 1976 - Vancouver Island). Solid line represents the relationship between median spawning date and latitude for chinook salmon (Adopted from Healy, 1991).

important mechanism in initiation of breeding in many seasonally-breeding mammalian species (King and Moody, 1982; Budde, 1983; Verme and Ozoga, 1987; Mead, 1989; Bubenik et al., 1990), other environmental factors, such as temperature, food availability, and body condition can synchronize timing of reproduction in many mammalian species (Reimers et al., 1983; Bowyer, 1991; Rachlow & Bowyer, 1991; Berger, 1992; Byres and Hogg, 1995), including mink (Martinet et al., 1985; Tauson, 1993).

Several studies indicate that in many species of mammals a female must reach a critical body weight or accumulate a critical amount of fat to conceive (Kennedy and Mitra, 1963; Clutton-Brock et al., 1986; Bronson, 1989; Butler and Whelan, 1994; Caro, 1994; Ruthven et al., 1994; Gerhart, 1995). In species with delayed implantation, such as the mink, pregnancy involves ovulation during the mating period, as well as implantation up to 55 days later (Mead, 1989). That the male mink had high values of body condition in early spring, and the two females caught in early June had higher indices of body condition than those of nonreproductive or lactating females, suggest that no food limitation occurred during that part of the year. Although the difference in body condition of females was not statistically significant because of small sample size, it indicates that females were able to increase their body condition in late spring. Therefore, it seems that the delay in breeding recorded in this study was not a result of food limitation during early spring.

Lactation is the most energetically demanding component of mammalian reproduction (Robbins, 1993; Oftedal, 1994). Natural selection should favor individuals that produce young at the time of high food abundance, thus enabling females to meet the nutritional requirements of lactation. On Chichagof Island, mink relied heavily on salmon carcasses as soon as they became available in early July (Ben-David, 1996; Ben-David et al., in review *a*). This food item is abundant in the area from early July to late November as different species migrate upstream to their spawning grounds (See chapter 1; Ben-David et al., in review *a*). Adjusting

time of parturition to coincide with the beginning of the salmon run provides the female mink with unlimited food availability throughout lactation. For all species of Pacific salmon, spawning migration occurs later with decreasing latitudes (Burgner, 1991; Healy, 1991; Heard, 1991; Salo, 1991; Sandercock, 1991). This trend is similar to the trend of timing of reproduction in mink along the Pacific Northwest coast (Figure 13), suggesting that timing of reproduction in female mink in this geographic area is adjusted to coincide with optimal food availability. In comparison, female martens captured in the same study area on Chichagof Island (Ben-David and Flynn, *in press*) did not shift their timing of reproduction. Levels of blood progesterone obtained from female martens suggest that parturition occurred in late April to early May (Ben-David and Flynn, in press). Although martens feed on salmon carcasses during years of low availability of rodents, this food is ignored when rodents are plentiful (See chapter 3; Ben-David et al., in review *b*), suggesting that martens are less dependent on salmon than are mink.

Male mink in the study area had enlarged testes as early as mid-March, and testicle size declined soon after mating. Similarly, Johnson (1985) captured male mink with enlarged testes as early as February 23 on Prince of Wales Island and testicle size declined during early July. Hatler (1976) reported similar dates for changes in testicle size for male mink from Vancouver Island. These observations suggest that male mink in the coastal Pacific Northwest are reproductively active from February - March as would be expected from day length in these latitudes. In all three locations (Chichagof Island, Prince of Wales Island, and Vancouver Island) males seemed to be capable of mating long before copulations occurred, and testicle size in each location declined shortly after mating. Therefore male mink likely responded primarily to photoperiodism in initiating reproduction, but timing of reproduction in female mink, along the coastal Pacific Northwest, is shifted in response to the dynamics of food availability. The observation that timing of mating of mink on Chichagof Island, Prince of Wales Island, and

Vancouver Island has shifted instead of a change in the length of the embryonic diapause suggests that mink are limited in their capability to maintain a longer delay of blastocyst implantation. This in turn raises questions about the cost, and adaptive significance of delayed implantation, and merits further investigation.

Acknowledgment

I wish to thank J. Simonson, C. Zank, M. Kemp, N. Olmstad, M. Rosing, B. Wissing, and S. Lewis for valubale assistance in the field. Drs. D. R. Klein, D. M. Schell, R. T. Bowyer, M. W. Oswood, T. A. Hanley, and J. E. Blake provided helpful comments on earlier versions of the manuscript. Funding for the project was provided by the USDA Forest Service, Pacific Northwest Research Station, Juneau; Alaska Cooperative Fish and Wildlife Research Unit; Water Research Center, University of Alaska Fairbanks.

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Chapter 3–Annual and seasonal changes in diets of martens: evidence from stable isotope analysis

Merav Ben-David, Rodney W. Flynn, and Donald M. Schell

Abstract

Theory predicts that generalist predators will switch to alternative prey when preferred foods are not readily available. Studies on the feeding ecology of the American marten (*Martes americana*) throughout North America suggest that this mustelid is a generalist predator concentrating largely on voles (*Microtus* sp.; *Clethrionomys* sp.). We investigated seasonal and annual changes in diets of martens in response to the changing abundance of small rodents (*Peromyscus keeni*, and *M. longicaudus*) on Chichagof Island, Southeast Alaska, using stable isotope analysis. We hypothesized that martens would feed primarily on small rodents during years with high abundance of these prey species, whereas during years of low abundance of prey, martens would switch to feed primarily on the seasonally available carcasses of salmon. We also hypothesized that home-range location on the landscape (i.e., access to salmon streams) would determine the type of food consumed by martens, and martens feeding on preferred prey would exhibit better body condition than those feeding on other foods. We live captured 75 martens repeatedly, from mid-February to mid-December 1992–1994. We also obtained marten carcasses from trappers during late autumn 1991 and 1992, from which we randomly sub-sampled 165 individuals. Using stable isotope ratios and a multiple-source mixing model, we noted that salmon carcasses composed a large portion of the diet of martens in autumn during years of low abundance of rodents (1991 and 1992). When small rodents were available in high numbers (1993 and 1994), they composed the bulk of the diet of martens in autumn, despite salmon carcasses being equally available in all years. Selection for small rodents occurred only in seasons in which abundance of small rodents was low. Logistic regression revealed that individuals with access to salmon

streams were more likely to incorporate salmon carcasses in their diet during years of low abundance of small rodents. Using stable isotope analysis on repeated samples from the same individuals, we explored some of the factors underlying feeding habits of individuals under variable ecological conditions. We were unable to demonstrate that body weights of live-captured male and female martens differed significantly between individuals feeding on marine-derived or terrestrial diets. Therefore, martens, as true generalist predators, switched to alternative prey when their principal food was not readily available on a seasonal or annual basis. Although salmon carcasses were not a preferred food for martens, they provided a suitable alternative to maintain body condition during years when small rodents were not readily available.

Introduction

Studies on the feeding ecology of the American marten (*Martes americana*) throughout North America suggest that this mustelid is a generalist predator, feeding on a large variety of prey such as small mammals, birds, invertebrates, fish, ungulate carrion, and vegetation (Martin, 1994 for review). Most studies identified voles (*Microtus* sp. and *Clethrionomys* sp.) as the most common prey in diets of marten (Buskirk and MacDonald, 1984; Douglas et al. 1983; Martin, 1987; Thompson and Colgan, 1990; Weckwerth and Hawley, 1962; Martin, 1994). These studies, however, differed in their conclusion as to whether martens responded opportunistically to prey abundance (Campbell, 1979; Gordon, 1986; Soutiere, 1979) or actively selected for this prey (Buskirk and MacDonald, 1984; Douglas et al. 1983; Martin, 1987; Thompson and Colgan, 1990). Foraging theory predicts that animals will select food items that result in energy returns equal to or higher than the energy expended on locating, capturing, and consuming that food (Pyke et al., 1977), and that generalist predators will switch to alternative prey when preferred foods are not readily available (Taylor, 1984). During years of low abundance of small rodents encounter rates of martens with these prey, would likely be reduced. Under such circumstences, other food items, should be of increased dietary importance. Dietary specialization, through resource selection (i.e., resource use disproportionate to its availability; Manly et al., 1993), can lead to increased vulnerability and possibly a numerical response of predators when the availability of principal food declines (King and Moors, 1979). During our study of the ecology of martens on Chichagof Island, Southeast Alaska from 1991 to 1994, rodent populations (*Peromyscus keeni*, and *Microtus longicaudas*) fluctuated widely. We investigated seasonal and annual changes in diets of martens in response to the changing abundance of small rodents.

From late summer through autumn, spawning Pacific salmon (*Oncorhynchus* sp.) carry marine-derived nutrients into streams and rivers along the Pacific Northwest, and subsequently fertilize those systems through their decomposition

and consumption (Cederholm et al., 1989; Kline et al., 1989; Kline et al., 1993; Piorkowski, 1995; Richey et al., 1975). Salmon carcasses are easy for martens to obtain during spawning runs because other predators such as brown bears (*Ursus arctos*), bald eagles (*Haliaeetus leucocephalus*), and river-otters (*Lutra canadensis*) often leave carcasses partially eaten (Cederholm et al., 1989). We hypothesized that martens would feed principally on small rodents during years with high abundance of these prey species, whereas during years of low abundance martens would include more salmon carcasses in their diet, as these salmonids became seasonally available.

Cederholm et al. (1989) reported that <4% of all salmon carcasses were washed down stream, and most were retained in the riparian zone. Because salmon carcasses usually occur in the vicinity of streams (Cederholm et al., 1989), and martens typically exhibit intrasexual territoriality (Powell, 1994), only resident martens with home ranges adjacent to salmon streams would have this resource available. Individuals without access to salmon streams would not benefit from such a resource. Therefore, we hypothesized that location of the home range on the landscape (i.e., access to salmon streams) would determine the diet of martens.

Small mustelids, including the American marten, store little body fat compared with other mammals (Harlow, 1994), and show little seasonal variation in accumulation of body fat (Buskirk and Harlow, 1989). Martens appear to compensate for their deficiency in accumulating fat by using several physiological (e.g., metabolism of muscle tissue) and behavioral adaptations, one of which is optimizing food intake by diet selection (Harlow, 1994). We investigated body condition of martens with different diets, and hypothesized that martens feeding on rodents would exhibit better body condition than those feeding on other foods.

We used stable isotope ratios to indicate marten diets. In nature carbon and nitrogen each occur as two stable isotopes: ^{12}C and ^{13}C ;^{14}N and ^{15}N. Ratios of the

two isotopes as compared with standards are noted as ^{13}C for carbon and ^{15}N for nitrogen, and are measured in parts per thousand (‰; Ehleringer and Rundel, 1988). The analysis of food webs using natural abundance of stable isotope ratios compares the ^{13}C and ^{15}N values of tissues from predator and prey. Values of ^{13}C differ between terrestrial and marine food sources due to differential assimilation of ^{13}C by primary producers in these ecosystems, and enable tracing food webs (Fry and Sherr, 1988; Tieszen and Button, 1988). Values of ^{15}N increase with transfer between trophic levels and therefore reflect both diet and trophic levels (DeNiro and Epstein, 1981). The specific combination of values of ^{13}C and ^{15}N result from the dietary interaction of species or individuals (Ambrose and DeNiro, 1986; Gearing, 1991; Hobson, 1991; Schell et al., 1988; Schoninger and DeNiro, 1984). Applying this technique to tissues, such as blood, allows repeated sampling of known individuals throughout the year (Hobson, 1991). Using this technique, on repeated samples from the same individuals, enabled us to investigate, for the first time, some of the factors underlying feeding habits of individuals in different seasons and years.

Methods

Study area

Our study area was located on Chichagof Island in Southeast Alaska, USA (Tenakee Springs at 57° 52' N 135° 18' W; Figure 1). The island, one of the three large northern islands of the Alexander Archipelago, is part of the Tongass National Forest. The archipelago has a maritime climate; summers are cool and wet and winters are characterized by deep snow (2,360 mm annual precipitation). The snow-free period extends from early May to early November at lower elevations. Vegetation at higher elevations is typically alpine tundra, and in lower elevations coastal, old-growth forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with well-developed understory (mainly *Oplopanax horridus*, *Vaccinium* sp., *Menziesia ferruginea*, and *Rubus* sp.). Our study area encompasses six streams that support an annual run of spawning Pacific salmon (*Onchorhynchus gorbuscha*, *O. keta*, and *O. kisutch*), from late summer to late autumn. Potential prey among the mammalian fauna of the island include: Keen's deer mice (*Peromyscus keeni*), long-tailed voles (*Microtus longicaudas*), red squirrels (*Tamiasciurus hudsonicus*), common shrews (*Sorex cinereus*), and Sitka black-tailed deer (*Odocoileus hemionus sitkensis*). The resident avian fauna includes Steller's jay (*Cyanocitta stelleri*), spruce grouse (*Dendragapus canadensis*), and winter wren (*Troglodytes troglodytes*). Other song birds such as dark-eye junco (*Junco hyemalis*), robin (*Turdus migratorius*), varied thrush (*Ixoreus naevius*), hermit thrush (*Catharus guttatus*), and Swainson's thrush (*Catharus ustulatus*), arrive on the island for the breeding season in early May and depart during September.

Sampling martens

We live captured 75 martens repeatedly, from mid-February to mid- December in 1992 to 1994, using Tomahawk live traps (models 203 and 205; Tomahawk Live Trap Co., Tomahawk, WI). After immobilization with an injection of Ketamine Hydrochloride (15 mg/kg body weight; Aveco, Fort Dodge, IW) and Xylazine

Hydrochloride (2 mg/kg body weight; Vedco, St. Joseph, MI), each individual was measured, weighed (to nearest 5 g), and marked with ear tags (size 1, style 1005; National Band and Tag Co., Newport, KY) or a passive integrated transponder (PIT) tags (Biosonics, Seattle, WA). A vestigial first premolar was extracted from all newly captured martens for age determination using counts of cementum annuli (Poole et al., 1994; Matson's Laboratory, Milltown, MT). A blood sample of 2 cc was drawn from the jugular vein, and stored in a glass or plastic vial. Most new captures were fitted with radiocollars (Telonix, Mesa, AZ), and radiocollars were replaced on recaptured martens as needed. A 30-g radio collar (MOD-070, expected life of 8 months) was placed on females, and a 49-g collar (MOD-080, expected life 18 months) was placed on males. Upon recovery from sedation, we released animals at their sites of capture. Blood was spun at 3,000 rpm for 5 min., using a manual centrifuge, within 2 hours after collection, and serum was siphoned into a separate vial. Both serum and samples of clotted blood-cells were then frozen until analysis. In later analyses, samples were pooled by season,based on ecological changes. For instance, summer samples were those collected from late-May to the end of August, covering the time of vegetation green-up and breeding of song birds. Autumn samples were those collected from September to late-December, representing the period of the main abundance of salmon carcasses. Winter- Spring samples were those collected from mid-February to early May representing the period of snow cover.

We obtained 610 carcasses of martens from trappers on Chichagof Island during the December 1991 to January 1992 and December 1992 trapping seasons. For each marten carcass, data on site and date of capture were recorded. We determined sex, measured body length, and weight (to nearest 5 g) for each carcass before removal of viscera, uterus, ovaries, and premolar teeth. Carcasses of 165 martens were selected randomly for this analysis. From each of these individuals, a muscle sample of 5 to 10 g was excised from the hind leg for stable

isotope analysis. Carcasses were subsequently aged using cementum annuli of premolar teeth (Matson's Laboratory, Milltown, MT).

Position of home range on the landscape

We located radio-collared martens from a small aircraft (Mech, 1974; Kenward, 1987) during daylight hours every 2 weeks throughout the year. The location of each marten was plotted on high-resolution, orthophoto maps (scale 1:31,680) while circling in the aircraft above the location. Error was determined by retrieving dead individuals and was estimated at 110 m. Aerial locations were plotted on digital versions of the orthophoto maps using geographic information system (GIS) on a personal computer to determine x, y coordinates. We estimated annual home ranges of resident martens from the radio-telemetry locations using the computer program HOME RANGE (Ackerman et al., 1990). Locations were tested for independence (Swihart and Slade, 1985), and outliers were examined (Samuel et al., 1985). Locations were not significantly autocorrelated ($P > 0.05$), and therefore no locations were excluded. We used 95% minimum convex polygons (MCP) to describe home range area for each marten (Ackerman et al., 1990). This method excludes irregular excursions from the delineation of the home range area, but tends to underestimate home range size. Animals that moved over an area > 2 home ranges within any season sampled, and covered areas that were occupied by resident martens, were considered transients. Digital GIS maps of the study area were obtained from the USDA Forest Service, Tongass National Forest. These maps demarcated stream segments used by anadromous fish and beach fringe habitats. Landscape position of home range for each marten was determined by over-laying the home range plot on the GIS maps. A home range that included a segment of an anadromous fish stream or beach fringe habitat was considered to have marine resources available.

Abundance of Small Rodents

We monitored annual trends in abundance of Keen's deer mice, and long tailed voles by trapping along 3 permanent transects during autumn (September–October) of each year from 1991 to 1994. Each transect consisted of 25 stations at 15 m intervals. Two snap traps (museum specials) were placed at each station, baited with rolled oats and peanut butter, and set for 3 consecutive nights. Seasonal changes in abundance of small mammals were monitored at 7 to 13 trapping grids during summer (mid-May to mid-August), autumn (October to November), and spring (March to early May) from summer 1992 to autumn 1993. Each grid contained 25 Sherman live traps set in 20 by 20 m arrangement, baited with rolled oats and peanut butter, and set for 3 consecutive nights. Keen's deer mice and long-tailed voles, were marked with paint on their nape and released; a sub-sample of 2 individuals per species per trap site was selected randomly, and euthanized with Halothane (Halocarbon, River Edge, NJ). A muscle sample was collected from each euthanized individual for stable isotope analysis. We expressed abundance of small rodent as number caught per 100 trap nights during the three night of sampling. Recaptures were not included in this count. All methods used in this study were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks.

Sampling prey

Muscle samples from Keen's deer mice, long tailed voles, and red squirrels were collected from small rodents trapped on the grids, and from a companion study by T.A. Hanley (USFS, Pacific Northwest Station), for stable isotope analysis. The remainder of each carcass was prepared as a museum specimen (including frozen tissues) and archived at the University of Alaska Museum. Tissue samples from salmon carcasses, deer carcasses were collected when encountered (permit ADFG 90-16) or obtained from hunters. Song birds (winter wrens, dark-eye juncos, robins, and thrushes) were collected when encountered (permit ADFG 90-16). Berry samples were collected from 11 vegetation transects

(500 m long) from the riparian to the upland habitats and at 100 m intervals. Additional samples of berries were collected at higher elevations and at beach fringe habitats. The berry samples included: blueberries (*Vaccinium* sp.), salmon berries (*Rubus spectabilis*), cloudberries (*Rubus chamaemorus*), stink current (*Ribes bracteosum*), Pacific crab apple (*Malus fusca*) and devil club (*Oplopanax horridus*).

Analysis of Stable Isotope Ratios

Tissues (clotted blood-cells, muscle samples, and vegetation samples) were kept frozen until preparation for determination of stable isotope ratios. Samples were dried at 60° to 70° C for 48 hours and then ground to fine powder using a Wig - L - Bug grinder (Cresent Dental Co.). Subsequently, a sub-sample (1– 1.5 mg for animal tissues and 8-10 mg for plant tissues) was weighed into a miniature tin cup (4 by 6 mm) for combustion. We used a Europa C/N continuous flow mass-spectrometer to obtain the stable isotope ratios. Each sample was analyzed in duplicate and results were accepted only if the variance between the duplicates did not exceed that of the peptone standard (CV = 0.1).

We determined the diet source for each marten based on the combined values of ^{13}C and ^{15}N. We developed a dual-isotope multiple-source mixing model, based on the conceptual one proposed by Kline et al. (1993), to estimate of the contribution of each prey to the diet of the predator. This model uses the mean ^{13}C and ^{15}N value of each type of prey. This mean value (*A, B, C,* etc.) is then corrected for the enrichment in predator ratios compared with its diet (i.e., fractionation values; *A′, B′, C′,* etc.; DeNiro and Epstein, 1981; Kline et al., 1993; Tieszen and Button, 1988; Figure 14). Euclidean distance between the corrected isotopic values of prey and each individual predator (i.e. the length of the line connecting *A′* and *P, B′* and *P,* etc.; Figure 14) is then calculated by $z = \sqrt{x^2 + y^2}$. The contribution of each prey to the diet of the predator is inversely related to the distance between the corrected signature of the prey and the predator (i.e., the shorter the distance the greater the contribution). Because of this inverse relationship, the relative

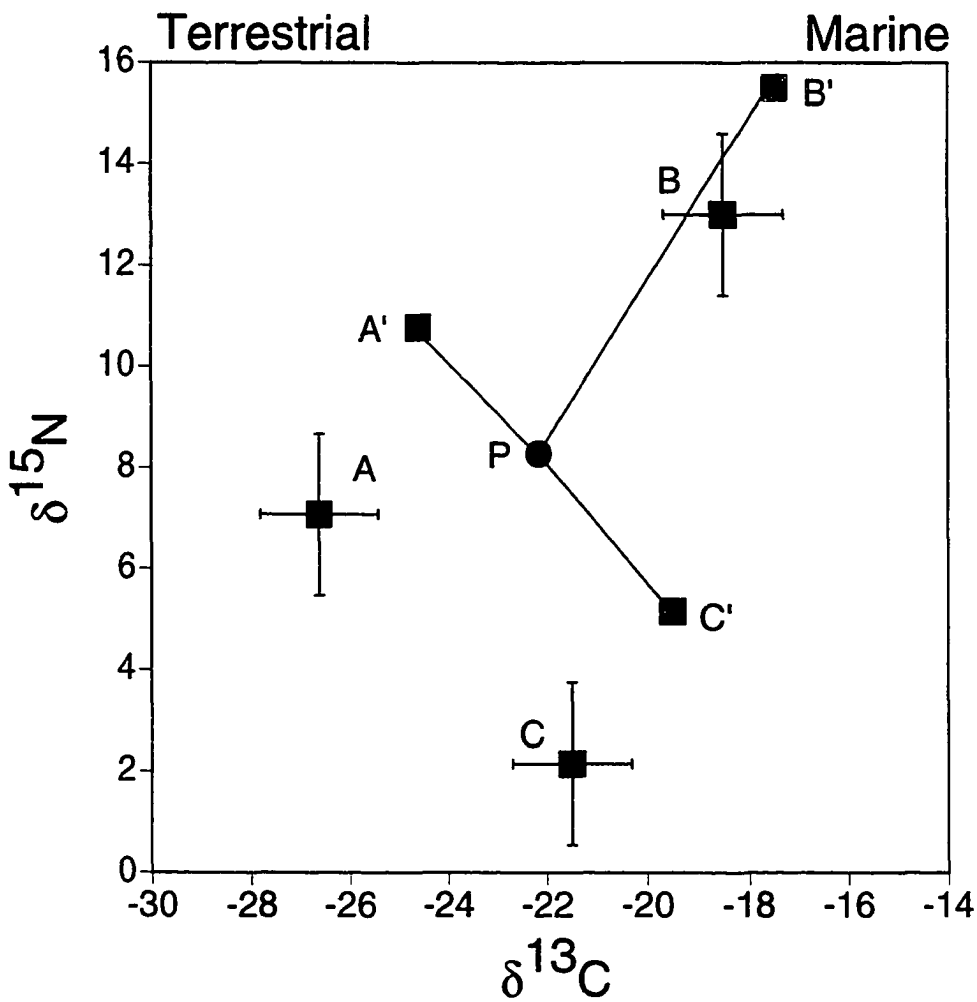

Figure 14. Dual isotope, three-source mixing model with variable fractionation values. This model uses the mean ^{13}C and ^{15}N value of each type of prey in a bivariate space. This mean value (*A, B, C*, etc.) is then corrected for the enrichment in predator ratios compared with its diet (i.e., fractionation values; *A', B', C'*, etc.). Euclidean distance between the corrected isotopic values of prey and that of each individual predator (i.e. the length of the line connecting *A'* and *P*, *B'* and *P*, etc.), is then calculated by $z = \sqrt{x^2 + y^2}$. The relative contribution of each prey to the predator's diet is inversely related to the distance between the corrected signature of the prey and that of the predator (i.e. the shorter the distance the greater the contribution).

contribution of each prey is calculated by:

$$\% X \text{ in diet} = \frac{PX'^{-1}}{PA'^{-1} + PB'^{-1} + PC'^{-1}} \times 100, \qquad \text{where } X' \text{ is } A', B' \text{ or } C'.$$

The mixing model requires that isotopic values of all prey be significantly different from each other. This model assumes that each individual predator consumes all possible types of prey. Therefore this model will tend to overestimate the proportion of food items that are rarely consumed and underestimate the proportion of commonly used prey. Consequently, we used the model as an index of prey consumption rather than as actual proportions in the diet.

We used fractionation values of 2 ‰ for carbon when mammalian prey, avian prey, and berries were consumed, and 1 ‰ when salmon was consumed, based on results from feeding experiments in captivity (Appendix A; S. Farley and C. Robbins, pers. comm.). Also, we used fractionation values of 3 ‰ for nitrogen when mammalian prey, avian prey, and berries were consumed and 2 ‰ when salmon was consumed (Appendix A). Because stable isotope values of clotted blood-cells did not differ significantly from those of muscles in experiments on captive mink (Appendix A), we pooled data obtained from live animals and those of carcasses in some of our analyses.

Statistical Analysis

We employed K nearest-neighbor randomization test (Schilling, 1986; Appendix C; Rosing et al., in review) to investigate whether stable isotope ratios of all possible prey types sampled were significantly different from each other by season. In this test the values of ^{13}C and ^{15}N are treated as spatial data because the unit of measurement in both variables is equal and stable. This test uses the Bonferroni correction when all food items are compared with each other (Appendix C; Rosing et al., in review). After calculating the relative contribution of each food item to the diet of each individual marten using the multiple-source mixing-model, we calculated the mean (± SE) for the entire sample in each season.

We then explored the changes in percentages of each food item between seasons and years using Kruskal-Wallis test with multiple comparisons (Zar, 1984; BMDP; Dixon, 1990).

We compared abundance of small rorents between seasons and years using Pearson's χ^2 test (BMDP; Dixon, 1990). Changes in stable isotope ratios of marten tissues (from live captured animals and carcasses) were investigated with one-way ANOVA with multiple comparisons (SAS, 1985). To test our hypothesis that diet of martens changed in relation to abundance of small rodents, we compared the results of the stable isotope analysis with abundance of small rodents using correlation analysis (Zar, 1984). To test whether the proportion of small rodents in marten diets differed in relation to their seasonal abundance we used a χ^2 goodness-of-fit test, and selection ratios (w_i) with Bonfferoni confidence intervals (Manly et al., 1993). In this analysis we used the proportions of small rodents obtained from the mixing model divided by the proportion of rodents captured in our surveys. Our analysis differs from the conventional use of selection ratios (Manly et al., 1993), because we used a measure of abundance of rodents (captures/ trap night) rather than a proportion of total food availability.

To identify the factors affecting diets of martens (for live captured martens only) as represented by stable isotope ratios, we introduced the following variables to a logistic-regression model (BMDP; Dixon, 1990): sex, age, year (as representative of prey abundance), season, and home range location on the landscape (Table 8). For the step-wise logistic regression, marine diets were coded 1, and terrestrial diets were coded 0 (Hosmer and Lemeshow 1989). We controlled for multicollinearity at $r > |0.45|$, and ensured that these data did not depart from a logistic-regression model with Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow, 1989).

To test our hypothesis that body weight will be related to prey choice and season, we used a two-way ANOVA on ranks with multiple comparisons (Conover

Table 8. Description of variables collected from live martens (n = 75) that were captured repeatedly between June 1992 and October 1994, on Chichagof Island, Southeast Alaska (total samples n = 155).

VARIABLE	DEFINITION AND METHODS
DEPENDENT VARIABLE	
Diet	Marine source (> 50% of diet as determined from the mixing model) coded 1, terrestrial source (> 50% of diet as determined from the mixing model coded 0.
INDEPENDENT VARIABLES	
Sex	Categorical variable coded 1 for males and 2 for females.
Age	Continuous variable as determined from cementum annuli.
Year	Categorical variable coded 1992, 1993 and 1994 representing low, moderate, and high small rodent abundance respectively.
Season	Categorical variable coded 1 for summer, 2 for autumn,and 3 for spring.
Home range location	Categorical variable coded 1 for home ranges located within 150m from salmon stream or beach fringe habitat, 2 for home ranges located further than 150 m from salmon stream or beach fringe habitat, and 3 for transient animals.

and Iman, 1988; SAS, 1985) on data collected from live-captured male and female martens.

Results

The K nearest-neighbor randomization test revealed that in each season (Figures 15 - 18) the stable isotope ratios of prey were significantly different from each other, except for deer mice and voles ($P = 0.2606$), and the different species of berries ($P = 0.1643$). Therefore, we were unable to measure the contribution of voles in the diet independently of deer mice using the stable isotope analysis and pooled them as one diet group, which we termed small rodents. Similarly, we treated all species of berrie as one category. Isotopic signatures of squirrels were enriched in ^{13}C (Figures 15 - 18) because of enrichment in ratios of spruce seeds (Appendix B), rather than from consumption of marine-derived nutrients. We were unable to capture voles in spring and therfore were unable to measure their contribution to the diet in that season. If the signature of voles is not significantly different than that of deer carcasses, then our results for the proportion of deer carcasses in the diet were inflated.

Diets of martens in autumn showed high variability in composition (Figure 15 and Figure 16). Some individuals relied heavily on salmon carcasses (> 35 % of diet; Table 9), whereas others fed mainly on small rodents (> 35 % of diet; Table 9). The other individual martens ate differing combinations of all types of food (Table 9). Berries composed 14% ± 0.3 (Mean ± SE) to 31% ± 2.2 of the diet , and squirrels between 15% ± 0.4 and 22% ± 0.8 (Table 10). The average percent of berries in the diets of martens increased significantly between autumn 1992 and autumn 1993, and between autumn 1993 and autumn 1994 (Table 10; Kruskal-Wallis, $P < 0.001$), as did small rodents (Table 10; Kruskal-Wallis, $P < 0.001$). At the same time, the average percent of salmon decreased significantly (Table 10; Kruskal-Wallis, $P < 0.001$). Percentages of squirrel in the diet significantly decreased only between autumn 1993 and autumn 1994 (Table 10; Kruskal-Wallis, $P = 0.005$).

In spring (Figure 17), 91% of 56 martens ate a combination of small rodents, winter-killed deer carcasses, and squirrels. Some martens (9%, n = 56), however,

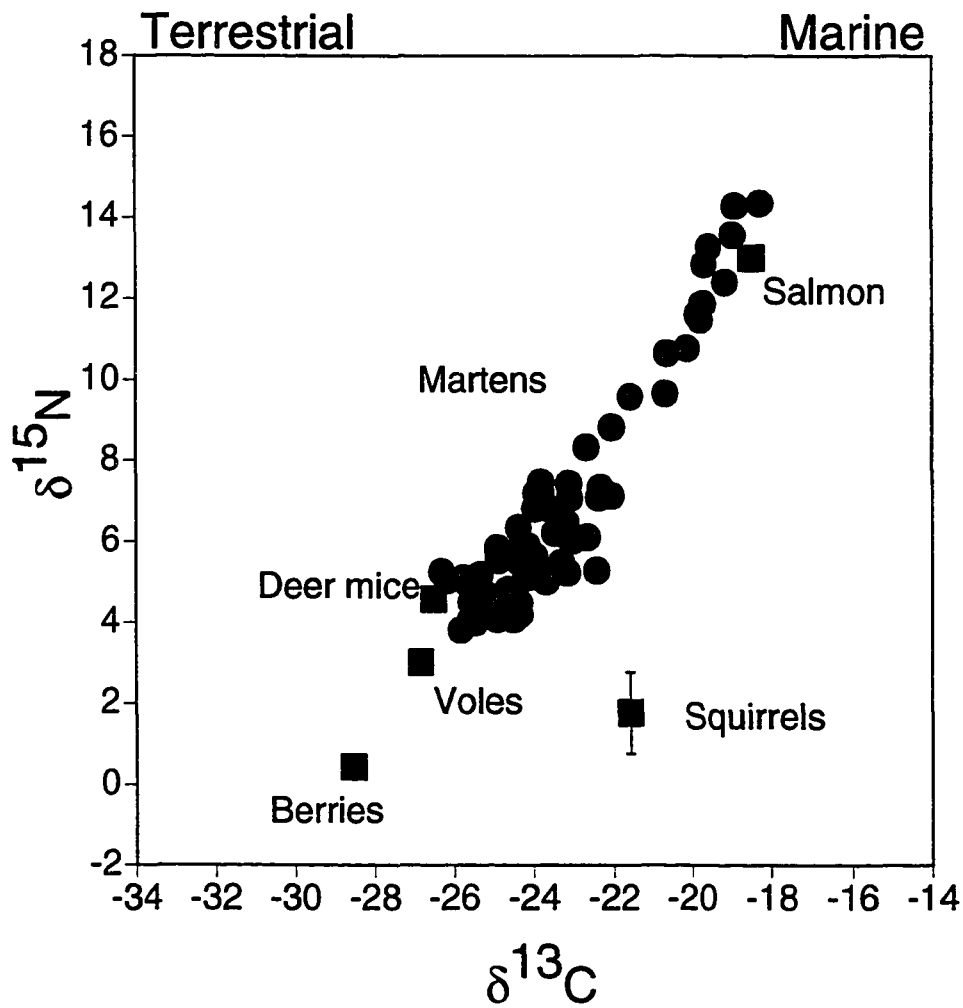

Figure 15. ^{13}C and ^{15}N values for live martens captured in autumn 1992 - 1994, on Chichagof Island, southeast Alaska (n = 75). Mean values ± SE are given for berries (n = 8), squirrels (n = 8), deer mice (n = 26), voles (n = 23), and salmon (n = 18)

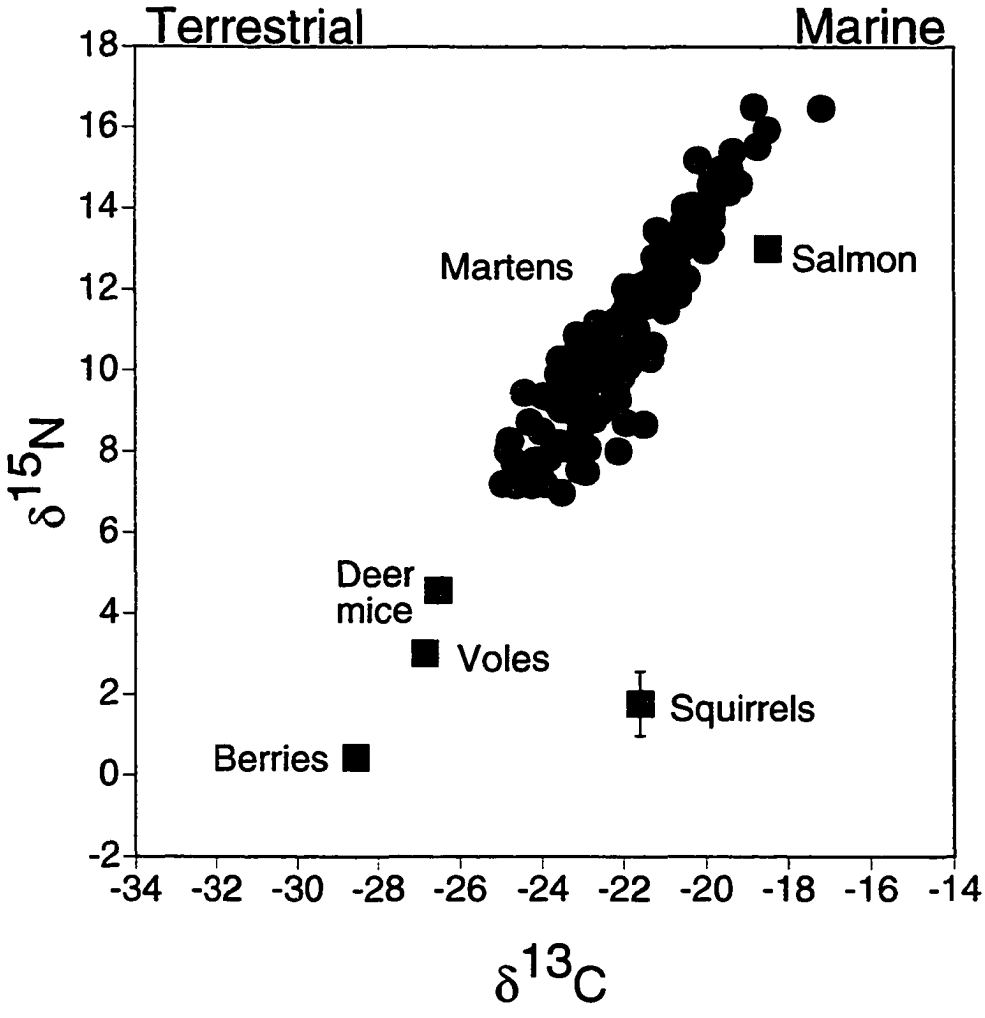

Figure 16. ^{13}C and ^{15}N values for marten carcasses collected in autumn and early winter 1991 - 1992, on Chichagof Island, southeast Alaska (n = 165). Mean values ± SE are given for berries (n = 8), squirrels (n = 8), deer mice (n = 26), voles (n = 23), and salmon (n = 18).

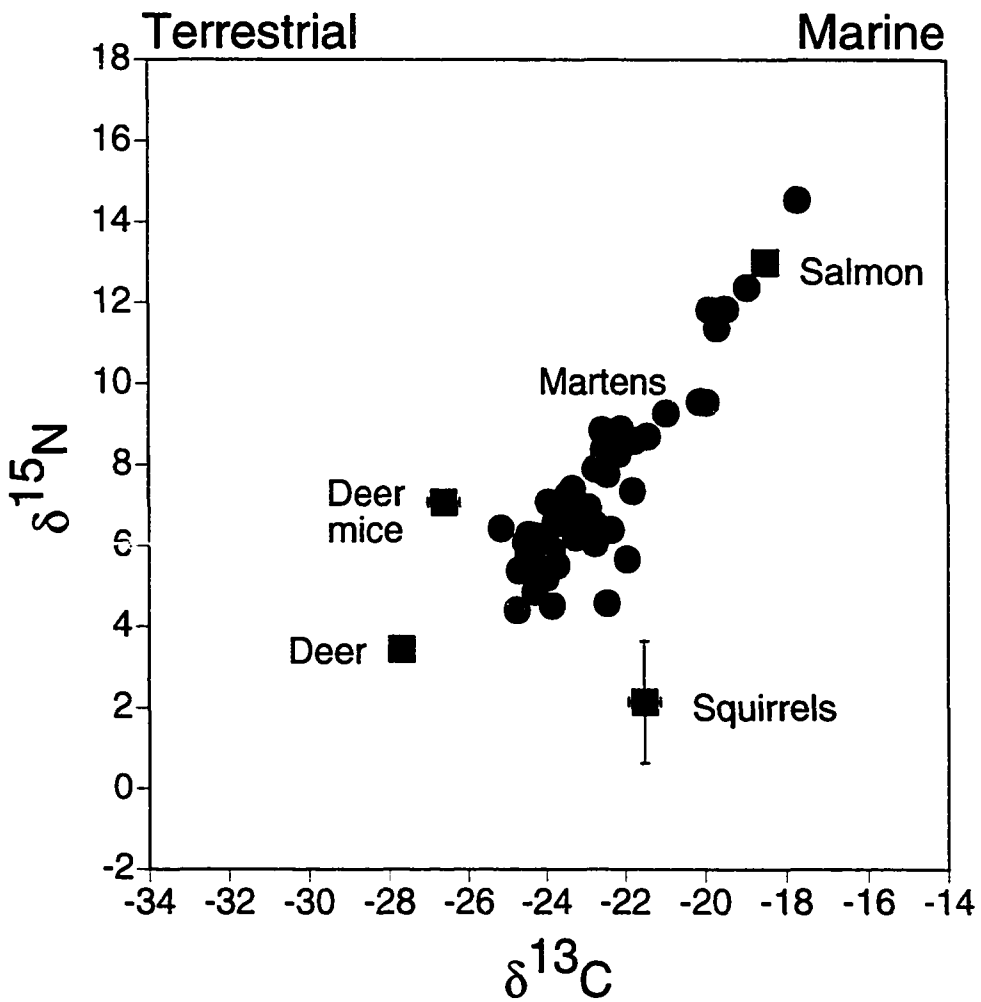

Figure 17. ^{13}C and ^{15}N values for live martens captured in spring 1993–1994, on Chichagof Island, southeast Alaska (n = 40). Mean values ± SE are given for deer (n = 14), squirrels (n = 5), deer mice (n = 18), and salmon (n = 18).

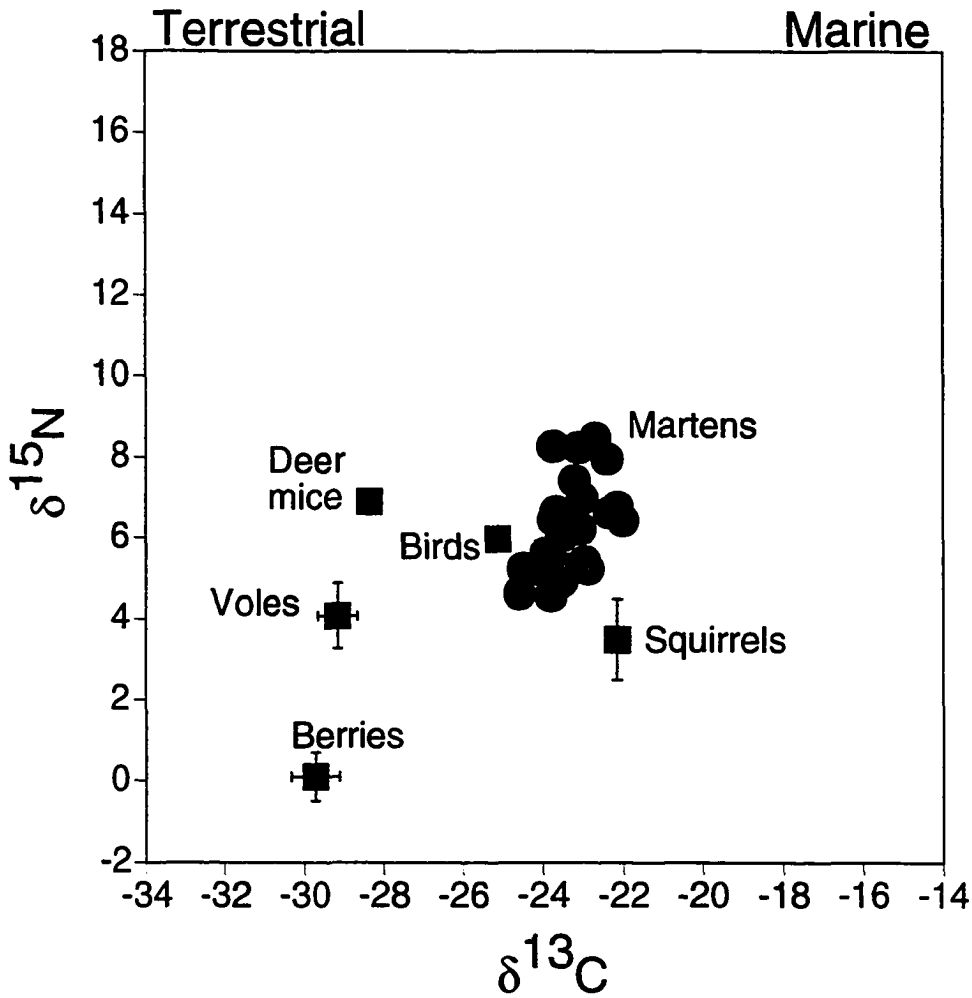

Figure 18. ^{13}C and ^{15}N values for live martens captured in summer 1992–1994, on Chichagof Island, southeast Alaska (n = 25). Mean values ± SE are given for berries (n = 57), squirrels (n = 10), deer mice (n = 55), birds (n = 24), and voles (n = 5).

Table 9. Proportions of martens that include >35% of salmon in their diet, and >35% of small rodents in their diet. Samples collected on Chichagof Island, Southeast Alaska From 1991 to 1994. Percentages of prey in the diet were calculated by the multiple-source mixing model.

Year	n	Proportion of martens
Small Rodents		
1991	39	0.41
1992	133	0.46
1993	40	0.65
1994	28	0.93
Salmon		
1991	39	0.28
1992	133	0.39
1993	40	0.10
1994	28	0.00

had a stable isotope signature characteristic of marine-derived diet (Figure 17). The average percent of deer carcasses in the diet increased in spring 1994 (Table 10; Kruskal-Wallis, $P = 0.032$), corresponding to a significant decrease in the percentage of marine derived-nutrients (Table 10; Kruskal-Wallis, $P = 0.029$).

Martens ($n = 25$) fed on different combinations of small rodents, berries, squirrels, and birds in summer (Figure 18). The average percentage of berries increased significantly in summer 1994 compared with the previous two summers (Table 10; Kruskal-Wallis, $P = 0.015$). Similarly, a significant increase occurred in the percentage of small rodents in summer 1994 (Table 10; Kruskal-Wallis, $P = 0.027$). Although the percentage of birds decreased between summer 1992 and 1993 (Table 10; Kruskal-Wallis, $P = 0.011$), no change occurred between summer

Table 10. Relative contribution (mean ± SE) of prey item to the diet of martens (n), captured on Chichagof Island, Southeast Alaska, during 1992–1994. Percentages were calculated using the multi-source mixing model. Letters represent significant difference in percent at $\alpha = 0.05$ (Kruskal-Wallis test with multiple comparisons).

	Percent in diet of martens					
	Summer 92 n = 8		Summer 93 n = 7		Summer 94 n = 9	
	%	SE	%	SE	%	SE
Berries	13[a]	2.1	15[a]	2.1	22[b]	2.0
Small Rodents	18[a]	1.4	17[a]	0.8	21[b]	0.4
Birds	47[a]	5.5	33[b]	3.4	30[b]	1.8
Squirrels	22[a]	2.4	35[b]	2.5	27[c]	0.8

	Autumn 91 n = 39		Autumn 92 n = 133		Autumn 93 n = 40		Autumn 94 n = 28	
	%	SE	%	SE	%	SE	%	SE
Berries	15[a]	0.5	14[a]	0.3	20[b]	1.2	31[c]	2.2
Small Rodents	37[a]	2.9	34[a]	1.4	40[b]	2.2	45[b]	2.6
Salmon	29[a]	2.5	33[a]	1.7	13[b]	1.7	7[c]	0.2
Squirrels	20[a]	0.8	19[a]	0.4	22[a]	0.8	15[b]	0.4

	Spring 93 n = 21		Spring 94 n = 35	
	%	SE	%	SE
Deer Carcasses	34[a]	3.5	43[b]	2.3
Small Rodents	24[a]	1.5	25[a]	1.1
Salmon	18[a]	2.2	11[b]	1.0
Squirrels	23[a]	1.8	22[a]	1.0

1993 and 1994 (Table 10). Squirrels, however, increased in the diet between summer 1992 and summer 1993, but decreased in 1994 (Table 10; Kruskal-Wallis, $P < 0.001$).

Numbers of small rodents in our study area significantly differed between years (χ^2 test, $df = 3$, $P < 0.001$). In 1991, rodent numbers were in decline, especially long-tailed voles (Figure 19), and reached a minimum in 1992. In 1993, rodent numbers recovered to a moderate level, and in 1994 rodents were abundant (Figure 19). Our analysis showed that stable isotope ratios of marten tissues (live-captured and trapper caught) differed significantly between years (ANOVA; $P < 0.001$) (Figure 19). The proportion of squirrels in autumn diets did not significantly differ between 1991, 1992, and 1993 and decreased significantly in 1994 (Table 10), suggesting that the enrichment in ^{13}C values in martens tissues resulted from incorporation of salmon carcasses in the diet. The high correlation (r = -0.988) between the isotope ratios of carbon for marten tissues and abundance of small rodents suggests that during years of low abundance of small rodent (1991 and 1992) martens switched to feed on salmon carcasses (Figure 19). Nonetheless, when small rodents were available in high numbers (1993 and 1994), martens reduced the consumption of salmon carcasses, although these prey were as available to them as in previous years.

Seasonal changes in food availability resulted from several ecological phenomena. Breeding song birds arrived on our study area in early summer and departed in early autumn of each year. In addition, most species of berries produced fruits during summer (July - August). Only blueberries, berries of stink current and crab apples were available to martens in autumn (early October). Salmon carcasses became available to martens in late summer (August), and the spawning run extended into late November of each year. Winter-killed deer became available to martens in January, while carcasses from hunter kills were available as early as October. Numbers of small rodents changed significantly between seasons (χ^2 test, $df = 4$, $P < 0.001$) in 1992 and 1993. This difference was a result of change in numbers between summer and autumn (Figure 20), but no significant difference occurred between autumn and spring or spring and summer (Figure 20). This suggests that the rodent population in our study area

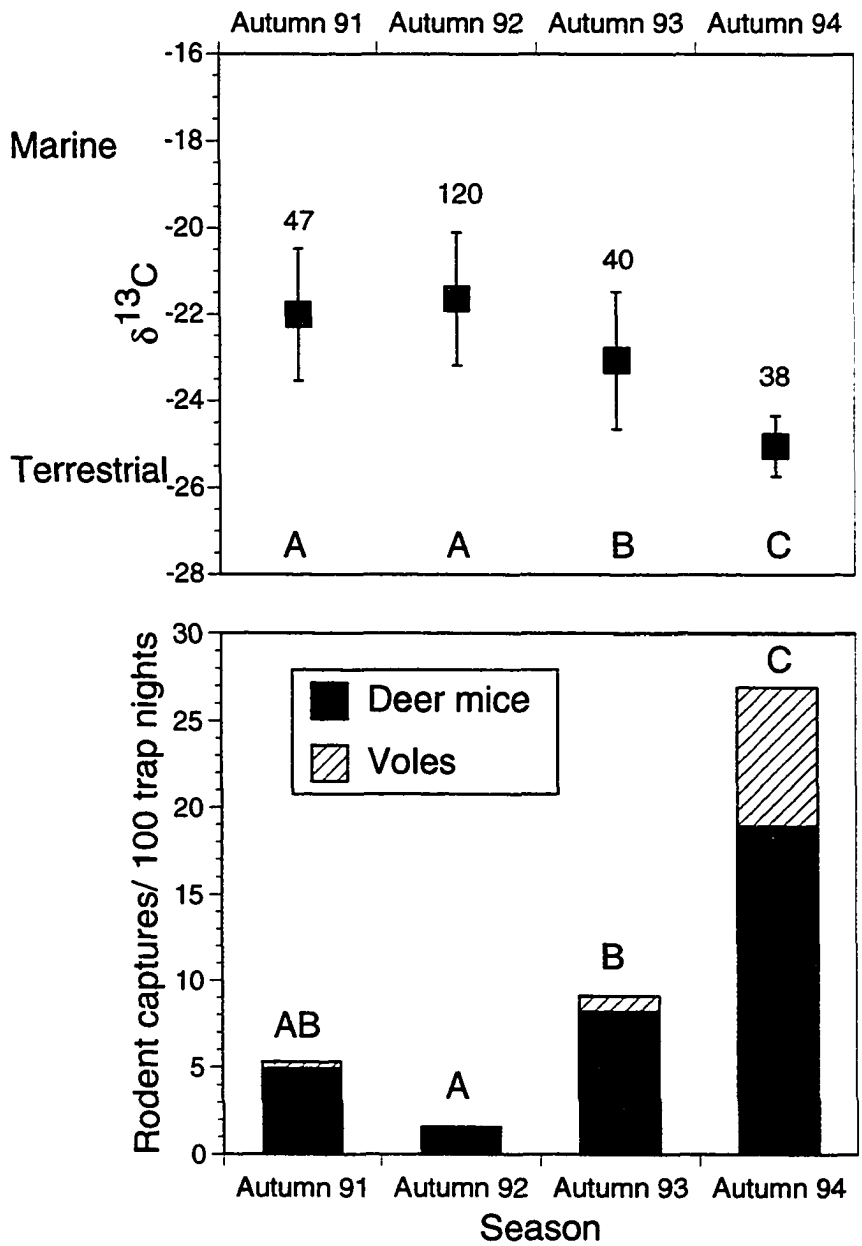

Figure 19. Mean and SE values of ^{13}C for marten carcasses and live martens captured in autumn 1991 - 1994, on Chichagof Island, southeast Alaska (top), and number of small rodent captures/ 100 trap nights during the same period (bottom). Sample sizes are provided above SE. Letters represent statistical difference at $\alpha = 0.05$.(ANOVA for values of ^{13}C; χ^2 test for rodent captures)

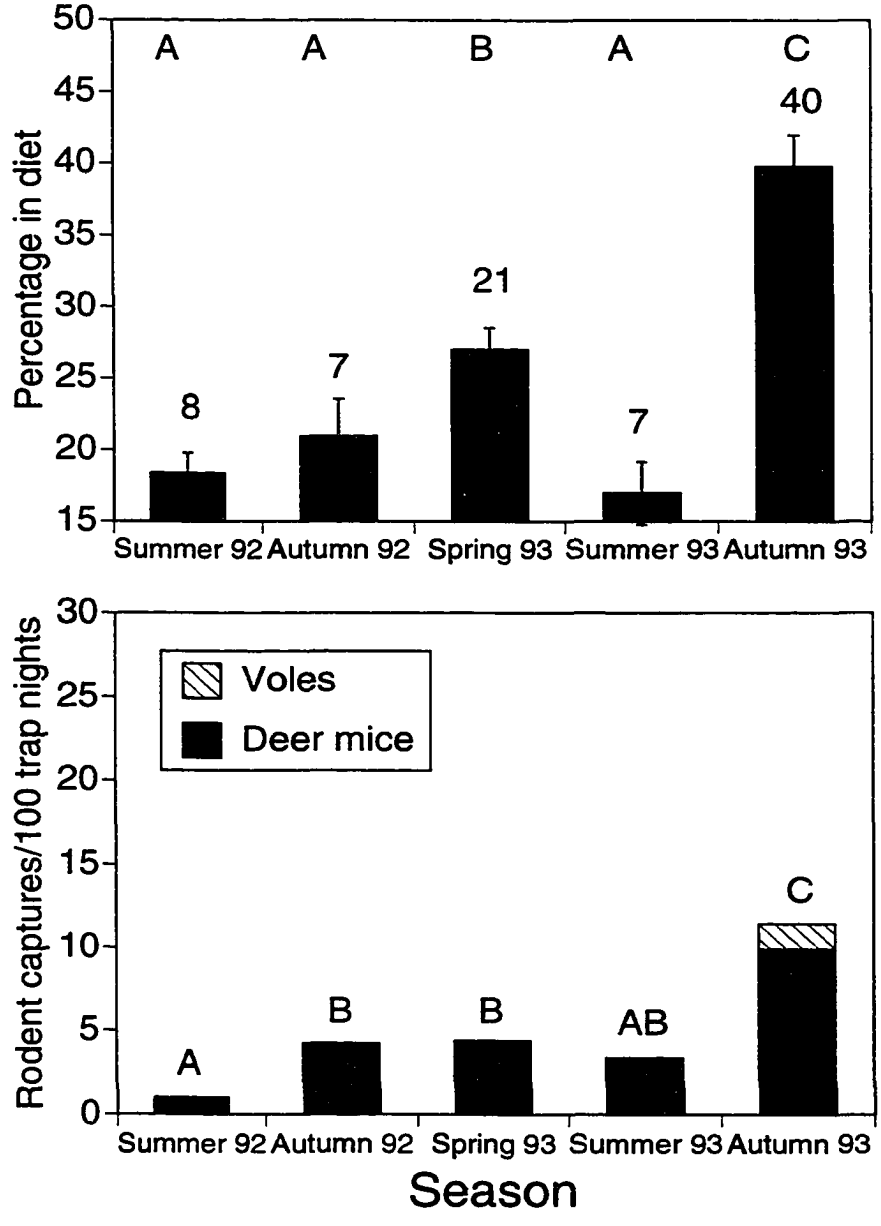

Figure 20. Proportion of small rodents in the diet of live martens captured in summer 1992 to autumn 1993, on Chichagof Island, southeast Alaska (top), and number of small rodent captures/ 100 trap nights during the same period (bottom). Sample sizes are provided above SE. Letters represent statistical difference at $\alpha = 0.05$. (Kruskal-Wallis test for precentages; χ^2 test for rodent captures)

experienced an increase in numbers because of reproduction during summer, and little winter mortality in these years. Using the multi-source mixing model, we determined the percentage of small rodents in the diets of live-captured martens, from summer 1992 to autumn 1993. These proportions differed significantly (Kruskal-Wallis, $P < 0.0001$). Multiple comparisons revealed that a significant increased occurred between autumn 1992 and spring 1993, followed by a significant decrease in summer 1993 (Figure 20). In autumn 1993, the mean percentage of small rodents in the diet significantly increased compared with spring or summer 1993 (Figure 20).

Comparing the percentages of small rodents in the diet with the seasonal abundance of small rodents revealed that while the percentage of rodents increased in the diet of martens between summer 1992 and autumn 1993, following the trend of increase in the small rodent population, selection (χ^2 goodness-of-fit test, $df = 4$, $P < 0.05$; $w_i > 1$; Manly et al., 1993) occurred only during summer 1992 ($w_i = 9$, CI = 2.9, 15.1), autumn 1992 ($w_i = 4$, CI = 1.23, 6.77), and spring 1993 ($w_i = 4.8$, CI = 1.1, 8.5). In summer 1993 ($w_i = 4.25$, CI = 0.95, 8.53), and autumn 1993 ($w_i = 3.01$, CI = 0.75, 5.27) martens fed on small rodents in relation to their availability.

To identify the factors affecting diets of martens (for live-captured martens only) as represented by the stable isotope ratios, we introduced the following variables to a logistic regression model (BMDP; Dixon 1990): sex, age, year (as representative of abundance of small rodents), season, and home range location on the landscape (Table 8). The logistic-regression model identified year, season, and home range location as the variables best separating marine from terrestrial diets ($P < 0.001$; Table 11). The model correctly classified 77% of all individuals to their respective dietary group (69% marine and 79% terrestrial). This result suggested that home range location (i.e., access to salmon streams) determined whether martens included salmon in their diet during years in which abundance of small rodents was low and in seasons when this resource was available (Figure

Table 11. Logistic regression model $P(y=j) = (e^{\beta o}+e^{\beta 1x1}+ e^{\beta 2x2....})/ (1 + e^{\beta o}+e^{\beta 1x1}+ e^{\beta 2x2....})$ where j is 0 or 1: coefficients, SE, and odds ratio for factors affecting diet selection (marine coded 1, terrestrial coded 0) in martens repeatedly captured between June 1992 and October 1994 on Chichagof Island, Southeast Alaska.

Variable		Coefficient	SE	Odds Ratio
Season	(1)	-9.34	0.05	-18.3
	(2)	-10.31	.0.46	-22.4
Year	(1)	7.98	1.17	6.85
	(2)	9.49	1.16	8.17
Home Range	(1)	2.7	1.11	2.43
	(2)	0.59	0.48	1.24
Constant	(1)	1.94	1.07	1.82

21). During years and seasons in which abundance of small mammals was high, home range location was not an important factor in determining diets of martens (Figure 21). Age and sex did not enter the model as they did not improve the fit of the model, suggesting that these variables did not significantly contributed to the differences in diets of martens.

In investigating differences in body weights of martens (Figure 22), we noted a significant effect of season but no significant effect of diet for males (ANOVA on ranks, overall $P = 0.0003$; season effect $P = 0.0002$, diet effect $P = 0.1755$). Multiple comparisons revealed that body weights of males were significantly lower in autumn compared with those in spring ($P < 0.05$). Female martens showed a marginal difference in body weights (ANOVA on ranks, overall $P = 0.0842$), and only the season effect was significantly different ($P = 0.0435$, diet effect $P = 0.5563$). Multiple comparisons revealed that body weights of females were significantly lower in autumn compared with those in summer ($P < 0.05$).

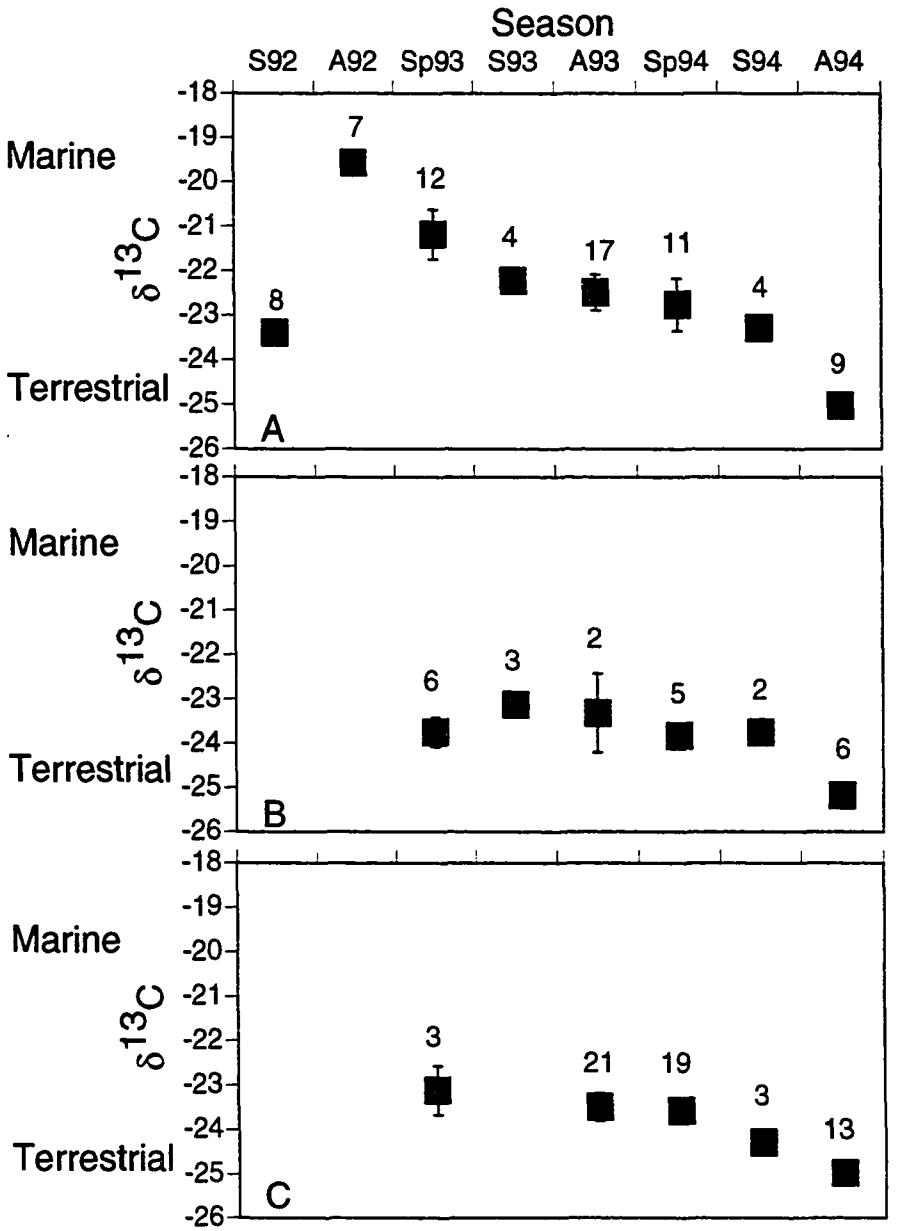

Figure 21. Mean and SE values of ^{13}C for live martens captured from summer 1992 to autumn 1994, on Chichagof Island, southeast Alaska, in home ranges with access to salmon streams (A), without access to salmon streams (B) and transient animals (C). Sample sizes are provided above SE.

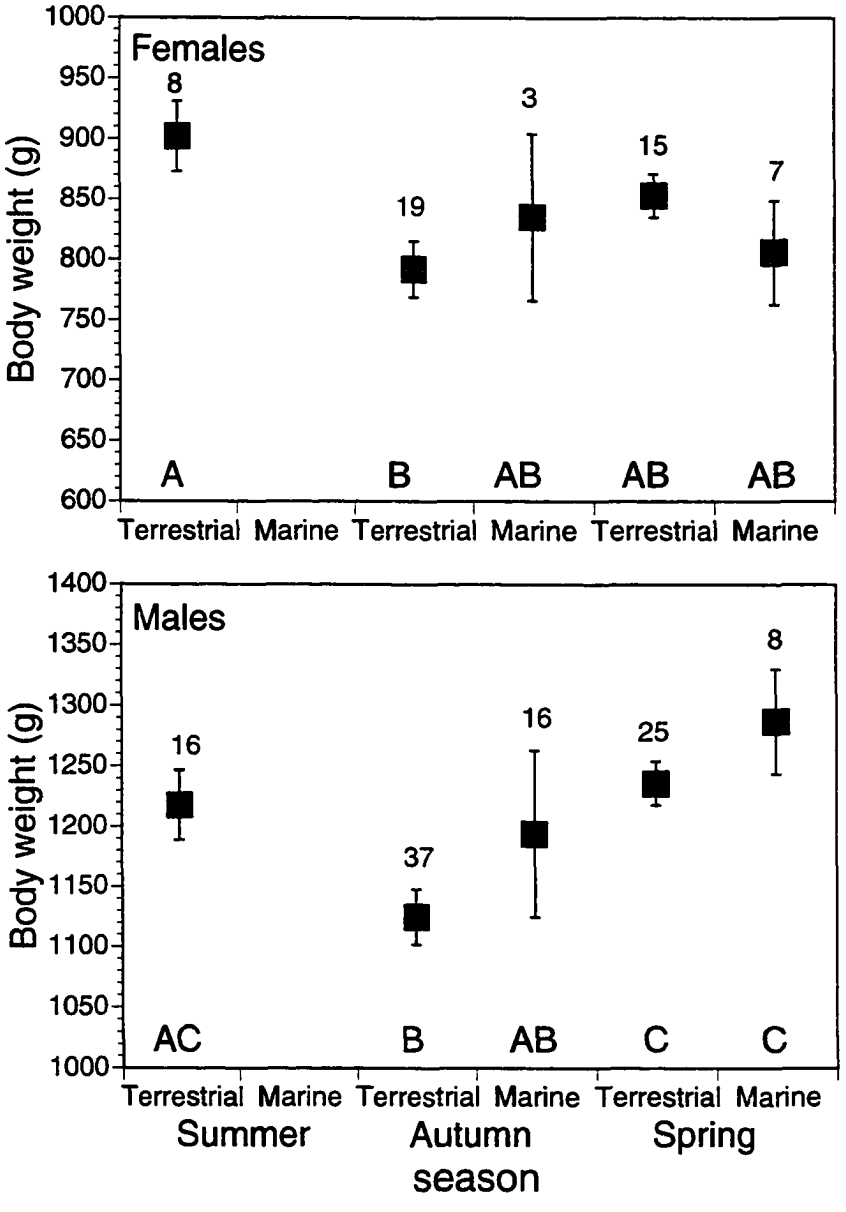

Figure 22. Mean and SE of body weight (g) for female (top figure) and male (bottom figure) martens, on Chichagof Island, southeast Alaska, by diet group (terrestrial vs. marine) in summer, autumn and spring.Sample sizes are provided above SE. Letters represent statistical difference at $\alpha = 0.05$. (Kruskal-Wallis test).

Discussion

Martens in our study area principally fed on small rodents in autumn when those were available in high numbers (1993 and 1994), despite salmon carcasses being as available to them as in other years (1991 and 1992). When small rodents occurred in high numbers, martens facing the choice between small rodents and salmon, selected small rodents. This is further supported by our finding that some individuals fed principally on small rodents even in years of low abundance of rodent (Table 9). Nonetheless, no selection occurred in summer and autumn 1993, suggesting that while martens increased the consumption of small rodents when those became more available, martens did not eat small rodents disproportionally to their availability. Martens may need to augment their diet with other foods to fulfill other dietary requirements (Robbins, 1993). Therefore, it seems that although martens responded to the increase in abundance of small rodent, they preferred rodents over salmon carcasses, and demonstrated selection for it only during seasons of low abundance of small rodents. This is in agreement with results of other studies that concluded that martens responded opportunistically to the abundance of voles (Campbell, 1979; Soutiere, 1979; Gordon, 1986), whereas others have shown selection for this prey (Douglas et al. 1983; Buskirk and MacDonald, 1984; Martin, 1987; Thompson and Colgan, 1990). Nonetheless, many of these studies address diet as a secondary objective and differ in their evaluation of prey abundance and estimation of selection. On the other hand, it is possible that these studies observed martens at different levels of prey availability and therefore some observed selection, and others only an opportunistic response. Our study clearly shows that selection occurred when numbers of rodents were low, but no selection occurred when number of rodents were high, although the proportion of small rodents in the dietof martens increased with the increase in numbers of small rodents.

The logistic-regression model revealed that one important factor affecting diet composition in martens was the location of their home range on the landscape.

Individuals with access to salmon streams were more likely to feed on salmon carcasses during years of low abundance in small rodent. This agrees with the prediction based on the optimal foraging theory (Pyke et al., 1977) that during years of low abundance of rodents, encounter rates of rodents will be reduced and other foods, such as salmon carcasses will be consumed to a larger extant. The logistic-regression model correctly classified 77% of all individuals to their respective dietary group (terrestrial vs. marine). This outcome suggests that although prey abundance (i.e., year and season), and home range location are important factors in determining diets of martens, additional factors such as differences in predatory specialization or imprinting can contribute to diet selection by martens.

In spring, carcasses of winter-killed deer seemed to be an important component in the diet of martens, composing 34 to 43% of the diet in that season. Nagorsen et al. (1989) reported deer remains in 20% of gastrointestinal tracts of martens obtained from trappers in winter on Vancouver Island, British Columbia, suggesting that this food was important for insular populations of martens in the Pacific Northwest. In spring, marine-derived foods were less available to martens in our study area because the salmon runs end in mid- to late November. Nonetheless, some carcasses of salmon may remain available as they thaw from the snow on stream banks or because they were cached by martens (Henry et al., 1990) or other predators such as mink (*Mustela vison*) (Ben-David, et al., in review). Other possible marine-derived foods were intertidal organisms exposed at low tide; we observed remains of salmon as well as crab shells in marten feces collected in spring. This outcome could explain the occurrence of stable isotope signatures in marten tissues characteristic of marine-derived foods during that season. Others studies have shown that island-inhabiting martens fed on intertidal organisms in winter (Nagorsen et al., 1989; Nagorsen et al., 1991), as did other species of mustelids (Ben-David et al., 1996; Bowyer, et al., 1994).

Marten predation on small rodents increased when rodents increased in numbers continued in spring, whereas selection seemed to occur only during periods with low abundance of small rodents. In summer 1993, small rodents were less common in the diet of martens than they were in spring 1993, although abundance of rodents did not decrease significantly. In summer, squirrels and birds became important components in the diet, even in summers with high numbers of small rodents (1993 and 1994). During that season nestlings and juvenile squirrels are encountered at a higher rate and easier to capture than voles or deer mice (Zielinski et al., 1983). Therefore, martens likely responded to the increase in availability of these prey. In addition, the availability of berries in summer affects dietary composition of martens as they compose 13 - 22% of the diet. Berries are an important seasonal food in diets of martens throughout their range (Simon, 1980; Hargis and McCullough, 1984; Martin, 1987; Nagorsen et al., 1989).

We were unable to demonstrate that body weights of live-captured male and female martens differed significantly between individuals feeding on marine-derived or terrestrial diets. This finding contradicted our hypothesis that those martens feeding on rodents would exhibit better body condition than those feeding on other foods. Thus, switching to alternative prey enables martens to maintain body condition in spite of a decline in preferred prey numbers. Nonetheless, we did record a significant change in body weights of male and female martens between seasons. Our results showed that in females the significant difference in body weight resulted from a reduction in weight between summer and autumn, whereas in males the difference resulted from a reduction in weight between summer and autumn and an increase in body weight between autumn and spring. Whether seasonal changes in body weight are a result of food availability, reproductive activity, dispersal, or changes in general levels of activity merits further investigation.

Our results suggest that martens, as true generalist predators, switch to alternative prey when preferred food is not readily available on a seasonal or annual basis. Such a short-term functional response could reduce the long-term numerical decline in predator populations, which usually follows shortages in availability of preferred foods (Taylor, 1984). Thompson and Colgan (1987) recorded a numerical decline in a marten population in Northcentral Ontario following a decline in the local population of voles. Similarly, Weckwerth and Hawley (1962) reported a decline in numbers of martens in Montana following a decline in abundance of prey. Although marten numbers in our study area changed among years, the relationship to abundance of small rodents needs clarification. Ben-David and Flynn (in press) demonstrated that reproductive and nonreproductive females martens did not differ in diet selection and that reproductive females feeding on salmon were able to maintain body condition similar to that of reproductive females feeding on small rodents. This suggests that although salmon carcasses are not a preferred food for martens, they act as a suitable alternative to maintain body condition and allow successful reproduction even in years when small rodents are not readily available (Ben-David and Flynn, in press).

Acknowledgments

We thank J. Simonson, C. Zank, M. Kemp, N. Olmstad, M. Rosing, B. Wissing, and S. Lewis for their assistance in collecting data in the field. We are also grateful to the trappers of Chichagof Island for providing us with marten carcasses. Special thanks to G. Blundell and T. Schumacher for processing the carcasses, obtaining the radio-locations, as well as collecting most of the blood samples in 1993 and 1994. N. Haubenstock and B. Barnette performed the stable isotope ratio analysis. We wish to thank Drs. D. R Klein, R. T. Bowyer, M. W. Oswood, and J. A Blake for helpful comments on earlier versions of the manuscript. Funding for the project was provided by the Alaska Department of Fish and Game; USDA Forest

Service, Pacific Northwest Research Station, Juneau; USDA Forest Service, Chatam Area, Sitka; Alaska Cooperative Fish and Wildlife Research Unit and the Water Research Center, University of Alaska Fairbanks.

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Chapter 4–Diet and reproductive performance in female martens, *Martes americana*

Merav Ben David, and Rodney W. Flynn

Abstract

Previous studies established a positive relationship between body condition and reproductive performance in several species of mammals. Among small mustelids, with limited ability to accumulate fat reserves, optimization of food intake through diet selection may partially determine reproductive success of females. In this study, we investigated diets and body condition of female martens (*Martes americana*) that were reproductive and nonreproductive in Southeast Alaska from 1991 to 1993. We hypothesized that reproductive females would have a greater portion of rodents in their diet than did nonreproductive ones. We also hypothesized that those females feeding on rodent prey would exhibit better body condition than those females feeding on other foods. We collected marten carcasses from trappers during late autumn in 1991 and 1992, from which we subsampled 52 adult females (>1 year, as determined from cementum annuli). Stable isotope analysis of muscle tissue was used to indicate diet for each individual. Reproductive status was established using counts of corpora lutea, whereas body condition was determined from carcass weight and fat scores. Diet, as indicated by stable isotope ratios, was established for 12 female martens live-captured in spring 1993. Reproductive status of these females was determined from blood progesterone levels, whereas body weight was used as an indicator of body condition. During the pre-implantation period, we observed no difference in diet between reproductive and nonreproductive females. Female martens grouped by their diet and reproductive performance were not significantly different in carcass weight or fat scores. During the period of active pregnancy, body weights of reproductive females were not different from nonreproductive ones, and females with a terrestrial diet did not differ from

females with a diet based on marine organisms. Although salmon carcasses were not a preferred food, they provided an alternative food source for female martens that allowed them to maintain body condition and reproduce successfully even in years when preferred foods were not readily available.

Introduction

Reproductive success of female mammals depends on longevity, fecundity, mating success, and survival of offspring (Clutton-Brock 1988). Reproductive performance of many female mammals is related to body condition (Caro 1994, Clutton-Brock et al. 1986, Gerhart 1995, Kennedy and Mitra 1963, Ruthven et al. 1994). These and other studies indicate that in many species, a female must reach a critical body weight or accumulate a critical amount of fat to conceive (Bronson 1989; Butler and Whelan 1994). Small mustelids, including the marten, store little body fat compared with other mammals (Harlow 1994), and show little variation in accumulation of body fat between seasons (Buskirk and Harlow 1989). Martens compensate for their deficiency in accumulating fat by using several physiological and behavioral adaptations, one of which is optimizing food intake by diet selection (Harlow 1994). In species with delayed implantation or embryonic diapause, pregnancy involves ovulation during the mating period and implantation of the embryo up to 7 months later (Mead 1994). Martens breed in summer and the embryos implant during the following spring (March and April) with births occurring 35 days later (Mead 1994). Therefore, nutrition and body condition of females during mating, prior to implantation, and postimplantation will be important factors in determining reproductive success.

During our study of the ecology of martens in Southeast Alaska , rodent populations (*Peromyscus keeni* and *Microtus longicaudas*) fluctuated widely (see chapter 3; Ben-David et al., in review *a*). Martens preferentially fed on small rodents (terrestrial) when those were abundant in 1994. When rodent numbers were low (1991 and 1992), some martens fed primarily on scavenged salmon carcasses (marine), whereas others selected rodents (Ben-David et al., unpubl. data *a*). During 1991-1992 and 1992-1993, pregnancy rates and the number of corpora lutea per female within our study area were low (Flynn and Blundell 1992; Flynn 1993; Strickland and Douglas 1987). Reproductive rates of martens had increased to high levels by 1993-1994 (Flynn and Schumacher 1994).

In this study, we compared diets of reproductive and nonreproductive female martens during the pre-and post-implantation periods. Also, we compared body condition of reproductive and nonreproductive females consuming marine and terrestrial diets. We hypothesized that reproductive females would have a greater portion of rodents in their diet than nonreproductive females. We also hypothesized that those females feeding on rodent prey would exhibit better body condition than those females feeding on other foods.

Stable isotope analysis

We used stable isotope ratios to indicate marten diets. In nature, carbon (C) and nitrogen (N) each occur as two stable isotopes: ^{12}C and ^{13}C; ^{14}N and ^{15}N. Ratios of the two isotopes, measured in parts per thousand (‰), are compared with standards and noted as ^{13}C for carbon and ^{15}N for nitrogen (Ehleringer and Rundel 1988). Values of ^{13}C differ between terrestrial and marine sources of food because of differential assimilation of ^{13}C by terrestrial and marine plants. Because ^{15}N is concentrated with consumption, ^{15}N values reflect dietary and trophic levels. The analysis of food webs using natural abundance of stable isotope ratios compares the ^{13}C and ^{15}N values of predator and prey tissues (Hobson 1991; Schell et al. 1988). The combination of ^{13}C and ^{15}N result from the dietary interaction of species or individuals (Gearing 1991, Hobson 1991, Schell et al. 1988, Schoninger and DeNiro 1984).

Methods

Our study area is located on Chichagof Island in Southeast Alaska, USA (Figure 1). The island is one of the three large islands in the northernAlexander Archipelago (Tenakee Springs at 57° 52' N 135° 18' W) and is part of the Tongass National Forest. The archipelago has a maritime climate; summers are cool and wet and winters are characterized by deep snow (236 cm annual precipitation). The snow-free period extends from early May to early November at lower elevations. Vegetation at higher elevations is typified by alpine tundra and at lower elevations by coastal, old-growth forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with a well-developed understory (mainly *Oplopanax horridus, Vaccinium* sp., *Menziesia ferruginea,* and *Rubus* sp.). Our study area encompasses six streams that support an annual run of spawning Pacific salmon (*Onchorhynchus gorbuscha, O. keta,* and *O. kisutch*) from late summer to late autumn. The island mammalian fauna includes: Keen's deer mice (*Peromyscus keeni*), long-tailed voles (*Microtus longicaudas*), tundra voles (*Microtus oeconomus*), red squirrels (*Tamiasciurus hudsonicus*), common shrews (*Sorex cinereus*), mink (*Mustela vison*) , river-otters (*Lutra canadensis*), brown bears (*Ursus arctos*), and Sitka black-tailed deer (*Odocoileus hemionus sitkensis*).

Sampling

We live-captured martens repeatedly throughout the year using Tomahawk live traps (model 203; Tomahawk Live Trap Co., Tomahawk, WI). Each marten we captured was immobilized with an injection of ketamine hydrochloride (Vetalar) (15 mg/kg body weight; Aveco, Fort Dodge, IW) and xylazine hydrochloride (Rompun) (2 mg/kg body weight; Vedco, St. Joseph, MI). We measured, weighed, and marked animals with ear tags (Size 1, Style 1005, National Band and Tag Co., Newport, KY) or a passive integrated transponder (PIT) tag (Biosonics, Seattle, Washington). Two first premolar teeth were extracted for age determination by cementum analysis (Matson's Laboratory, Milltown, MT). A blood sample of 2 cc

was drawn from the jugular vein and stored in a glass or plastic vial. Martens were held in the trap until fully recovered, and then released at the site of capture. A manual centrifuge was used to spin the blood at 3,000 rpm for 5 minutes within 2 hours after collection. Blood serum was siphoned into a separate vial. Serum and samples of clotted blood-cell were frozen until analysis. All methods used in this study were approved by an independent Animal Care and Use Committee at the University of Alaska Fairbanks.

We collected 610 marten carcasses from trappers on Chichagof Island during the December 1991 through January 1992 and December 1992 trapping seasons (Flynn and Blundell 1992). For each marten carcass, we recorded the site and date of capture, and determined sex, body measurements, and weight for each carcass before the removal of the viscera, uterus, ovaries, and premolars. One-hundred and sixty carcasses of marten were selected randomly for the stable isotope analysis. We selected 52 adult females > 1 year (as determined from tooth cementum). From each carcass, a piece of muscle 5 to 10 g was excised from the hind leg for stable isotope analysis. Carcasses were aged using cementum annuli of four premolar teeth (Matson's Laboratory, Milltown, Montana).

Analysis of Stable Isotope Ratios

Tissues (clotted blood-cell and muscle samples) were kept frozen between collection and preparation for determination of stable isotope ratios. Samples were dried in 60° to 70° C for 48 hours and then ground to powder using a Wig - L - Bug grinder. Subsequently, a sub-sample of 1-1.5 mg was weighed into a miniature tin cup (4 by 6 mm) for combustion. We used a Europa C/N continuous flow massspectrometer to obtain the stable isotope ratios. Each sample was analyzed in duplicate and results were accepted only if the variance between the duplicates did not exceed that of the peptone standard (CV = 0.1). Values of ^{13}C and ^{15}N for the samples of marten were used to compare diets of reproductive and nonreproductive females. Because the ^{13}C and ^{15}N values were highly

correlated ($r = 0.89$), we used carbon values alone to determine diet grouping (marine and terrestrial) in subsequent analysis. The extreme values of ^{13}C for female marten tissues ranged from -24.79 ‰ for a predominantly terrestrial diet (rodent ^{13}C values ranged from -28.8 ‰ to -26.1 %) to -19.87 ‰ for a predominantly marine diet (salmon ^{13}C values ranged from -21.2 % to -18.5 ‰). We assumed that marten tissues with values $^{13}C < -22.4$ ‰ represented a greater portion of rodents in the diet (see chapter 3; Ben-David et al.,in review *a*).

Fat Scores

Using an ocular estimation procedure developed by Flynn and Blundell (1993), we assigned an index of internal and external body-fat content to each marten carcass. Values for external and internal body-fat index were recorded as whole numbers from 0 (none observed) to 6 (abundant fat). We determined an appropriate body-fat index by comparing each carcass with a photographic example of each body-fat category. For further analysis, we combined external and internal fat indices to produce total fat score for each carcass.

Counts of Corpora Lutea

Reproductive status of female martens at death was established by the presence of corpora lutea in their ovaries. We selected 52 adult females > 1 year (as determined from tooth cementum) from the 160 marten carcasses used for stable isotope analysis. From each carcass, we extracted the ovaries from the reproductive organs of females and preserved them in 10% formalin. All ovaries were washed in water and sent to Matson's Laboratory (Milltown, MT) for evaluation for the presence and number of corpora lutea (Strickland and Douglas 1987). We termed females with one or more corpora lutea as reproductive, whereas females lacking corpora lutea were termed nonreproductive.

Progesterone Level Analysis

Levels of blood progesterone of live-trapped female martens were determined using a Diagnostic Products iodinated solid-phase RIA kit (by R. Mead, University of Idaho, Moscow, Idaho).We used levels of blood progesterone from female martens trapped in July as a standard for nonreproductive levels of progesterone (<5 ng/ml; Table 1). We applied this standard to blood samples obtained from female martens trapped from mid-March to mid-May. Females with levels <5 ng/ml were termed nonreproductive, whereas females with levels >5 ng/ml were termed reproductive.

Statistical Analysis

To test our hypothesis that reproductive females would have a greater portion of rodents in their diet than nonreproductive females, we employed *k* nearest-neighbor randomization test (see Appendix C; Schilling, 1986; Rosing et al., in review) to detect differences in diets between reproductive and nonreproductive female martens. In this test, the ^{13}C and ^{15}N values are treated as spatial data because the unit of measurement in both variables is equal and stable. We compared differences between proportions of reproductive females in the marine and teresstrial diet groups using the Z-test (Zar 1984). The Mann-Whitney *U*-test (Zar 1984) was used for two-sample comparisions with small sample sizes. We hypothesized that those females feeding on rodent prey would exhibit better body condition than those females feeding on other foods. To test this hypothesis, female martens were placed into four diet-reproductive groups: nonreproductive terrestrial diet, nonreproductive marine diet, reproductive terrestrial diet, and reproductive marine diet. We employed Kruskal-Wallis one-way analysis of variance (BMDP - Dixon 1990; Zar 1984) to investigate differences in carcass weight and fat scores among the four categories.

Results

Of the 52 adult female martens we collected in late autumn 1991 and 1992, 47% had a stable isotope signature indicating a predominantly rodent diet, whereas 53% had a stable isotope signature suggesting a diet of predominantly salmon carcasses. We were unable to detect differences in diets of reproductive and nonreproductive females (Figure 23; K nearest-neighbor randomization test; $P = 0.48$). Similarly, the proportion of reproductive females feeding mainly on rodents (46% of 24) did not significantly differ from the proportion of reproductive females feeding mainly on salmon carcasses (25% of 28) ($Z = 1.6$, $P > 0.05$). We observed no significant difference in carcass weight among all 4 diet reproductive groups of female martens (Figure 24; Kruskal-Wallis, $P = 0.98$). Similarly, no significant difference was detected in fat scores among the 4 groups of females (Figure 25; Kruskal-Wallis, $P = 0.16$).

Of the 12 females live-trapped in spring 1993, six had progesterone levels exceeding 5 ng/ml, suggesting initiation of active pregnancy, and were termed reproductive (Table 12). Of those reproductive females, two had a stable isotope signature that was predominantly marine ($\delta^{13}C > -22.4‰$), and four had a predominantly terrestrial signature ($\delta^{13}C < -22.4‰$). Of the nonreproductive females, three females had terrestrial signatures, and two had marine signatures (Table 12). One of the nonreproductive females (MR87; Table 12) had isotope ratios typical of a diet composed predominantly of squirrel (Ben-David et al., unpubl. data*a*) and was excluded from further analysis.

Body weights of females with diets from terrestrial sources did not differ significantly from those of females with diets from marine sources (Mann-Whitney, $P > 0.2$). Similarly, body weights of reproductive females did not differ from those of nonreproductive females (Mann-Whitney, $P > 0.2$). Of the three females with progesterone levels indicating implantation when captured in spring and recaptured in July (Table 12), only MR24, which fed on marine-derived foods, showed evidence of lactation.

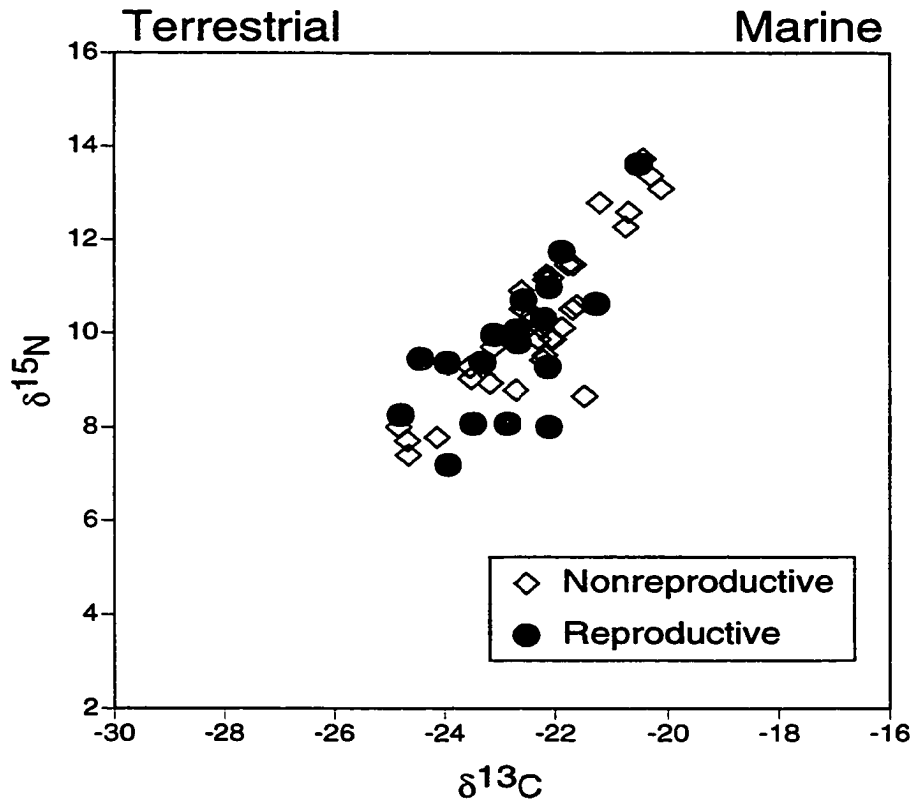

Figure 23. Stable isotope ratios (^{13}C - ‰, and ^{15}N - ‰) of reproductive (n = 18) and nonreproductive (n = 34) female martens, from Chichagof Island, Southeast Alaska, 1991 and 1992.

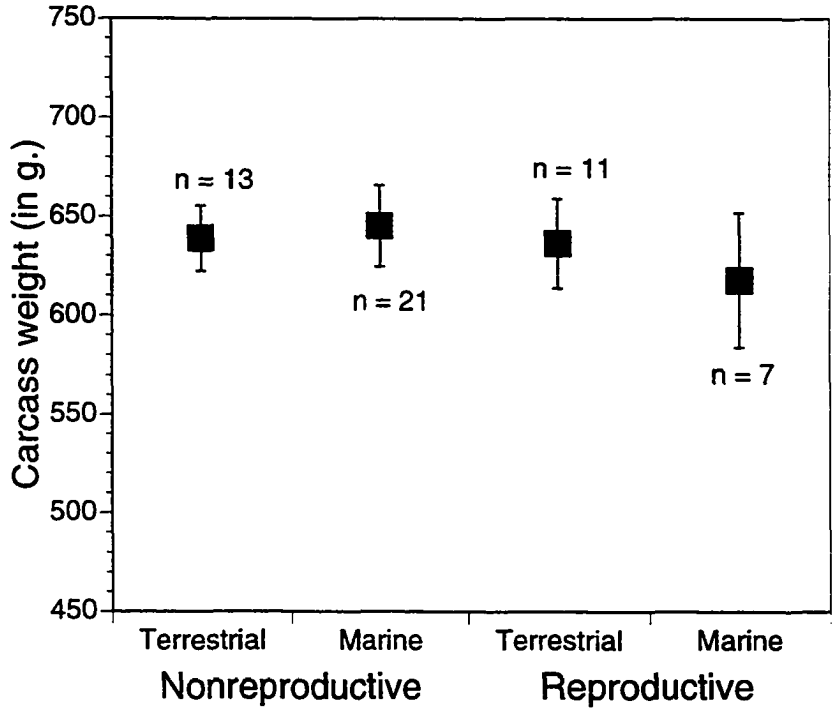

Figure 24. Mean carcass weight (g) for reproductive and nonreproductive female martens by diet group (terrestrial vs. marine), from Chichagof Island, Southeast Alaska, 1991 and 1992.

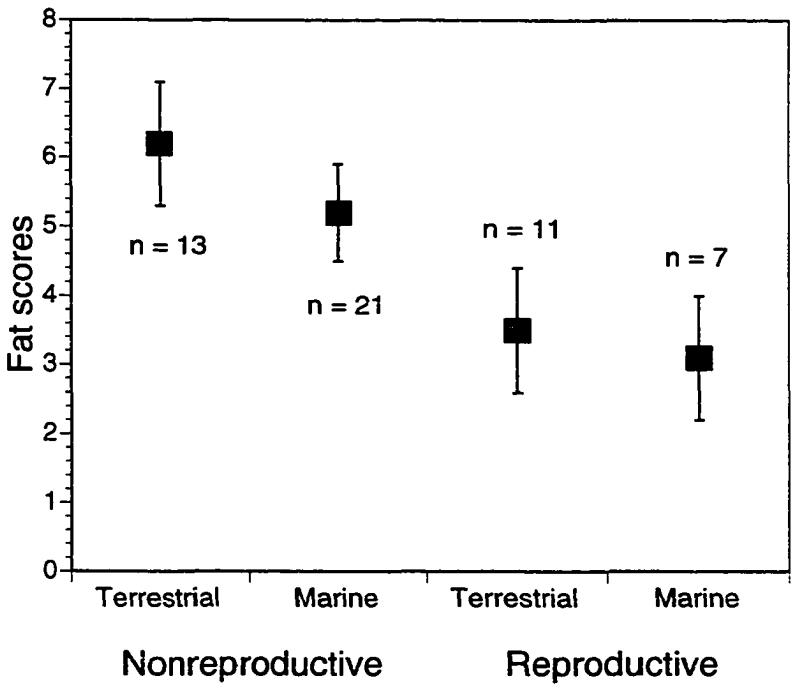

Figure 25. Mean fat scores (±SE) for reproductive and nonreproductive female martens by diet group (terrestrial vs. marine), from Chichagof Island, Southeast Alaska, 1991 and 1992.

Table 12. Blood progesterone levels, body weights, and stable isotope values for female martens caught in spring and summer 1993, on Chichagof Island, Southeast Alaska

	Animal ID	Date of capture	Body weight (g)	Progesterone (ng/ml)	^{13}C (‰)	^{15}N (‰)
Spring	MR52	3/19/93	980	7.8	-24.54	6.09
	MR85	4/28/93	940	4.8	-24.05	5.96
	MR58	4/14/93	830	17.4	-23.50	6.70
	MR48	3/10/93	895	4.6	-23.26	6.22
	MR83	4/08/93	845	3.	-23.15	6.30
	MR62	3/15/93	880	5.7	-22.76	6.53
	MR86	5/02/93	840	8.3	-22.75	6.07
	MR12	5/14/93	800	7.8	-22.40	7.96
	MR84	4/27/93	785	4.2	-22.15	8.28
	MR77	4/27/93	940	2.9	-22.09	8.88
	MR24	3/16/93	880	9.6	-19.87	11.83
	MR87	5/02/93	940	3.4	-21.94	5.67
Summer	MR06	7/25/92	800	2.3	-23.71	6.45
	MR13	7/06/93	975	2.1	-22.13	6.76
	MR58	7/07/93	960	3.5	-22.88	5.23
	MR24	7/07/93	820	4.4	-21.99	6.43

Discussion

We suspect that the high number of nonreproductive female martens (65%) in our 1991 and 1992 sample probably resulted from poor body condition during the preceding summer, which is the mating season for this species (Mead 1994). Thompson and Colgan (1987) reported lower ovulation rates in martens during years of food scarcity in Northcentral Ontario than in years with plentiful foods. In 1991 and 1992, rodent numbers were low in our study area, and salmon carcasses did not become available to martens until the end of July (see chapter 3; Ben-David et al., in review *a*). Feces and stable isotope analyses showed that martens relied heavily on berries and birds during this season (see chapter 3; Ben-David et al., in review *a*). Therefore, availability of these two foods during low rodent abundance could determine body condition and rates of ovulation in female martens. Studies on ovulation rates in other mustelids demonstrated an increase in ovulation rate with increasing age (Doktor et al., 1987; Shea et al., 1985), especially during years of low availability of food (Kartashov, 1989). Therfore, our sample of nonreproductive females may consist largely of younger females. Nonetheless, diet composition of martens in our study are did not vary with sex or age (see chapter 3; Ben-David et al., in review *a*), suggesting that any differences between reproductive and nonreproductive females could be attributed to reproductive status and not to age.

Our results show that by early winter (pre-implantation period), no differences occurred in diets of reproductive and nonreproductive females. Also, body condition of reproductive and nonreproductive females was not significantly different, and no difference was detected between females that fed mainly on salmon carcasses and those that fed mainly on rodents. This finding does not support our hypotheses that females feeding on rodent prey would exhibit better body condition than those that fed mainly on salmon carcasses and that reproductive females will feed more heavily on rodent prey compared with nonreproductive females. Although salmon carcasses are not a preferred food

item for martens (see chapter 3; Ben-David et al., in review *a*), they are an alternate food to sustain body condition for some females and may allow successful implantation even in years when rodents are not readily available.

Optimal foraging theory predicts that animals will select foods that result in energy returns equal or higher than the energy expenditure on locating, capturing, and consuming that food (Pyke et al. 1977). During years of low abundance of rodent , encounter rates of such prey will be reduced and other foods such as salmon carcasses will be used. Salmon carcasses are easy for martens to feed on during the spawning period because other predators (e.g., bears, eagles, and otters) often leave partially eaten carcasses exposed on land. This food resource, occurred only near streams, and is available to martens with home ranges adjacent to salmon streams. Thus, for some females, specializing on mammalian prey optimizes food intake, whereas for others, switching to feed on alternative prey assists in maintaining body condition. Whether differences in diet among females are a result of location of their home-range on the landscape or a result of differences in predatory specialization merits further investigation.

During Spring 1993, feces and analysis of stable isotope ratios showed that while most martens ate rodents and deer (from carcasses), some depended predominantly on marine-derived foods (see chapter 3; Ben-David et al., in review *a*). In spring, marine-derived foods are less available to martens in our study area because the salmon spawning ends in late November. Nonetheless, some salmon carcasses may remain available as they thaw from the snow on stream banks or have been cached by other predators such as mink (see chapter 1; Ben-David et al., in review *b*). Other possible marine-derived foods were intertidal organisms exposed at low tide. fecal analysis (M. Ben-David and T.V. Schumacher, unpubl. data) showed remains of salmon and crab shells in marten scats collected in spring. Other studies have shown that island-inhabiting martens feed on intertidal organisms in winter (Nagorsen et al. 1989; Nagorsen et al. 1991). We suggest that marine-derived foods can provide female martens with adequate

resources for the more demanding stages of active pregnancy. For example, reproductive female MR24, which fed on marine-derived foods in spring, showed evidence of lactation when recaptured in July. Thompson and Colgan (1987) reported that few female martens produced young and lactated during periods of low abundance of mammalian prey. The availability of marine-derived foods to martens in our study area may reduce the effects of shortages in preferred foods during the 3 periods of pregnancy: embryonic diapause, active pregnancy, and lactation.

Acknowledgments

We thank the trappers of Chichagof Island for providing marten carcasses. Special thanks to G. Blundell for processing the carcasses and obtaining most of the blood samples in spring 1993. N. Haubenstock and B. Barnette performed the stable isotope ratio analysis. We wish to thank Drs. D. R. Klein, D. M. Schell, R. T. Bowyer, and M. Oswood for helpful comments on earlier versions of the manuscript. The project .was funded by the Alaska Department of Fish and Game; USDA Forest Service, Pacific Northwest Research Station, Juneau; USDA Forest Service, Chatam Area, Sitka; and the Water Research Center, University of Alaska Fairbanks.

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Synopsis

This study has demonstrated the following:

•The stable isotope ratios of most potential prey items (end members of mixing model) of both mink and martens differed significantly from each other. Nonetheless, no significant difference occurred between several pairs of foods, and therefore the relative contribution of these items to the diets of mink and martens could not be assessed.

•A deterministic multi-source mixing model was developed to calculate the relative contribution of each prey item to the diet of individual mink and marten, based on isotopic signatures obtained from predator and prey tissues. This model assumes that each individual predator consumes all possible prey types, and therefore will tend to overestimate the proportion of prey that are rarely consumed and underestimate the proportion of commonly used prey. Consequently, this model is used as an index of prey consumption rather than as actual proportions.

•Seasonal abundance of freshwater fish sampled in this study significantly changed between seasons. Stable isotope ratios of small fish changed between summer and autumn, and autumn and spring. Stable isotope ratios of large fish did not change between seasons.

•Riverine mink on Chichagof Island, Southeast Alaska, rely on marine-derived nutrients throughout the year through the consumption of adult dolly varden in early summer, consumption of spawning pink, chum, and coho salmon in summer and autumn, and consumption of emerging juvenile salmonids in spring

•Seasonal abundance of most intertidal organisms sampled in this study did not change between seasons. Nonetheless, stable isotope ratios of most intertidal organisms changed between seasons.

•Coastal mink make use of several kinds of intertidal organisms in all seasons, but mainly consume intertidal fish in spring and summer. In autumn salmon carcasses are incorporated into coastal mink diets.

•Coastal and riverine mink in Southeast Alaska differ in their diets in spring and summer, but individuals from both groups rely on the abundant salmon carcasses during autumn.

•Blood progesterone levels, body condition, and testicle length measurements suggest that wild, free-ranging mink on Chichagof Island mate during the late part of April to early May, and parturition occurs in late June to early July. Although male mink seem to respond to photoperiodism in initiating reproduction, timing of reproduction in female mink, in the study area, appears to shift so that lactation coincides with the availability of Pacific salmon carcasses.

•During our study, abundance of rodents (*Peromyscus Keeni*, and *Microtus longicaudas*) in the study area fluctuated widely. Martens preferably fed on small rodents in autumn when those were available in high numbers (1993 and 1994), despite the fact that salmon carcasses were available to them as they had been in years of low abundance of rodents (1991 and 1992). Therefore, although martens responded to the increase in small rodent abundance, they demonstrated selection for that food.

•In spring, winter-kill deer carcasses seemed to be an important component in the diet of martens. In summer, squirrels, birds and berries became important components in the diet of martens, even in summers with high small-rodent numbers.

•One important factor affecting diet composition in martens is the location of their home range on the landscape. Individuals with access to salmon streams were more likely to switch to feed on salmon carcasses during years of low small rodent abundance. Other factors such as age and sex did not seem to determine diet selection of martens.

•Investigation of body condition (i.e., body weight and fat scores), and reproductive performance (i.e., corpora lutea counts, and blood progesterone levels) revealed that there was no significant difference in diet composition or body condition between reproductive and non-reproductive female martens. Although salmon carcasses are not a preferred food for martens, they act as a suitable alternative to maintain body condition and allow successful reproduction even in years when more preferred food is not readily available.

•Stable isotope analysis enabled tracking changes in diets of individuals through time, and exploring factors associated with such changes (i.e., changes in prey availability, and location of home range on the landscape). Nonetheless, this approach does not allow the determination of the contribution of all possible prey items to the diet because some prey items do not have a distinct isotopic signature. Therefore, this technique will be best utilized in conjunction with other approaches to dietary investigation (i.e., scat or gastrointestinal analyses).

As in many other scientific works, new questions arise from the results obtained in this study. Some of these questions are outlined below:

The connection between prey abundance and prey availability.

What is the relationship between abundance of small rodents and their availability to mink and martens as predators? How important is the phenomenon of stranding of small fish in off-channel pools to the predatory success of mink? How many of the salmon carcasses are available to mink and marten during summer, autumn, and spring?

The dynamics of prey abundance and changes in their isotopic signatures.

Are the changes in prey abundance observed in this study a result of changes in their numbers or a result of their behavior? What are the factors associated with changes of isotopic signatures of the different prey species of mink and martens?

Stable isotope analysis vs. scat or gastro-intestinal analysis.

Will scat analysis and gastro-intestinal analysis provide different results for the diet composition of mink and marten from the same area and time periods? How much of this will be due to the difference between assessing excretion of indigestible parts vs. assimilation of nutrients derived from prey?

Stochastic vs. deterministic multi-source mixing models.

Will the results of a stochastic mixing model be different from those obtained from the deterministic model used in this study? Which one provides better estimation of mink and marten diets?

Feeding-niche selection of mink.

Are mink that live along the coast truly a distinct group from mink living along rivers? Do individuals remain loyal to one feeding environment throughout their lives? Does the difference separating these two groups occur due to imprinting on food while the young accompany their mother?

Factors involved in prey selection, spacing patterns and population dynamics of martens.

What additional factors besides small rodents abundance and location of home range on the landscape determine diet selection by martens? If rodent populations decline to lower levels than observed in this study, would the spacing patterns of martens change? Will martens that did not consume salmon during our investigation change their diets under such conditions? Does the availability of salmon carcasses affect home range size of martens? What are the causes of the seasonal change in body weights of martens?

Breeding biology of mink and martens.

Why do mink change timing of mating rather than change the length of implantation? Do female marten differ in timing of implantation depending on quality of their home ranges? What other factors beside food availability determine reproductive success of mink and marten in Southeast Alaska?

Incorporation of marine-derived nutrients into the terrestrial system.

Do marine-derived nutrients become incorporated into terrestrial vegetation? What are the decomposition and cycling processes involved in such incorporation? How does the incorporation of marine-derived nutrients into terrestrial vegetation affects the productivity of these species and the herbivores and frugivores that use them? How does the landscape affect such incorporation?

Appendix A - Isotopic fractionation and response curves of carbon and nitrogen in mink.

Summary.

In order to establish the fractionation values of carbon and nitrogen between predators and prey (Hobson, 1991; Schoeninger & DeNiro, 1984), and monitor the response curves associated with changes in diets, a controlled experiment was performed in captivity. Thirty farmed mink (wild type) were chosen as a model for predator species. The animals (6 males and 24 females) were allowed 3 weeks for acclimation to their new environment while feeding on their original diet. After 3 weeks a blood sample of 2 cc was drawn from the jugular vein and the animals were randomly assigned to three groups, and fed with three experimental diets: marine originated food (fish), terrestrial originated food (beef) and a mixture of the two (beef + fish). The experiment lasted 77 days with weekly and bi-weekly bleeding sessions, after which all animals were euthanized with Halothane (Halocarbon, River Edge, NJ). Blood was spun at 3,000 rpm for 5 min. within 2 hours after collection, and serum was siphoned into a separate vial. Stable isotope ratios (^{13}C and ^{15}N) from the food, clotted blood cells and muscle tissue from the mink were obtained using Europa C/N continuous flow mass-spectrometer. Stable carbon and nitrogen ratios did not significantly differ with age or sex (Kruskal- Wallis, $P > 0.05$; Figure 26). Assimilation of carbon and nitrogen from fish diet was slower than that of beef or the mixed diet (Figures 27 - 29). This resulted in different fractionation values (signature of blood minus signature of diet) at the end of 56 days (Figure 30). Stable carbon ratios of clotted blood cells (-19.3 ±0.3, n = 24) significantly differred from those of muscle tissue (-19.6 ± 0.2, n = 24; ANOVA, $P = 0.04$) at the end of the experiment, however, this difference was within the machine error. Stable nitrogen ratios of clotted blood cells (12.8 ± 1.7, n = 24) did not significantly differ from those of muscle tissue (13.4 ± 0.9, n = 24; ANOVA, $P = 0.1$) at the end of the experiment.

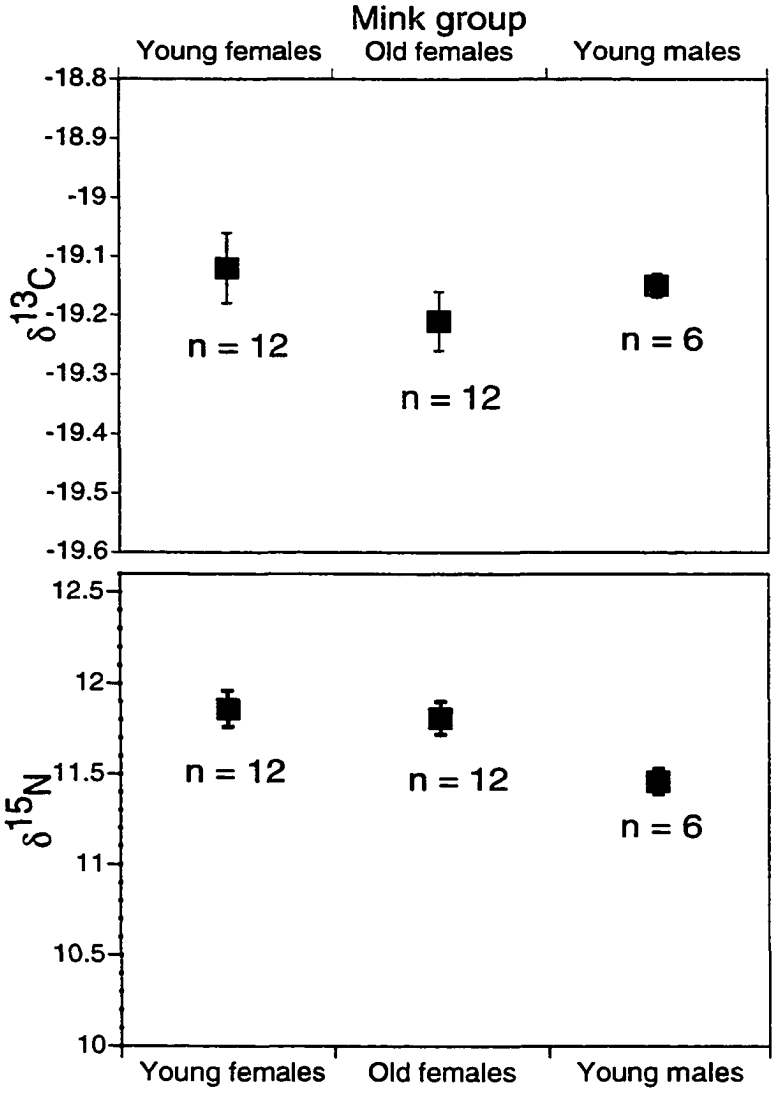

Figure 26. Values of ^{13}C and ^{15}N plotted against mink group for farmed mink held in captivity at the University of Alaska Fairbanks. Animals have been fed on the same diet on which they have been raised at Oragon State University.

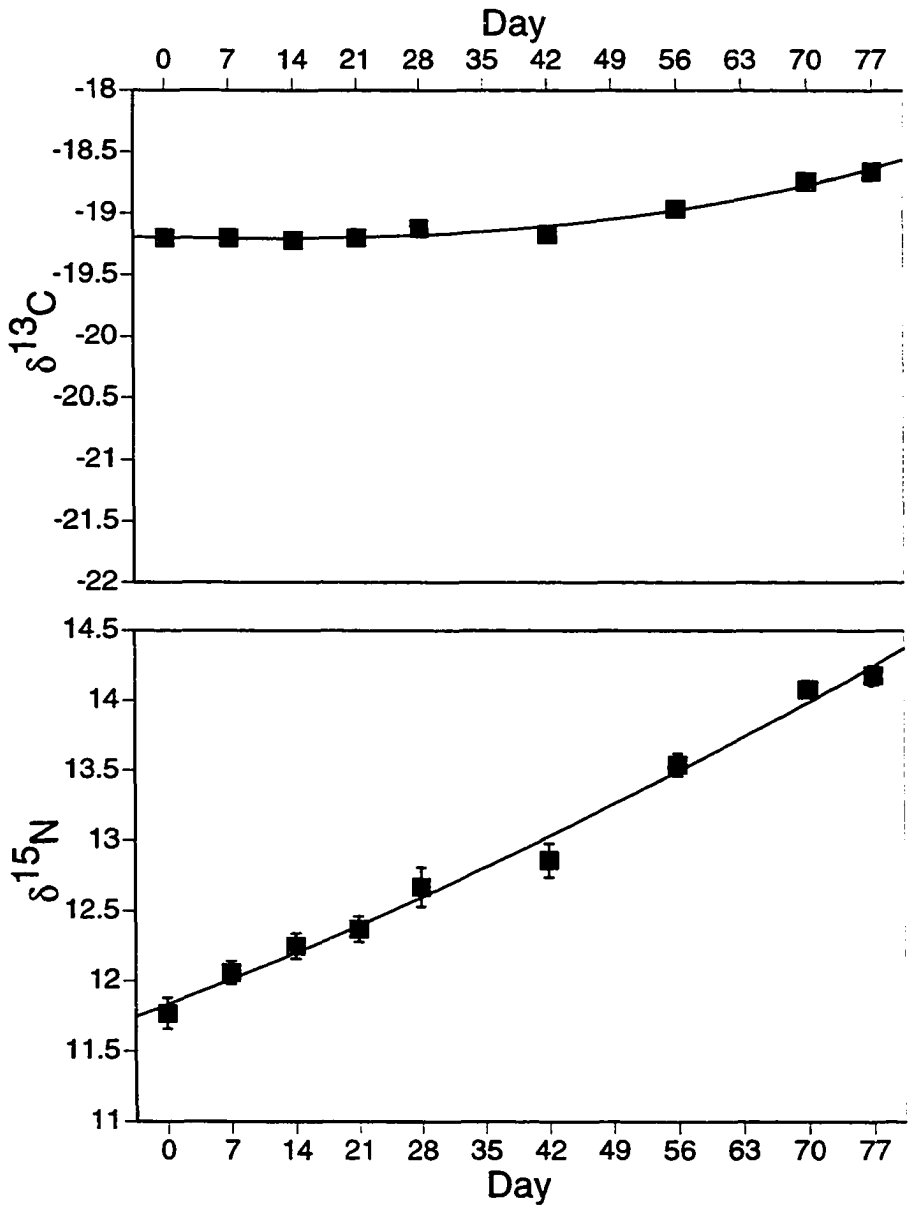

Figure 27. Values of ^{13}C and ^{15}N of clotted blood cells of captive mink (n = 10) plotted against days from begining of experimental feeding on fish diet.

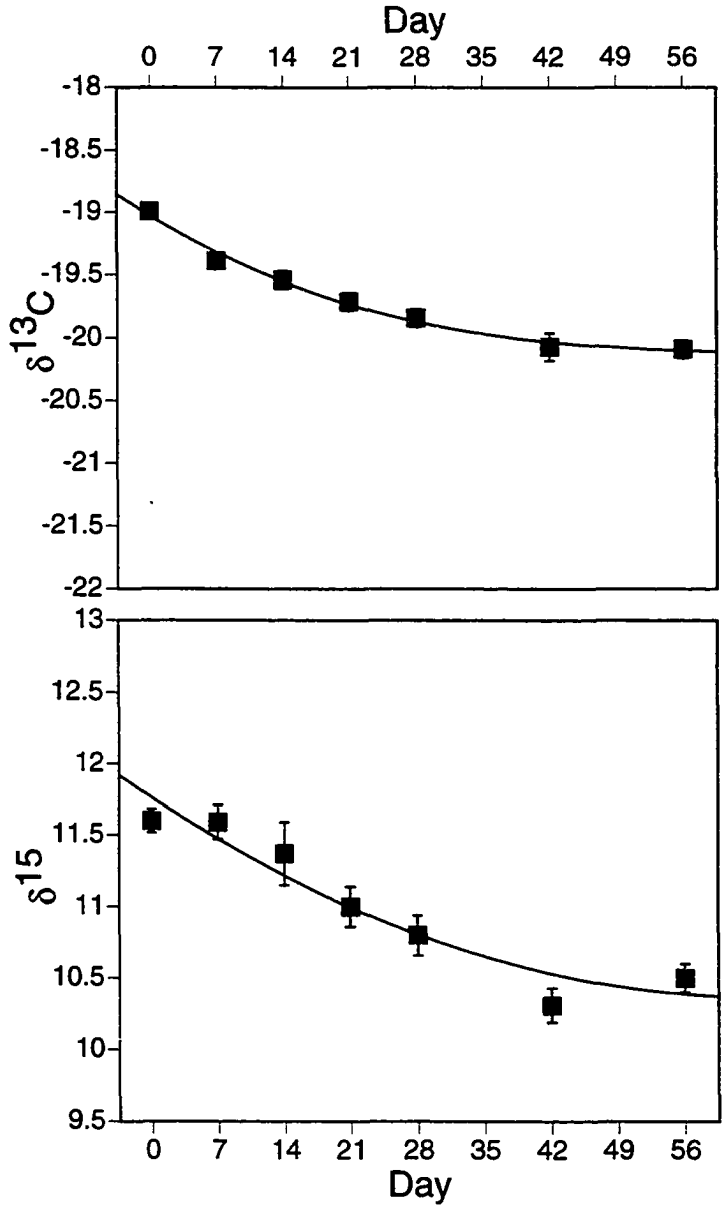

Figure 28. Values of ^{13}C and ^{15}N of clotted blood cells of captive mink (n = 7) plotted against days from begining of experimental feeding on beef diet.

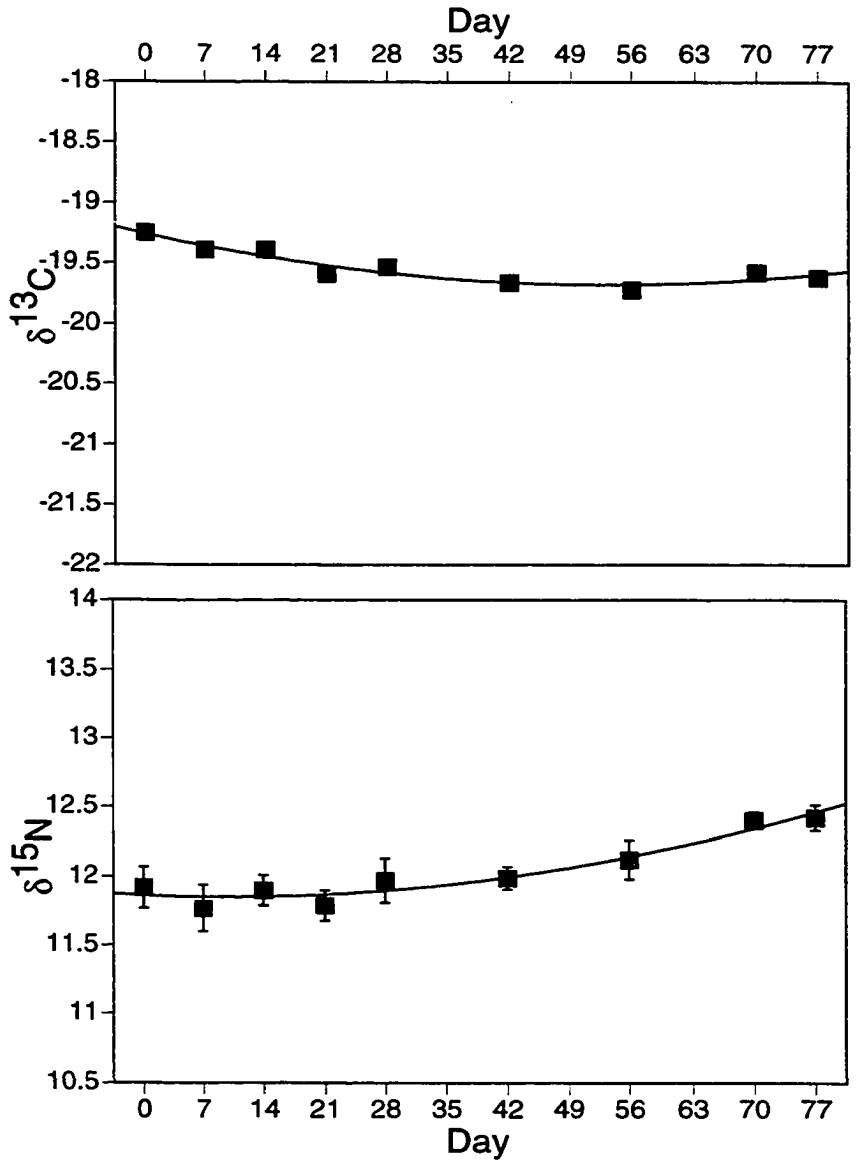

Figure 29. Values of ^{13}C and ^{15}N of clotted blood cells of captive mink (n = 8) plotted against days from begining of experimental feeding on beef and fish diet.

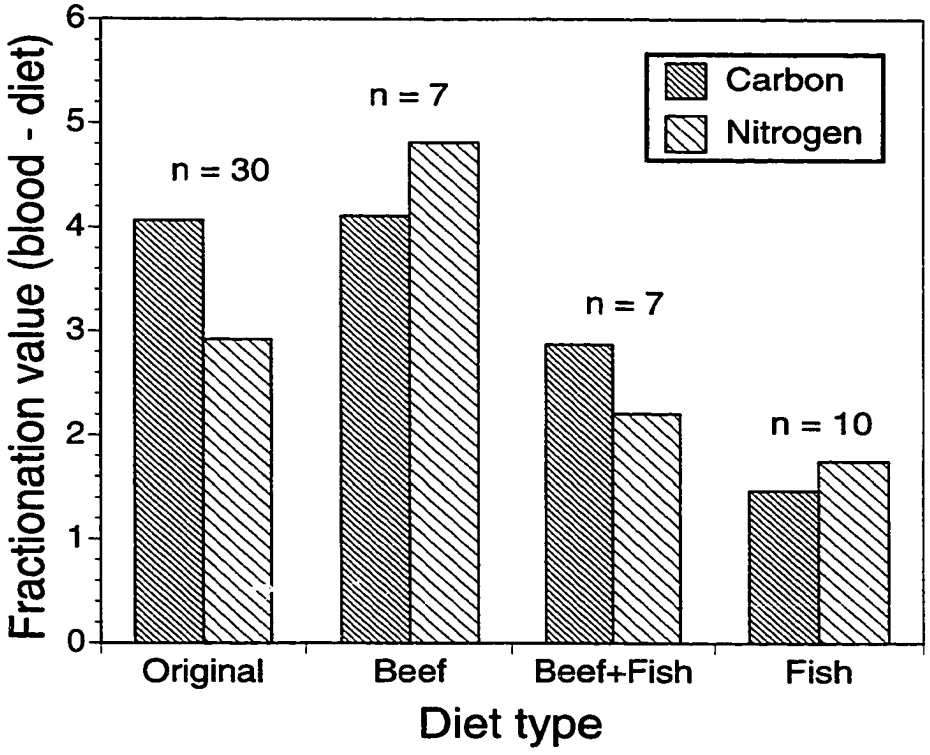

Figure 30. Fractionation values of ^{13}C and ^{15}N (mink blood minus diet) for the original diet (at day 0 of the experiment), and three experimental diets (at day 56 of the experiment).

Appendix B - Values of stable isotope for all samples

Table 13: Stable Isotope Data - Blue Berries

Date	C - A	N - A
7/19/92	-30.22	4.69
7/19/92	-29.96	1.88
6/26/93	-29.24	2.86
6/26/93	-30.73	1.35
6/27/93	-31.08	-0.17
6/28/93	-29.65	1.75
6/28/93	-30.27	1.06
7/5/93	-30.14	3.14
7/5/93	-31.54	2.97
7/5/93	-32.35	2.54
7/5/93	-32.07	0.18
7/5/93	-32.75	0.77
7/9/93	-28.64	-6.53
7/9/93	-29.67	-4.24
7/9/93	-29.55	-5.55
7/9/93	-28.04	-2.92
7/9/93	-26.05	2.62
7/9/93	-27.93	-3.39
7/9/93	-28.76	-5.78
7/9/93	-27.21	-3.23
7/12/93	-31.09	1.17
7/12/93	-32.9	0.07
7/12/93	-31.14	0.65
7/12/93	-32.78	-1.84
7/12/93	-33.08	-0.66
7/12/93	-32.21	-0.19
7/12/93	-29.33	-2.03
7/15/93	-31.43	2.19
7/15/93	-30.35	2.14
7/15/93	-32.89	-0.1
7/15/93	-30.2	-3.94
7/15/93	-31.73	1.03

Table 13: Stable Isotope Data - Blue Berries

Date	C - A	N - A
7/15/93	-30.68	3.92
7/15/93	-32.21	1.19
7/15/93	-28.23	-4.03
7/15/93	-27.46	-4.52
7/15/93	-29.61	0.64
7/4/94	-28.65	2.13
7/4/94	-29.12	1.62
7/4/94	-27.92	-0.81
7/4/94	-29.28	4.32
7/4/94	-30.09	0.2
7/4/94	-30.45	0.57
7/4/94	-29.34	2.14
7/5/94	-30.51	4.83
7/5/94	-30.91	1.45
7/5/94	-28.58	-3.29
7/5/94	-26.36	-3.27
7/5/94	-27.63	-2.63
7/5/94	-29.65	-3.46
7/5/94	-32.28	-4.64
7/21/94	-29.44	0.58
7/21/94	-29.85	1.38
7/21/94	-32.18	-0.72
7/21/94	-32.54	-1.94
7/21/94	-33.04	-2.2
7/24/94	-32.22	-1.21
7/24/94	-27.95	-4.5
7/24/94	-27.94	-2.08
7/24/94	-29.44	-1.62
7/24/94	-28.67	-6.62
7/24/94	-31.74	1.63
7/24/94	-30.45	-4.55
8/21/94	-31.87	3.07
8/21/94	-31.48	0.3
8/21/94	-30.34	-5.97
8/21/94	-28.33	-8.04

Table 13: Stable Isotope Data - Blue Berries

Date	C - A	N - A
8/21/94	-28.39	-5.97
8/21/94	-32.53	0.67
8/21/94	-30.18	2.25

Table 14: Stable Isotope Data - Devil's Club Berries

Date	C	N
7/19/92	-28.86	4.71
7/5/93	-30.9	3.16
7/5/93	-28.23	1.66
7/12/93	-31.54	1.54
7/12/93	-30.42	1.42
7/12/93	-28.91	-1.01
7/12/93	-29.85	-0.88
7/12/93	-29.24	-0.49
7/12/93	-30.45	1.55
7/12/93	-29.05	-2.42
7/15/93	-28.51	2.28
7/15/93	-30.07	1.53
7/15/93	-30.81	1.23
7/15/93	-26.56	2.67
7/15/93	-31.67	-1.12
7/15/93	-28.41	0.98
7/4/94	-30.56	5.62
7/4/94	-28.5	2.3
7/4/94	-29.92	3.71
7/4/94	-29.71	4.84
7/4/94	-25.49	-1.97
7/4/94	-25.98	0.75
7/4/94	-31.18	6.44
7/4/94	-28.1	5.51
7/4/94	-30.76	2.26
7/4/94	-30.68	1.86
7/4/94	-29.84	2.01
7/5/94	-30.79	7.28

Table 14: Stable Isotope Data - Devil's Club Berries

Date	C	N
7/19/92	-28.86	4.71
7/5/94	-25.57	-3.83
7/5/94	-28.46	-4.05
7/5/94	-30.96	-3.34
7/21/94	-31.26	2.55
7/21/94	-28.47	-0.59
7/21/94	-29.06	-0.73
7/21/94	-30.88	1.49
7/21/94	-30.48	-3.04
7/21/94	-30.76	-1.11
7/21/94	-31.22	-1.5
7/24/94	-26.87	-1.64
7/24/94	-27.64	-4.12
7/24/94	-25.86	-1.28
7/24/94	-27.46	-3.98
7/24/94	-25.41	-0.34
7/24/94	-29.79	-1.74
7/24/94	-30.87	-7.63
7/24/94	-25.16	-0.75
7/24/94	-27.09	0.55
8/21/94	-30.93	0.05
8/21/94	-30.18	-1.14

Table 15: Stable Isotope Data - Cloud Berries

Date	C	N
6/27/93	-27.11	8.03
7/12/93	-31.37	2.37
7/12/93	-26.65	1.39
7/12/93	-30.4	1.55
7/15/93	-27.38	3.47
7/15/93	-29.13	1.36

Table 16: Stable Isotope Data - Stink Current Berries

Date	C	N
8/21/94	-25.55	1.93
8/21/94	-28.65	-1.29
8/21/94	-29.85	2.5
8/21/94	-27.02	-0.34
8/21/94	-27.71	0.28
10/23/94	-30.56	-0.58
10/24/94	-27.9	2.61

Table 17: Stable Isotope Data - Salmon Berries

Date	C	N
6/26/93	-29.93	-1.97
6/26/93	-28.51	1.06
7/5/93	-28.49	5.3
7/5/93	-31.91	7.56
7/5/93	-32.27	5.76
7/5/93	-31.06	5
7/5/93	-32.79	9.49
7/9/93	-27.45	2.48
7/9/93	-26.35	5.02
7/9/93	-27.18	-3.82
7/9/93	-28.16	-0.51
7/10/93	-28.83	0.64
7/12/93	-31.05	-1.54
7/12/93	-32.5	3.66
7/12/93	-32.79	4.69
7/12/93	-32.5	4.81
7/12/93	-30.31	2.4
7/12/93	-32.12	8.97
7/12/93	-31.69	4.19
7/12/93	-27.36	3.47
7/13/93	-30.45	-1.36
7/15/93	-28.79	-0.57

Table 17: Stable Isotope Data - Salmon Berries

Date	C	N
6/26/93	-29.93	-1.97
7/15/93	-31.35	2.8
7/15/93	-31.85	3.47
7/15/93	-32.03	6.24
7/15/93	-34.75	-0.33
7/15/93	-33.78	5.79
7/15/93	-31.08	6.37
7/15/93	-33.85	5.71
7/15/93	-33.58	7.98
7/4/94	-28.83	8.71
7/4/94	-27.97	2.39
7/4/94	-27.36	-1.12
7/4/94	-27.53	2.05
7/4/94	-28.5	2.19
7/4/94	-29.93	4.76
7/4/94	-30.13	3.97
7/4/94	-28.68	12.67
7/4/94	-30.31	9.66
7/4/94	-32.49	9
7/5/94	-26.84	3.56
7/5/94	-29.1	0.45
7/5/94	-29.66	3.92
7/5/94	-29.55	2.55
7/21/94	-27.86	2.83
7/21/94	-29.99	1.95
7/21/94	-29.67	-1.57
7/21/94	-30.67	-2.18
7/21/94	-30.39	-0.26
7/21/94	-31.54	-0.9
7/21/94	-28.81	5.16
7/21/94	-31.7	6.3
7/24/94	-29.94	-2.21
7/24/94	-29.51	-2
7/24/94	-29.2	-1.85
7/24/94	-28.85	-3.42

Table 17: Stable Isotope Data - Salmon Berries

Date	C	N
6/26/93	-29.93	-1.97
7/24/94	-26.5	1.42
7/24/94	-28.76	-0.3
7/24/94	-29.01	-2.47
7/24/94	-31.63	4.62
7/24/94	-27.24	7.49
7/24/94	-26.63	7.85
7/24/94	-28.47	5.83
7/24/94	-26.59	4.07
7/24/94	-29.12	8.35
7/24/94	-29.61	3.01

Table 18: Stable Isotope Data - Spruce Seeds

Date	C	N
7/5/93	-25.21	1.28
7/5/93	-26.13	-3.79
7/5/93	-27.38	-1.44
7/5/93	-26.79	-2.46
7/14/93	-25.97	0.57
7/14/93	-27.29	-5.34
7/14/93	-26.23	-1.96
7/14/93	-25.33	-1.81
7/14/93	-27.33	-1.06
7/15/93	-26.15	-1.7
7/15/93	-26.89	-4.42
7/15/93	-25.64	0.28
7/15/93	-24.83	-0.84
7/15/93	-26.55	-0.39
5/18/94	-25.7	-5.41
5/19/94	-25.17	-4.11
5/20/94	-24.86	-5.76
5/20/94	-24.45	3.31
5/20/94	-24.98	-3.06

Table 18: Stable Isotope Data - Spruce Seeds

Date	C	N
7/5/93	-25.21	1.28
5/21/94	-24.52	-0.61
5/21/94	-24.46	0.49
5/21/94	-24.91	-6.31
5/21/94	-25.05	-7.33
5/21/94	-25.02	-2.22
5/21/94	-25.32	-10.64
5/21/94	-25.47	-10.5
5/21/94	-25.72	1.47
5/21/94	-27.06	2.19
5/21/94	-25.69	0.25
5/21/94	-24.06	1.73
5/21/94	-26.22	0.05
5/21/94	-26.2	-4.39
5/21/94	-25.89	-2.49
5/21/94	-24.25	1.22
7/4/94	-25.72	3.52
7/4/94	-24.28	1.29
7/4/94	-24.02	3.96
7/4/94	-24.6	3.17

Table 19: Song Birds - Stable Isotope Data

Date	Age	Weight	C	N
6/11/92	Adu.	28.7	-25.34	5.96
6/16/92	Adu.	33.5	-24.84	6.94
7/13/92	Juv.	19.5	-24.87	5.66
7/16/92	Juv.	14.5	-25.7	5.79
7/16/92	Juv.	70	-23.97	8.31
7/20/92	Juv.	25	-25.89	6.83
7/21/92	Juv.	23	-25.05	4.74
7/22/92	Juv.	9.5	-26.14	5.95
7/27/92	Juv.	28	-26.12	4.84
7/28/92	Juv.	27	-25.89	6.06
7/29/92	Juv.	25	-25.8	5.27
7/29/92	Adu.	23	-24.99	6.38
7/29/92	Adu.	34	-25.73	4.95
7/30/92	Adu.	29.5	-25.55	7.41
7/31/92	Juv.	25	-25.47	4.56
8/16/92	Adu.	30	-25.93	4.58
4/18/93	Adu.		-23.01	5.11
6/4/93	Adu.	73	-22.73	7.5
6/4/93	Adu.	81	-22.46	8.54
6/4/93	Juv.	4	-24.19	8.11
6/19/93	Juv.	7.5	-25.96	6.06
6/20/93	Juv.	7.5	-25.8	5.86
6/26/93	Juv.	8.5	-25.91	6.2
7/6/93	Juv.	19	-24.37	5.05
7/8/93	Juv.	69.5	-25.08	4.6

Table 20: Ducks - Stable Isotope Data

Date	Age	Weight	C	N
11/22/93	Adu.		-24.94	11.86
11/23/93	Adu.		-19.19	14.35
11/23/93	Adu.		-23.96	12.12
11/24/93	Adu.		-21.41	11.11
11/24/93	Adu.		-26.28	11.27
11/24/93	Adu.		-24.48	7.03

Table 21: Deer - Stable Isotope Data

Date	Age	Sex	C	N
Fall 92	?	?	-28.02	3.28
1/11/93	?	?	-28.08	4
1/11/93	Subadult	female	-28.08	4.59
1/11/93	Subadult	female	-26.64	4.77
11/1/93		?	-26.15	4.46
11/1/93		?	-26.27	3.24
11/17/93	?	?	-27.07	2.48
11/17/93	?	?	-26.86	2.86
11/17/93	1	male	-27.74	2.28
11/25/93	Juv.	female	-28.45	1.52
12/1/93	1.5	male	-29.3	4.03
12/1/93	Subadult	male	-28.75	4.8
1/1/94	?	?	-27.03	1.75
9/30/94	young	male	-29.13	4.29

Table 22: Coho Salmon - Stable Isotope Data

Sex	Date	C	N
F	10/30/92	-19.036	12.431
F	11/1/92	-18.279	12.551
F	11/8/92	-18.819	14.069
F	11/8/92	-17.884	13.088
F	11/9/92	-17.889	11.971
F	10/19/93	-20.05	13.4
F	11/5/93	-16.57	13.78
F	11/6/93	-18.59	12.91
M	10/30/92	-18.891	12.535
M	11/1/92	-17.906	13.227
M	11/3/92	-18.853	12.821
M	11/4/92	-18.558	13.835
M	11/8/92	-18.775	13.487
M	11/8/92	-18.25	13.487
M	11/9/92	-18.569	12.913
M	11/9/92	-17.679	13.466
M	11/12/92	-19.89	12.699
M	10/18/93	-19.6	12.33
M	11/9/93	-19.6	12.2
M	11/26/93	-18.65	12.59

Table 23: Chum Salmon - Stable Isotope Data

Sex	Date	C	N
F	6/29/93	-20.51	10.77
F	7/5/93	-19.92	11.72
M	7/11/93	-20.44	12.22

Table 24: Dolly Varden - Stable Isotope Data

Sex	Date	C	N
?	6/27/92	-17.73	13.25
?	6/27/92	-18.3	13.39
?	6/27/92	-18.33	12.95
?	6/28/92	-17.06	12.76
?	6/28/92	-17.1	12.75
?	6/28/92	-17.29	13.43
F	5/14/93	-20.18	14.05
F	5/18/93	-19.01	14.27
F	5/21/93	-19.37	13.57
F	5/21/93	-20.11	13.31
F	5/21/93	-19.34	15.05
F	6/15/93	-19.13	14.75
F	6/15/93	-19.1	13.12
F	6/15/93	-18.84	13.86
F	6/22/93	-21.42	16.13
F	6/22/93	-21.12	14.76
F	6/22/93	-18.06	13.09
F	10/23/93	-19.23	13.33
M	5/20/93	-22.77	14.01
M	6/6/93	-19.73	13.11
M	6/6/93	-20.02	14.23
M	6/15/93	-19.54	13.35
M	6/15/93	-19.44	13.63
M	6/22/93	-19.35	13.92

Table 25: Pink Salmon - Stable Isotope Data

Sex	Date	C	N
F	8/1/92	-20.57	10.87
F	8/2/92	-20.42	10.81
F	8/3/92	-19.79	11.71
F	8/4/92	-21.27	10.07
F	8/5/92	-19.54	12.26

Table 25: Pink Salmon - Stable Isotope Data

Sex	Date	C	N
F	8/6/92	-20.85	10.45
F	7/9/93	-21.67	11.24
F	7/9/93	-22.51	11.54
F	7/11/93	-20.54	11.64
F	7/12/93	-21.87	11.14
M	7/31/92	-20.49	10.84
M	8/1/92	-20.46	10.95
M	8/4/92	-21.58	11.2
M	8/5/92	-19.81	11.1
M	8/5/92	-20.92	11.26
M	8/6/92	-19.45	11.5
M	7/9/93	-23.69	11.59
M	7/9/93	-24.43	11.52
M	7/9/93	-21.61	12.15

Table 26: Juvenile Coho Salmon - Stable Isotope Data

Fork length	Date	Weight	C	N
3.8	6/12/92	0.4	-22.99	10.97
5.5	6/12/92	1.3	-24.27	10.76
5.5	6/12/92	1.5	-22.99	11.29
5.8	6/12/92	2	-22.72	11.19
6.9	6/12/92	3.4	-22.62	12.07
4.1	6/13/92	0.5	-23.38	10.97
4.7	6/13/92	0.7	-24.04	10.18
6	6/18/92	2	-26.49	9.6
6.3	6/18/92	2.6	-25.26	11.04
6.4	6/18/92	2.5	-27.54	11.19
6.6	6/18/92	2.4	-25.43	10.57
6.7	6/18/92	3.1	-29.41	8.95
7.4	6/18/92	3.9	-20.98	14.79
8.5	6/18/92	6.1	-21.33	14.34
5.7	6/21/92	2.2	-22.9	11.78
5.7	6/21/92	1.6	-26.64	9.48
6.4	6/21/92	2.7	-25.51	8.2

Table 26: Juvenile Coho Salmon - Stable Isotope Data

Fork length	Date	Weight	C	N
6.4	6/22/92	2	-24.48	8.73
6.4	6/22/92	2.2	-24.27	8.76
6.9	6/22/92	3.6	-24.23	10.79
5.7	6/23/92	1.8	-23.75	12.09
6.4	6/23/92	2.3	-23.53	11.81
6.7	6/23/92	3.2	-24.97	10.36
6.8	6/23/92	2.9	-22.4	12.72
7.6	6/23/92	4.1	-22.83	13.04
6	6/2[illegible]/92	2.4	-22.77	12.25
6.3	6/29/92	2.7	-25.96	9.72
6.7	6/29/92	3	-22.95	12.45
7	6/29/92	3.7	-23.02	12.64
7.4	6/29/92	2.5	-23.45	12.04
5.4	7/1/92	1.6	-24.82	10.79
5.7	7/1/92	2	-23.89	11.17
7.3	7/1/92	4.3	-22.23	14.5
9.1	7/1/92	8.6	-24.21	12.85
6.8	8/7/92	3.6	-22.94	11.22
8.6	8/7/92	7	-22.76	13.02
9.8	8/7/92	12.8	-21.59	13.86
4.9	11/1/92	1.4	-22.63	13.12
5.3	11/1/92	1.6	-22.7	13.92
4.6	11/9/92	1	-22.59	12.93
4.6	11/9/92	1.1	-22.33	13.11
4.8	11/9/92	1.4	-23.19	11.96
7.8	11/9/92	3.6	-23.45	13.11
4.3	11/10/92	1	-23.86	11.57
4.4	11/10/92	1	-22.65	13.32
4.7	11/10/92	1.2	-22.49	13.19
4.8	11/10/92	1.3	-23.57	11.82
4.9	11/10/92	1.3	-22.71	13.2
5.5	11/10/92	1.6	-23.03	12.74
5.6	11/10/92	1.7	-25.36	9.78
7.9	11/10/92	5.8	-22.82	13.04
10.2	11/10/92	13.2	-23.08	13.56

Table 26: Juvenile Coho Salmon - Stable Isotope Data

Fork length	Date	Weight	C	N
5.7	11/11/92	2	-21.67	13.85
8.9	11/11/92	9.2	-22.63	13.44
4.5	11/12/92	1	-23.19	12.31
7.9	11/12/92	7.2	-23.12	13.74
4.6	11/13/92	1	-23.39	12.98
5.9	11/13/92	2.6	-23.01	13.33
5.2	11/14/92	1.8	-23.64	13.02
6.7	11/14/92	4	-23.56	12.81
7.1	11/14/92	4.5	-23.96	11.92
4.6	11/17/92	1.1	-23.14	12.547
9.6	11/17/92	11	-22.68	13.95
10	11/17/92	11.8	-22.25	14.16
7.7	11/18/92	5	-27.27	9.2
8.1	11/18/92	5.3	-23.56	12.84
8.9	11/18/92	8.6	-22.44	14.08
9.8	11/18/92	11.8	-21.69	14.01
5	3/30/93	1.13	-24.54	10.91
5.2	3/30/93	1.37	-26.62	10.64
7.2	3/30/93	3.68	-25.04	10.47
6	4/4/93	2.22	-22.13	13.32
8.2	4/4/93	5.17	-22.86	12.97
11.5	4/4/93	17.41	-21.39	14.89
5.9	4/7/93	1.96	-29.56	10.06
6.8	4/7/93	2.93	-22.32	13.41
5.4	4/8/93	1.16	-32.15	9.09
5.7	4/8/93	1.56	-31.11	8.56
6.8	4/8/93	3.38	-31.45	9.67
5.2	4/9/93	1.18	-23.11	11.62
7.4	4/9/93	3.69	-29.24	9.7
3.3	4/19/93	0.17	-22.12	14.79
4.6	4/19/93	0.83	-24.95	9.75
5.2	4/19/93	0.97	-21.48	13.87
5.7	4/19/93	1.86	-22.07	13.67
5.7	4/19/93	1.9	-23.42	12.02
5.8	4/19/93	1.77	-22.85	12.95

Table 26: Juvenile Coho Salmon - Stable Isotope Data

Fork length	Date	Weight	C	N
6.7	4/19/93	2.19	-23.26	13.37
6.7	4/19/93	1.46	-25.91	9.39
6.8	4/19/93	3.19	-22.68	13.01
8.6	4/19/93	5.1	-24.73	9.43
8.9	4/19/93	6.13	-21.92	13.39
10.7	4/19/93	11.57	-21.36	13.91
4.7	4/20/93	0.84	-21.93	13.97
6.2	4/20/93	2.56	-22.33	13.77
6.4	4/20/93	2.56	-21.65	13.93
7.8	4/20/93	4.81	-22.2	13.2
6.1	4/21/93	1.52	-22.38	12.43
3.2	5/15/93	0.25	-21	15.22
7.6	5/15/93	3.28	-26.08	8.38
8.4	5/15/93	3.46	-25.05	9.81
3.6	5/16/93	0.19	-22.66	14.7
3.8	5/16/93	0.18	-22.21	14.33
9.1	5/16/93	4.75	-23.49	13.41
10.8	5/16/93	7.87	-22.21	13.56
6.8	5/17/93	1.99	-21.04	14.46
8.8	5/17/93	4.52	-22.73	13.83
7.5	5/19/93	3.32	-22.66	14.56
8	5/19/93	4.57	-25.53	11.3
8.2	5/19/93	4.34	-23.74	11.55
9.6	5/19/93	7.33	-21.31	13.98
10.2	5/19/93	8.93	-28.67	10.19
7.3	5/25/93	3.07	-21.92	13.64
8.8	5/25/93	3.91	-24.79	10.15
3.3	5/27/93	0.22	-21.87	14.16
5.6	5/27/93	1.48	-25.68	11.06
6.6	5/27/93	1.99	-25.54	11.04
8.1	5/27/93	4.65	-24.01	11.95
5.3	6/12/93	1.19	-22.65	12.01
6	6/12/93	2.14	-23.48	11.29
6.7	6/12/93	2.77	-24.08	10.59
6.8	6/12/93	2.29	-24.53	10.39

Table 26: Juvenile Coho Salmon - Stable Isotope Data

Fork length	Date	Weight	C	N
7	6/12/93	2.95	-23.96	9.85
4.6	6/13/93	0.51	-25.1	8.53
3.4	6/17/93	0.22	-20.97	15.82
5.7	6/17/93	1.45	-22.47	14.33
7.3	6/17/93	3.8	-23.53	13.78
3.3	6/19/93	0.18	-20.83	15.9
3.7	6/19/93	0.26	-21.49	15.26
3.3	6/27/93	0.18	-21.97	12.78
3.3	6/27/93	0.19	-22.55	12.82
3.5	6/27/93	0.28	-20.76	14.35
4.5	6/27/93	0.65	-24.38	11.34
7	6/27/93	2.84	-24.82	10.72
7.3	6/27/93	3.78	-24.15	12.67
8.6	6/27/93	4.88	-24.7	12.69
4.9	6/29/93	1.03	-24.16	11.27
5.3	6/29/93	1.77	-23.72	11.13
6.2	6/29/93	2.51	-24.38	11.75
6.5	6/29/93	3.05	-21.86	10.99
6.6	6/29/93	3.6	-24.87	12
6.6	6/29/93	3.35	-23.17	13.06
6.9	6/29/93	3.61	-26.52	10.98
7.9	6/29/93	5.3	-25.17	11.25
3.9	10/22/93	0.83	-22.21	13.76
4.4	10/22/93	0.71	-21.64	13.92
4.6	10/22/93	1.19	-23	13.96
4.1	10/23/93	0.74	-24.85	10.95
4.3	10/23/93	1.1	-21.98	13.66
8.8	10/23/93	8.09	-25.46	11.05
9.5	10/23/93	10.17	-22.08	12.18
3.6	10/24/93	0.49	-23.01	11.6
5.6	10/24/93	1.78	-22.53	12.96
3.9	10/25/93	0.7	-26.92	10.31
4.4	10/25/93	0.89	-24.95	9.26
4.5	10/25/93	0.98	-24.78	9.46
7.2	10/25/93	4.51	-23.78	13.3

Table 26: Juvenile Coho Salmon - Stable Isotope Data

Fork length	Date	Weight	C	N
9.2	10/25/93	8.05	-25.37	11.45
3.7	10/26/93	0.55	-23.22	10.98
5	10/26/93	1.41	-26.1	8.45
5.4	10/26/93	1.74	-21.91	13.53
5.5	10/26/93	2.33	-25.77	9.77
5.7	10/26/93	2.44	-23.24	13.5
5.7	10/26/93	2.24	-23.06	14.36
5.8	10/27/93	2.14	-22.62	13.44
3.9	11/4/93	0.53	-23.25	12.86
4.1	11/4/93	0.55	-25.16	10.75
4.5	11/4/93	0.76	-24.22	12.52
5.4	11/6/93	1.43	-26.18	11.1
5.9	11/6/93	1.89	-23.34	12.87
7.3	11/6/93	3.86	-24.57	12.78
8.2	11/6/93	5.81	-22.25	13.42
4.7	11/7/93	0.91	-22.44	13.92
5	11/7/93	1.23	-22.92	13.82
6.1	11/7/93	2.3	-23.24	13.14
7.1	11/7/93	3.32	-22.07	13.81
7.8	11/7/93	4.74	-22.54	13.05
8	11/7/93	6.33	-23.17	12.85
8.1	11/7/93	5.87	-22.41	13.03
10.8	11/7/93	14.24	-22.57	15.19
11.8	11/7/93	18.5	-22.55	15
4	11/8/93	0.56	-21.93	12.25
4.3	11/12/93	1.02	-25.34	10.95
5.1	11/12/93	1.44	-23.34	13.03
5.3	11/12/93	1.4	-22.61	12.39
5.7	11/12/93	1.76	-23.87	12.42
6.6	11/12/93	2.67	-24.47	11.12
6.6	11/12/93	2.61	-24.14	12.81
7.6	11/12/93	4.45	-23.16	12.46
8.6	11/12/93	6.24	-26.41	9.76
8.8	11/12/93	7.08	-23.9	12.26
11	11/12/93	14.83	-33.71	9.69

Table 26: Juvenile Coho Salmon - Stable Isotope Data

Fork length	Date	Weight	C	N
11.4	11/12/93	14.16	-32.89	9.03

Table 27: Juvenile Chum Salmon - Stable Isotope Data

Fork length	Date	Weight	C	N
3.8	4/19/93	0.32	-20.51	13.2
4.1	4/19/93	0.28	-21.15	12.46
3.5	4/20/93	0.32	-20.01	12.65
3.7	4/20/93	0.36	-20.74	12.49
3.8	4/20/93	0.44	-21.74	12.34
4.1	4/20/93	0.43	-21.22	11.61
3.8	5/15/93	0.28	-21.51	13.73
3.6	5/16/93	0.26	-20.84	13.3
3.6	5/16/93	0.19	-20.92	13.76
3.5	11/4/93	0.25	-23.36	12.12

Table 28: Juvenile Dolly Varden - Stable Isotope Data

Fork length	Date	Weight	C	N
11.6	6/12/92	16.5	-21.72	13.78
8.9	6/18/92	6.6	-24.52	10.4
5.6	6/21/92	1.4	-23.47	11.54
6.1	6/21/92	2	-27.8	9.47
6.5	6/21/92	2.4	-23.78	10.08
8.6	6/21/92	6.8	-24.06	11.16
9.4	6/21/92	7	-22.43	12.44
9.6	6/21/92	8.6	-26.53	10.4
10.6	6/21/92	12.7	-22.23	13.3
8.9	6/23/92	7.5	-23.52	11.75
9.7	6/23/92	9.3	-22.63	12.87
12.3	6/23/92	21	-23.89	12.13
7.5	6/29/92	3.3	-23.78	11.07
8.7	6/29/92	6.6	-21.74	14.28
9.3	6/29/92	7.7	-22.26	12.92

Table 28: Juvenile Dolly Varden - Stable Isotope Data

Fork length	Date	Weight	C	N
7	7/1/92	3	-21.77	12.78
7.9	7/1/92	4.7	-25.13	10.13
10.8	7/1/92	11.2	-22.52	12.87
11.4	7/1/92	14.6	-21.31	13.99
7.8	8/7/92	4.4	-21.33	12.74
8.5	8/7/92	7.4	-22.95	12.7
9.7	8/7/92	9.6	-23.1	12.01
5.2	11/9/92	1.2	-24.14	11.58
9.6	11/9/92	11.2	-22.61	13.3
10.2	11/9/92	12.3	-25.52	9.72
11.8	11/9/92	18.3	-26.719	10.22
4.9	11/11/92	1.2	-24.29	11.8
6.6	11/12/92	2.9	-23.46	12.28
8.1	11/12/92	6.4	-23.16	13.08
6.2	11/17/92	2.2	-24.05	11.9
6.6	11/17/92	1.9	-23.49	12.49
8.6	3/30/93	6.18	-27.33	9.61
9.2	3/30/93	6.69	-25.96	9.77
5.8	4/7/93	1.61	-23.85	11.45
8.4	4/7/93	5.19	-24.29	12.82
11.1	4/7/93	13.23	-23.22	12.64
13.1	4/7/93	19.93	-23.61	12.9
5.7	4/9/93	1.23	-24.41	11
7.4	4/9/93	2.74	-24.91	7.95
11.1	4/9/93	11.14	-23.49	12.25
6.5	4/19/93	2.13	-27.4	8.2
9.2	4/19/93	7.49	-25.8	10.09
12.9	4/20/93	18.3	-21.7	14.25
9.4	4/21/93	6.85	-23.12	13.55
8	5/15/93	3.63	-26.18	9.91
10.3	5/15/93	8	-25.64	10.64
11.2	5/15/93	9.85	-25.96	11.52
11.3	5/15/93	12.19	-26.35	10.63
12.2	5/16/93	12.67	-23.1	12.24
13.8	5/16/93	16.87	-21.85	14.13

Table 28: Juvenile Dolly Varden - Stable Isotope Data

Fork length	Date	Weight	C	N
7.5	5/19/93	1.76	-22.8	13.71
9.1	5/19/93	4.74	-26.14	9.64
11.1	5/19/93	9.28	-25.24	12.69
11.6	5/20/93	12.08	-28.12	11.32
8.2	5/25/93	4.09	-21.97	13.51
8.8	5/25/93	6.06	-24.27	10.8
5.4	5/27/93	0.77	-26.58	11.39
7.2	5/27/93	2.94	-25.87	10.54
7.3	5/27/93	3.08	-25.33	12.01
9.7	5/27/93	9.32	-22.67	13.56
8.9	5/28/93	6.69	-23.18	13.18
6.8	6/12/93	2.62	-25.81	9.5
10.2	6/12/93	9.86	-22.42	12.77
15.5	6/12/93	32.66	-21.93	12.75
9.6	6/17/93	7.86	-22.62	14.25
10.3	6/17/93	9.62	-22.73	14.42
8.9	6/27/93	7.28	-27.23	9.72
9.2	6/27/93	5.73	-28.34	11.21
12	6/27/93	13.6	-23.97	9.31
13.5	6/27/93	21.85	-20.39	12.46
9.1	6/28/93	6.38	-25.2	8.54
6.9	6/29/93	3.54	-25.68	10.39
7.9	6/29/93	4.7	-31.14	9.13
15.2	7/6/93	30.28	-18.55	12.65
16.9	7/8/93	52.71	-18.81	13.25
18	7/8/93	69.25	-19.34	12.97
8.2	10/22/93	4.79	-30.05	8.82
11.5	10/23/93	18.97	-27.8	12.15
14.2	10/23/93	28.15	-22.23	14.4
6	10/25/93	2.1	-27.92	9.49
6.4	10/25/93	2.36	-25.33	7.09
5.2	11/6/93	1.17	-28.84	11.26
5.3	11/6/93	1.29	-23.95	11.97
10	11/6/93	10.59	-24.97	12.1
14.6	11/6/93	31.88	-22.84	13.73

Table 28: Juvenile Dolly Varden - Stable Isotope Data

Fork length	Date	Weight	C	N
6.1	11/7/93	1.56	-29.35	12.17
7.1	11/7/93	2.95	-25.58	8.21
9	11/7/93	6.29	-26.51	8.6
9.1	11/7/93	7.85	-27.79	9.17
10.5	11/7/93	14.21	-24.55	12.85
11	11/7/93	11.98	-38.12	7.01
4.4	11/12/93	0.99	-28.02	8.52
5.1	11/12/93	1.24	-26.72	9.16
9.3	11/12/93	7.6	-25.16	10.87
9.6	11/12/93	8.44	-24.49	12.33
9.9	11/12/93	9.3	-23.62	11.81
11.1	11/12/93	13.13	-23.65	12.14
9.5	11/14/93	9.26	-24.5	12.41
10.3	11/14/93	12.98	-24.45	11.31

Table 29: Juvenile Pink Salmon - Stable Isotope Data

Fork length	Date	Weight	C	N
3.1	3/31/93	0.12	-21.81	13.4
3.2	3/31/93	0.13	-22.26	13.95
3.1	4/8/93	0.1	-21.52	12.42
3.1	4/20/93	0.17	-22.21	12.49
3.2	4/20/93	0.19	-20.72	12.53
3.3	4/20/93	0.19	-21.83	12.9
3.3	4/20/93	0.21	-22.24	12.59
3	5/25/93	0.14	-22.99	12.7
3.2	5/27/93	0.11	-23.23	12.03
3.3	5/27/93	0.19	-22.73	12.09
3.4	5/27/93	0.17	-22.55	12.48
3	5/28/93	0.13	-21.67	13.94
3.2	5/28/93	0.15	-22.3	13.84
3.3	5/29/93	0.1	-22.16	13.41
3.2	?	0.11	-23.47	13.77

Table 30: Coast-Range Sculpin - Stable Isotope Data

Fork length	Date	Weight	C	N
9.2	6/12/92	9.4	-23.78	12.61
6.4	6/14/92	2.4	-24.79	11.65
8	6/18/92	4.7	-24.45	12.73
8.6	6/18/92	5.6	-23.49	13.03
9	6/18/92	6.8	-24.3	12.64
9.2	6/21/92	8.6	-23.46	12.03
9.4	6/21/92	9.6	-23.46	11.79
9.2	6/23/92	9.7	-21.4	12.81
10	6/23/92	11.8	-22.82	13.45
9.2	6/29/92	10.4	-22.29	12.61
6.6	7/1/92	3.1	-24.94	12.23
9.1	7/1/92	7.5	-22.81	11.55
9.4	7/1/92	11.1	-21.4	14.01
10.2	11/1/92	17.4	-22.6	13.02
4.4	11/9/92	0.9	-24.51	10.75
9.5	11/10/92	15.1	-22.72	12.25
8.8	4/4/93	6.99	-22.61	13.17
7.3	4/6/93	4.44	-25.15	10.76
9.1	4/6/93	10.81	-22.74	13.85
7.5	4/9/93	3.73	-26.1	10.74
4.4	4/19/93	0.65	-23.79	11.23
6.7	4/20/93	3.72	-24.23	12.49
7.7	4/20/93	5.31	-24.75	12.99
8.1	4/21/93	5.61	-25.98	8.73
8.2	4/21/93	6.24	-23.98	13.33
9.1	4/22/93	8.5	-22.74	13.24
6.3	5/17/93	1.64	-26.2	11.82
6.8	5/18/93	2.57	-28.34	11.85
8.4	5/19/93	4.72	-24	13.2
8.6	5/19/93	4.84	-23.83	13.12
6.9	5/21/93	4.01	-26.13	12.05
9.1	5/21/93	9.81	-24.18	12.02
7.5	6/12/93	3.08	-24.45	9.61
8.5	6/12/93	5.38	-22.79	11.11

Table 30: Coast-Range Sculpin - Stable Isotope Data

Fork length	Date	Weight	C	N
8.9	6/12/93	6.75	-23.25	10.31
9.3	6/12/93	8.87	-23.55	11.99
9.4	6/12/93	8.93	-23.18	11.68
8.8	6/17/93	8.29	-23.29	13.6
10.3	6/17/93	10.85	-22.15	13.84
10.1	6/27/93	14.46	-22.75	12.45
6.7	6/28/93	3.01	-27.4	11.01
7.2	6/28/93	4.85	-25.17	10.48
7.6	10/22/93	3.72	-25.4	9.99
7.8	10/22/93	6.31	-24.75	11.67
9.6	10/22/93	14.99	-23.17	13.94
7.7	10/25/93	5.62	-27.31	10.22
8.7	10/25/93	9.21	-25.82	10.31
9.1	10/25/93	14.89	-23.26	13.08
9.1	11/6/93	10.3	-22.76	12.52
9.3	11/6/93	11.8	-22.51	13.15
9.7	11/6/93	11.2	-22.91	13.74
7.7	11/7/93	4.28	-24.83	12.61
9	11/7/93	8.31	-25.76	13.26
5.5	11/12/93	1.35	-26.88	9.78
6.2	11/12/93	2.6	-22.97	11.94
8.4	11/14/93	8.09	-22.62	13.01
8.6	11/14/93	9.03	-23.66	12.71
9.6	11/14/93	4.35	-23.5	12.58

Table 31: Juvenile Steelhead - Stable Isotope Data

Fork length	Date	Weight	C	N
10.4	4/4/93	12.05	-22.39	14.3
10.2	6/12/93	9.46	-28.86	10.67
10.8	6/12/93	11.32	-22.93	11.09
6.6	6/17/93	2.44	-28.67	11.37
7.5	6/17/93	2.87	-24.36	13.45
11.8	6/27/93	17.03	-27.88	9.18
5.6	11/6/93	1.73	-25.39	12.5

Table 31: Juvenile Steelhead - Stable Isotope Data

Fork length	Date	Weight	C	N
5.6	11/6/93	1.06	-23.71	13.31
5.6	11/9/93	2.01	-23.04	11.93

Table 32: Three-spined Sticklebacks - Stable Isotope Data

Fork length	Date	Weight	C	N
4.8	6/18/92	0.9	-28.34	10.44
5.1	6/18/92	1	-32.37	8.04
5.5	6/18/92	1.2	-29.13	9.55
5.6	6/18/92	1.7	-29.37	10.1
5.6	6/18/92	1.2	-27.83	11.12
6	6/18/92	1.5	-30.87	9.72
6.1	6/18/92	1.6	-28.76	8.64
6.2	6/18/92	1.4	-30.3	9.55
6.2	7/1/92	2.2	-27.49	11.6
6.3	11/2/92	2.7	-29.99	10.26
4.5	11/18/92	0.8	-29.06	9.52
4.9	11/18/92	0.9	-29.1	9.4
5.8	11/18/92	1.5	-29.63	9.47
5.4	3/30/93	1.36	-28.55	10.59
5.5	3/30/93	1.24	-27.15	9.79
4.9	4/5/93	0.7	-31.22	7.96
3.2	4/19/93	0.28	-27.43	12.73
5.1	4/19/93	1.02	-31.87	9.33
5.4	4/19/93	1.35	-29.06	9.2
3.6	4/20/93	0.36	-33.86	9.36
3.9	4/20/93	0.46	-31.78	9.77
5	5/15/93	1.08	-27.67	10.73
5.5	5/15/93	1.03	-26.9	10.23
5.6	5/16/93	1.45	-25.43	11.72
6.6	5/16/93	2.25	-29.84	10.58
5.1	5/18/93	1.23	-30.03	9.53
6.2	5/18/93	2.44	-29.18	8.95
5.1	5/21/93	0.99	-29.61	10.74
4.6	10/22/93	0.94	-25.76	13.98

Table 32: Three-spined Sticklebacks - Stable Isotope Data

Fork length	Date	Weight	C	N
4.4	10/23/93	0.82	-31.44	9.49
5.4	10/23/93	1.43	-28.56	8.93
5.4	10/25/93	1.8	-28.93	12.14
4.8	11/7/93	1	-29.5	10.21
4.8	11/7/93	1.94	-29.74	9.88

Table 33: Marten Carcasses - Stable Isotope Data

Sex	Age	Date	Weight	Carbon	Nitrogen
F	1	12/7/91	550	-22.41	10.4
F	0	12/7/91	680	-20.9	12.23
F	0	12/7/91	570	-20.3	14.07
F	0	12/7/91	740	-23.37	9.66
F	0	12/9/91	755	-22.68	9.82
F	4	12/9/91	690	-22.2	10.31
F	1	12/9/91	790	-22.17	11.15
F	0	12/9/91	640	-19.8	14.51
F	0	12/10/91	820	-21.68	11.03
F	1	12/10/91	655	-24.31	8.73
F	1	12/11/91	470	-21.77	11.47
F	1	12/17/91	660	-21.69	10.52
F	2	12/28/91	645	-21.21	12.8
F	2	12/28/91	610	-23.12	9.71
F	1	12/28/91	610	-22.16	11.24
F	2	12/28/91		-22.6	10.53
F	1	12/28/91		-24.14	7.79
F	1	12/28/91		-22.9	9.94
F	3	12/28/91		-21.61	10.59
F	1	12/28/91		-20.12	13.1
F	1	12/31/91	565	-21.12	12.41
F	0	12/31/91	635	-21.46	12.12
F	0	1/5/92	605	-23.18	9.34
F	1	1/5/92	675	-20.44	13.74

Table 33: Marten Carcasses - Stable Isotope Data

Sex	Age	Date	Weight	Carbon	Nitrogen
F	0	1/5/92	700	-18.73	15.53
F	2	1/6/92	580	-24.65	7.18
F	3	1/6/92	605	-23.54	9.28
F	2	12/1/92	560	-21.87	10.12
F	0	12/1/92	540	-22.21	10.7
F	1	12/1/92	610	-22.24	10.11
F	0	12/1/92	559	-22.23	10.12
F	0	12/1/92	500	-21.01	12.97
F	3	12/1/92	600	-20.74	12.28
F	2	12/1/92	510	-23.32	9.38
F	2	12/2/92	700	-24.67	7.72
F	2	12/3/92	765	-23.1	9.97
F	1	12/4/92	580	-22.61	10.91
F	1	12/5/92	635	-22.22	9.43
F	1	12/5/92	680	-22.03	9.87
F	3	12/5/92	650	-22.06	9.89
F	2	12/5/92	690	-22.67	9.81
F	4	12/5/92	590	-23.93	7.2
F	2	12/5/92	620	-23.48	8.09
F	2	12/5/92	690	-21.68	11.47
F	3	12/6/92	690	-22.7	10.07
F	1	12/6/92	630	-20.51	13.63
F	7	12/7/92	560	-22.07	11.19
F	1	12/7/92	640	-22.31	9.87
F	1	12/7/92	660	-24.83	8.02
F	13	12/7/92	710	-22.18	9.53
F	1	12/7/92	795	-21.48	8.67
F	3	12/7/92	665	-22.11	10.99
F	1	12/7/92	760	-23.18	8.95
F	3	12/7/92	665	-22.72	8.8
F	2	12/7/92	660	-24.79	8.27
F	2	12/7/92	580	-23.95	9.37
F	0	12/9/92	680	-21.44	11.63
F	0	12/11/92	630	-21.91	12.07
F	2	12/12/92	615	-21.88	11.75

Table 33: Marten Carcasses - Stable Isotope Data

Sex	Age	Date	Weight	Carbon	Nitrogen
F	0	12/12/92	560	-21.52	12.09
F	2	12/12/92	580	-22.87	8.09
F	0	12/13/92	640	-20.18	15.2
F	1	12/13/92	720	-22.57	10.71
F	1	12/16/92	610	-20.3	13.54
F	2	12/16/92	700	-21.27	10.63
F	5	12/16/92	595	-24.44	9.45
F	1	12/16/92	710	-23.52	9.05
F	0	12/19/92	685	-22.82	9.13
F	0	12/19/92	615	-22.27	10.86
F	2	12/21/92	590	-22.13	9.29
F	2	12/21/92	590	-22.13	9.29
F	2	1/15/93	435	-22.11	8.02
F	8	1/15/93	620	-20.69	12.6
M	1	12/7/91	1295	-22.43	10.4
M	0	12/7/91	880	-22.96	9.93
M	2	12/7/91	970	-20.77	13.02
M	0	12/8/91	1030	-20.21	14.02
M	0	12/9/91	975	-21.91	10.5
M	2	12/10/91	1130	-23.83	7.86
M	0	12/10/91	1210	-20.67	11.87
M	2	12/10/91	810	-24.95	7.21
M	1	12/11/91	1020	-22.43	10.34
M	1	12/17/91	995	-20.2	13.58
M	10	12/17/91	1145	-20.33	13.62
M	2	12/17/91	1255	-20.97	11.6
M	3	12/28/91	895	-24.18	7.78
M	2	12/28/91	830	-21.79	11.01
M	2	12/28/91	760	-24.25	7.18
M	8	12/31/91	860	-20	12.97
M	1	1/6/92	1000	-23.6	9.92
M	1	1/9/92	850	-24.01	8.5
M	1	12/1/92	1135	-22.91	9.58
M	2	12/1/92	795	-19.51	14.77
M	3	12/1/92	685	-23.09	7.56

Table 33: Marten Carcasses - Stable Isotope Data

Sex	Age	Date	Weight	Carbon	Nitrogen
M	0	12/1/92	790	-18.5	15.94
M	1	12/1/92	970	-22.44	10.98
M	7	12/1/92	735	-23.57	8.21
M	1	12/1/92	690	-22.915	7.51
M	0	12/1/92	1020	-20.48	14.02
M	0	12/1/92	865	-22.25	9.71
M	2	12/1/92	900	-19.18	14.61
M	1	12/1/92	815	-22.1	10.96
M	1	12/1/92	750	-19.85	13.73
M	1	12/1/92	925	-19.4	14.95
M	3	12/1/92	1060	-23.13	10.5
M	0	12/1/92	1100	-22.64	11.18
M	1	12/1/92	875	-20.96	11.49
M	1	12/1/92	1240	-23.56	10.28
M	2	12/1/92	995	-21.94	12.01
M	2	12/2/92	910	-21.32	10.6
M	0	12/2/92	910	-19.45	14.4
M	0	12/2/92	830	-21.16	12.63
M	1	12/2/92	1105	-19.99	13.68
M	7	12/2/92	1040	-23.6	8.16
M	2	12/2/92	900	-20.16	13.45
M	4	12/2/92	1430	-23.35	10.18
M	0	12/2/92	900	-19.86	14.58
M	2	12/3/92	885	-21.6	11.63
M	2	12/3/92	860	-23.01	9.78
M	1	12/3/92	850	-19.75	14.42
M	2	12/3/92	1160	-21.14	12.83
M	1	12/3/92	930	-20.15	13.47
M	0	12/3/92	810	-20.73	12.91
M	3	12/3/92	1120	-24.05	7.51
M	4	12/6/92	1000	-22.33	9.89
M	2	12/6/92	1045	-21.93	8.72
M	2	12/6/92	1190	-21.16	13.46
M	2	12/6/92	1080	-19.58	14.98
M	2	12/6/92	1230	-23.53	9.25

Table 33: Marten Carcasses - Stable Isotope Data

Sex	Age	Date	Weight	Carbon	Nitrogen
M	2	12/6/92	1010	-20.58	13.01
M	2	12/7/92	960	-23.23	9.95
M	1	12/7/92	1075	-23.61	9.2
M	1	12/7/92	1010	-20.79	12.52
M	2	12/7/92	790	-19.87	13.21
M	0	12/7/92	850	-23.09	9.75
M	2	12/9/92	960	-20.88	12.73
M	0	12/9/92	925	-20.37	13.37
M	0	12/9/92	785	-19.62	14.73
M	2	12/9/92	1145	-22.56	8.99
M	1	12/9/92	900	-21.61	11.91
M	1	12/9/92	1000	-21.82	10.55
M	0	12/9/92	780	-20.89	13.04
M	0	12/9/92	810	-21.1	13.39
M	0	12/10/92	800	-23.15	10.88
M	2	12/11/92	845	-20.94	12.86
M	0	12/13/92	920	-19.76	14.72
M	8	12/15/92	1020	-19.83	14.86
M	3	12/15/92	950	-23.06	8.49
M	0	12/16/92	885	-21.96	11.47
M	0	12/16/92	800	-22.33	9.93
M	1	12/16/92		-21.32	12.2
M	0	12/16/92	830	-22.16	11.01
M	1	12/16/92		-22.07	9.91
M	5	12/16/92	890	-21.79	11.14
M	0	12/17/92	940	-20.12	13.76
M	0	12/20/92	980	-22.91	9.08
M	2	1/8/93	910	-20.81	12.49
M	9	1/8/93	980	-19.34	15.4
M	3	1/8/93	960	-19.85	14.05
M	2	1/15/93	755	-20.04	13.71
M	3	1/15/93	910	-20.16	13.73
M	1	1/15/93	865	-17.18	16.48
M	2	1/15/93	900	-18.82	16.51
M		10/21/93		-23.51	6.99

Table 33: Marten Carcasses - Stable Isotope Data

Sex	Age	Date	Weight	Carbon	Nitrogen
M		12/9/93		-20.45	12.27

Table 34: Live Martens - Stable isotope Data

Sex	Age	Date	Weight	C	N
F	1	7/25/92	800	-23.71	6.45
F	1	3/10/93	895	-23.26	6.22
F	5	3/15/93	880	-22.76	6.53
F	3	3/16/93	880	-19.87	11.83
F	3	3/19/93	980	-24.54	6.09
F	1	4/8/93	845	-23.15	6.3
F	2	4/12/93	860	-22.92	6.95
F	2	4/14/93	830	-23.5	6.7
F	3	4/27/93	940	-22.09	8.88
F	2	4/27/93	785	-22.15	8.28
F	1	4/28/93	940	-24.05	5.96
F	1	5/2/93	840	-22.75	6.07
F	1	5/2/93	940	-21.94	5.67
F	1	5/14/93	800	-22.4	7.96
F	2	5/20/93	920	-23.52	4.93
F	2	7/6/93	975	-22.13	6.76
F	3	7/7/93	820	-21.99	6.43
F	2	7/7/93	960	-22.88	5.23
F	3	7/10/93	1000	-22.96	5.41
F	0	9/26/93	810	-22.34	7.33
F	3	10/15/93	885	-23.06	6.02
F	0	10/21/93	720	-24.62	4.53
F	1	10/24/93	750	-23.94	7.19
F	0	10/29/93	730	-20.65	10.65
F	0	11/18/93	660	-24.34	4.49
F	1	12/11/93	740	-23.82	7.46
F	1	12/11/93	640	-23.98	5.64
F	2	12/14/93	965	-22.43	5.29
F	4	2/10/94	690	-22.44	4.58
F	2	2/15/94	670	-20.11	9.56

Table 34: Live Martens - Stable isotope Data

Sex	Age	Date	Weight	C	N
F	0	3/29/94	680	-19.47	11.85
F	1	3/30/94	920	-22.52	8.38
F	1	3/31/94	750	-21.78	7.36
F	0	3/31/94	800	-24.29	4.87
F	4	4/1/94	810	-23.84	4.52
F	0	4/2/94	840	-23.95	5.36
F	0	5/1/94	780	-24	5.21
F	9	5/4/94	885	-23.72	5.52
F	1	7/16/94	940	-23.47	5.23
F	0	9/28/94	880	-26.31	5.25
F	0	10/4/94	915	-25.25	4.74
F	5	10/5/94	800	-25.57	4.5
F	4	10/5/94	910	-24.26	5.6
F	1	10/6/94	865	-25.43	4.44
F	1	10/7/94	775	-25.82	3.82
F	1	10/7/94	980	-25.33	5.18
F	0	10/24/94	905	-24.89	5.54
F	0	10/25/94	700	-25.46	4.01
F	2	10/26/94	690	-25.4	4.56
F	4	10/26/94	800	-24.33	5.49
F	1	10/26/94	670	-24.17	5.9
F	3	10/27/94	760	-25.19	4.54
M	2	6/11/92	1330	-23.73	8.27
M	1	6/20/92	1200	-23.21	7.42
M	2	6/28/92	1160	-22.69	8.47
M	2	7/9/92	1380	-23.06	6.22
M	2	7/15/92	1280	-23.92	5.61
M	1	8/1/92	1000	-23.66	6.65
M	2	8/3/92	1275	-23.11	8.24
M	1	10/31/92	1175	-18.95	13.57
M	0	11/4/92	1210	-18.26	14.36
M	2	11/5/92	1250	-19.76	11.84
M	2	11/10/92	1340	-19.57	13.27
M	0	11/16/92	1200	-20.13	10.77
M	2	11/17/92	1250	-19.68	12.84

Table 34: Live Martens - Stable isotope Data

Sex	Age	Date	Weight	C	N
M	5	11/19/92	1360	-18.88	14.29
M	3	3/10/93	1295	-22.34	6.39
M	3	3/10/93	1245	-24.21	5.66
M	5	3/12/93	1425	-19.95	9.55
M	3	3/14/93	1240	-24.31	5.95
M	6	3/14/93	1350	-18.93	12.38
M	2	3/14/93	1080	-17.69	14.56
M	2	4/7/93	1495	-21.41	8.71
M	6	4/14/93	1180	-19.69	11.37
M	3	4/15/93	1230	-24.46	6.27
M	2	7/8/93	1200	-22.34	6.63
M	0	9/26/93	1100	-22.08	7.13
M	0	10/17/93	1090	-23.13	7.43
M	1	10/18/93	1210	-24.9	5.84
M	0	10/20/93	1045	-24.98	4.33
M	0	10/20/93	1050	-24.23	5.78
M	0	10/21/93	1050	-24.46	4.79
M	0	10/21/93	1050	-23.69	5.02
M	0	10/29/93	1270	-21.59	9.59
M	0	10/29/93	1100	-24.41	4.53
M	0	10/29/93	1150	-24.91	4.09
M	0	11/1/93	1030	-19.14	12.4
M	1	11/5/93	1190	-19.88	11.6
M	0	11/12/93	1075	-19.78	11.48
M	0	11/13/93	910	-24.16	5.12
M	0	11/15/93	1010	-23.82	7.23
M	0	11/17/93	1090	-24.33	4.21
M	0	11/18/93	1200	-24.5	4.08
M	0	11/18/93	1150	-20.69	9.66
M	0	11/18/93	1040	-22.68	8.33
M	0	11/18/93	1040	-23.16	5.24
M	0	12/9/93	1240	-23.47	6.21
M	0	12/9/93	1020	-24.61	4.57
M	0	12/9/93	1030	-23.31	5.48
M	1	12/10/93	1000	-23.11	7.07

Table 34: Live Martens - Stable isotope Data

Sex	Age	Date	Weight	C	N
M	0	12/11/93	1080	-23.2	6.46
M	1	12/11/93	1030	-22.38	7.08
M	0	12/12/93	1350	-19.7	11.87
M	3	12/12/93	1590	-24.21	5.5
M	0	12/13/93	1125	-22.05	8.82
M	5	12/13/93	1170	-22.67	6.11
M	4	12/13/93	1210	-23.81	5.28
M	3	2/11/94	1060	-24.04	5.71
M	1	2/13/94	1070	-23.84	5.89
M	1	2/13/94	1010	-23.93	7.07
M	1	2/13/94	1050	-23.79	6.54
M	0	3/28/94	1330	-23.31	7.41
M	0	3/29/94	1280	-22.73	7.91
M	0	3/29/94	1210	-24.33	6.25
M	0	3/29/94	1340	-22.56	8.86
M	3	3/29/94	1260	-23.31	6.48
M	3	3/29/94	1220	-20.94	9.28
M	0	3/29/94	1260	-21.74	8.6
M	1	3/30/94	1240	-23.44	7.26
M	0	3/31/94	1280	-23.54	6.66
M	1	4/2/94	1260	-24.41	6.19
M	0	4/2/94	1120	-24.48	5.78
M	5	4/3/94	1350	-24.12	6.18
M	0	4/4/94	1090	-22.43	7.78
M	1	4/29/94	1370	-24.47	5.46
M	0	4/29/94	1240	-22.75	6.44
M	0	4/29/94	1410	-25.16	6.43
M	1	4/30/94	1360	-24.12	6.2
M	0	4/30/94	1220	-24.75	4.41
M	3	5/2/94	1425	-24.07	5.65
M	0	5/4/94	1290	-24.32	5.74
M	0	5/5/94	1110	-24.7	5.39
M	0	5/19/94	1260	-23.33	6.21
M	1	5/20/94	1050	-23.01	6.98
M	4	5/21/94	1225	-23.25	6.55

Table 34: Live Martens - Stable isotope Data

Sex	Age	Date	Weight	C	N
M	1	5/22/94	1125	-23.52	6.05
M	0	5/23/94	1200	-24.48	5.24
M	0	6/15/94	1310	-24.57	4.63
M	3	6/15/94	1345	-24.02	5.2
M	0	7/8/94	1160	-23.79	4.58
M	0	10/2/94	1120	-25.44	4.79
M	0	10/3/94	1200	-26.18	5.04
M	0	10/3/94	1220	-25.19	4.6
M	0	10/3/94	1120	-25.59	4.05
M	0	10/4/94	1260	-25.76	5.1
M	0	10/5/94	1120	-25.21	4.54
M	0	10/5/94	1250	-24.94	4.61
M	0	10/7/94	1130	-25.66	4.98
M	0	10/22/94	1220	-24.2	5.23
M	1	10/24/94	1260	-24.38	6.33
M	0	10/24/94	810	-24.2	5.62
M	2	10/25/94	845	-23.65	6.82
M	0	10/26/94	1205	-24.63	4.82
M	0	10/26/94	1375	-24.43	5.75
M	1	10/27/94	1100	-23.97	6.81

Table 35: Long-tailed Voles - Stable Isotope Data

Sex	Age	Date	Weight	C	N
F	Subadult	9/20/90	39	-26.67	4.63
F	Subadult	9/20/90	34.4	-25.03	2.61
F	Adult	9/20/90	33.5	-26.04	3.71
F	Adult	7/20/92	53.7	-28.16	2.59
F	Adult	8/1/92	46.3	-30.92	2.6
F	Juv.	8/11/93	24	-29.29	6.44
F	Adult	9/30/94	38.4	-26.29	2.43
F	Adult	10/21/94	39.4	-27.07	2.39
F	Adult	10/21/94	54.5	-26.42	1.51
F	Adult	10/21/94	42.8	-26.74	3.1
F	Adult	10/21/94	39.9	-26.73	1.73

Table 35: Long-tailed Voles - Stable Isotope Data

Sex	Age	Date	Weight	C	N
F	Adult	10/22/94	37.4	-27.29	2.49
M	Subadult	9/20/90	34.1	-27.22	1.87
M	Adult	9/20/90	36.7	-25.35	1.76
M	Adult	9/20/90	36.7	-25.5	2.26
M	?	9/20/90	36.8	-25.31	2.73
M	Adult	8/10/93	34	-28.7	5.72
M	Subadult	8/11/93	28	-28.73	3.06
M	Adult	10/26/93	43.5	-27.26	7.95
M	Adult	11/8/93	34.5	-28.6	7.63
M	Adult	9/28/94	42.2	-28.56	3.07
M	Adult	9/29/94	44.1	-29.11	2.57
M	Adult	9/30/94	37.1	-26.7	2.23
M	Adult	10/20/94	38.9	-27.45	5.72
M	Adult	10/21/94	38.2	-29.23	1.13
M	Adult	10/21/94	38.3	-26.61	2.48
M	Adult	10/21/94	46.9	-26.51	1.98
M	Adult	10/21/94	37.3	-25.87	1.7

Table 36: Keen's Deer mice - Stable Isotope Data

Sex	Age	Date	Weight	C	N
F	Adult	9/19/90	37	-26.18	4.41
F	Adult	9/20/90	29	-25.77	4.05
F	Subadult	9/21/91	24.6	-24.93	3.62
F	Subadult	9/23/91	28.4	-25.78	4.7
F	Subadult	9/24/91	25.7	-24.97	2.48
F	Adult	10/13/91	30.95	-26.9	4.88
F	Adult	6/13/92	40.3	-27	7.56
F	Adult	6/20/92	33.5	-27.08	7.56
F	Adult	7/20/92	34.2	-26.68	5.95
F	Juvenile	7/24/92	18.7	-27.75	6.35
F	Subadult	7/27/92	23	-27.4	7.23
F	Adult	7/27/92	42.4	-29.7	8.15
F	Adult	7/27/92	51	-30.35	7.37
F	Juvenile	7/27/92	22.1	-29.75	6.56

Table 36: Keen's Deer mice - Stable Isotope Data

Sex	Age	Date	Weight	C	N
F	Juvenile	7/28/92	22.3	-28.62	8.07
F	Adult	7/29/92	39.3	-27	8.92
F	Subadult	7/29/92	23.1	-27.94	7.23
F	Adult	8/1/92	37	-31.06	5.83
F	Subadult	8/1/92	22.7	-30.49	4.55
F	Adult	8/1/92	35.1	-29.55	5.81
F	Subadult	8/2/92	20.2	-30.63	4.97
F	Subadult	8/2/92	22.5	-29.89	4.92
F	Adult	8/2/92	46	-30.92	5.5
F	Subadult	8/4/92	14.7	-29.98	5.24
F	Juvenile	8/4/92	14.1	-32.27	5.06
F	Juvenile	8/4/92	13.9	-27.23	9.97
F	Juvenile	8/5/92	16.6	-31.18	4.73
F	Juvenile	8/11/92	12.9	-26.96	6.92
F	Juvenile	8/11/92	14.1	-26.62	6.9
F	Adult	8/19/92	23.2	-27.1	8
F	Adult	8/27/92	37	-27.7	6.96
F	Subadult	8/29/92	21.5	-27.19	6.75
F	Adult	11/9/92	27	-25.56	5.58
F	Adult	11/10/92	25	-28.63	5.66
F	Adult	11/11/92	25	-25.45	6.51
F	Adult	11/18/92	20	-24.32	4.96
F	Adult	3/30/93	26.1	-29.82	6.96
F	Adult	4/12/93	23.3	-23.58	5.07
F	Adult	4/14/93	22.3	-22.51	4.75
F	Adult	4/20/93	27.2	-27.22	8.2
F	Adult	5/18/93	38.5	-27.89	8.17
F	Adult	5/19/93	42.5	-29.18	7.69
F	Adult	5/19/93	32	-28.17	7.15
F	Adult	6/4/93	34.5	-23.87	6.34
F	Adult	6/4/93	32.3	-23.08	7.64
F	Adult	6/14/93	35	-28.36	6.96
F	Adult	6/19/93	36.5	-29.79	7.09
F	Adult	6/25/93	41	-28.95	7.13
F	Adult	6/29/93	38.5	-29.54	8.43

Table 36: Keen's Deer mice - Stable Isotope Data

Sex	Age	Date	Weight	C	N
F	Adult	7/2/93	39	-28	6.94
F	Adult	7/20/93	34.5	-27.46	6.51
F	Juv.	7/22/93	21	-28.65	5.42
F	Adult	7/29/93	31.5	-28.37	7.77
F	Adult	8/11/93	26.5	-30	6.67
F	Juv.	8/18/93	20	-29.4	5.89
F	Adult	8/18/93	36.5	-30.72	5.77
F	Adult	11/7/93	18.75	-28.2	7.33
F	Adult	11/8/93	20.5	-28.39	6.82
F	Adult	11/9/93	22.75	-28.1	6.8
F	Subadult	11/12/93	20.1	-25.54	3.96
F	Adult	11/13/93	28	-27.32	5.32
F	Subadult	11/14/93	19.7	-25.73	4.98
F	Adult	10/21/94	33.2	-25.3	4.51
F	Adult	10/21/94	34.2	-25.9	2.33
F	Subad.	10/21/94	22.3	-26.61	0.73
F	Adult	10/21/94	29.8	-25.67	2.33
M	Adult	9/19/90	36.6	-25.86	4.57
M	Adult	9/20/90	30	-24.75	6.21
M	Adult	9/20/90	40	-25.08	5.64
M	Adult	9/20/90	33.6	-24.84	4.54
M	Subadult	9/20/90	19.8	-27.13	4.8
M	Subadult	9/21/91	27.6	-24.61	4.8
M	Subadult	9/21/91	22.2	-25.84	4.17
M	Subadult	9/23/91	29	-27.45	6.92
M	Adult	9/23/91	32.3	-25.22	3.83
M	Subadult	10/13/91	24.35	-27.46	5.86
M	Subadult	10/13/91	28.5	-28.24	4.58
M	Adult	6/12/92	36.2	-26.82	9.98
M	Adult	6/25/92	31.9	-28.2	8.68
M	Adult	7/3/92	36.1	-29.8	8.56
M	Juvenile	7/6/92	14.4	-28.66	9.47
M	Adult	7/19/92	30.2	-25.58	5.31
M	Juvenile	7/20/92	22.1	-26.55	7.01
M	Juvenile	7/21/92	19.8	-25.91	3.91

Table 36: Keen's Deer mice - Stable Isotope Data

Sex	Age	Date	Weight	C	N
M	Juvenile	7/24/92	20	-27.73	7.13
M	Adult	7/27/92	33.5	-27.68	8.03
M	Adult	7/27/92	30.7	-30.49	6.6
M	Adult	7/27/92	36.8	-29.67	6.83
M	Subadult	7/27/92	25.2	-29.08	6.48
M	Juvenile	7/27/92	14.5	-26.13	7.79
M	Adult	7/28/92	40.9	-28.32	9.15
M	Juvenile	7/28/92	20.6	-27.48	7.06
M	Juvenile	7/30/92	7.7	-28.5	8.91
M	Adult	8/1/92	35.3	-30.44	6.55
M	Adult	8/5/92	35.2	-27.71	7.25
M	Adult	8/9/92	37	-29.84	7.15
M	Adult	8/14/92	37.7	-30.4	6.835
M	Adult	8/15/92	32.8	-30.32	7.19
M	Subadult	8/16/92	28	-26.87	5.79
M	Adult	8/18/92	35.4	-26.27	7.12
M	Adult	8/19/92	31.3	-26.5	6.06
M	Adult	8/27/92	29.9	-28.34	6.29
M	Adult	8/28/92	30.5	-26.67	7
M	Subadult	11/2/92	23	-26.62	5.91
M	Adult	11/10/92	27	-28.66	5.45
M	Adult	11/17/92	25.3	-26.86	6.61
M	Adult	11/17/92	29.3	-27.05	6.39
M	Adult	11/17/92	25.5	-26.55	6.91
M	Adult	11/17/92	25	-28.83	7.3
M	Adult	4/8/93	25.1	-27.38	5.85
M	Adult	4/8/93	24.3	-26.36	8.13
M	Adult	4/8/93	32.5	-26.7	8.84
M	Adult	4/12/93	29.7	-22.19	5.78
M	Adult	4/12/93	32.5	-26.68	6.13
M	Adult	4/16/93	26.3	-25.4	7.66
M	Adult	4/20/93	32.1	-29.05	7.59
M	Adult	4/20/93	29.4	-26.27	6.9
M	Adult	4/21/93	26.9	-26.3	6.61
M	Adult	5/17/93	37.5	-27.55	7.51

Table 36: Keen's Deer mice - Stable Isotope Data

Sex	Age	Date	Weight	C	N
M	Adult	5/19/93	30	-26.64	8.34
M	Adult	5/28/93	28	-27.68	7.76
M	Adult	5/28/93	34.5	-30.44	6.48
M	Adult	5/29/93	35.6	-27.99	8.11
M	Adult	6/2/93	32	-21.48	5.9
M	Adult	6/5/93	23.6	-22.67	8.04
M	Adult	6/12/93	33.5	-30.39	8.05
M	Adult	6/25/93	30	-29.47	6.99
M	Adult	6/26/93	20.5	-30.73	7.1
M	Adult	6/26/93	37	-28.56	8.08
M	Adult	7/7/93	36	-28.25	7.48
M	Juv.	7/10/93	22	-29.34	6.69
M	Juv.	7/15/93	28.5	-25.69	5.89
M	Adult	7/20/93	28	-27.33	5.61
M	Juv.	7/20/93	23	-29.41	6.98
M	Adult	7/21/93	36.5	-29	7.8
M	Subadult	8/11/93	29	-28.92	6.56
M	Subadult	8/11/93	27.5	-30.29	5.4
M	Subadult	8/17/93	34	-30.36	5.24
M	Adult	10/25/93	26	-30.12	6.63
M	Adult	11/7/93	20	-28.48	7.2
M	Adult	11/14/93	25.9	-28.78	6.23
M	Subadult	11/19/93	22.8	-23.86	2.44
M	Subadult	11/19/93	24	-23.42	2.61
M	Adult	9/28/94	37	-26.48	3.28
M	Subadult	9/29/94	28.2	-24.94	3.48
M	Subadult	9/30/94	25.6	-27.24	3.97
M	Subadult	9/30/94	27.5	-24.22	3.08
M	Subad.	10/20/94	30.5	-23.8	4.7
M	Subad.	10/20/94	24	-26.01	1.37
M	Adult	10/21/94	28.1	-25.58	1.04
M	Adult	10/21/94	33.7	-26.13	1.12
M	Subad.	10/21/94	28.3	-25.15	0.6
M	Subad.	10/21/94	24.3	-25.86	1.33
M	Adult	10/22/94	31.9	-27.27	1

Table 36: Keen's Deer mice - Stable Isotope Data

Sex	Age	Date	Weight	C	N
M	Adult	10/22/94	6.12	-26.34	3.36

Table 37: Squirrels - Stable Isotope Data

Sex	Age	Date	Weight	C	N
F	Adult	6/23/92	183.6	-22.01	5.21
F	Adult	4/12/93	179.2	-21.36	5.17
F	Adult	7/1/93	206	-22.7	6.77
F	Adult	7/14/93	178.4	-21.92	2.02
F	Juvenile	7/31/93	114	-23.37	6.06
F	Subadult	10/1/93	138.9	-21.23	0.19
F	Subadult	10/1/93	113.9	-21.49	2.62
F	Adult	11/9/93	177.6	-20.74	3.79
F	Adult	3/30/94	197	-20.67	-2.72
F	Adult	10/1/94	155	-23.03	4.38
F	Adult	10/5/94	180	-22.35	3.65
M	Subadult	7/8/92	107	-22.95	4.35
M	Juvenile	7/22/92	80.2	-23.39	7.49
M	Adult	3/30/93	173.2	-21.76	4.44
M	Subadult	5/4/93	180.8	-20.87	-0.35
M	Juvenile	6/23/93	104.6	-21.28	3.65
M	Adult	10/1/93	155.4	-21.04	1.47
M	Subadult	10/1/93	163	-21.38	-0.51
M	Subadult	10/1/93	158.5	-21.43	-1.47
	Newborn	3/31/93		-22.85	4.19

Table 38: Mink carcasses - Stable Isotope Data

Sex	Age	Date	Weight	C	N
F	2	1/24/92		-16.96	15.12
F	3	12/1/92	530	-15.94	16.21
F	3	12/1/92	425	-15.65	16.39
F	2	12/1/92	340	-15.22	16.49
F	2	12/1/92	475	-19.89	14.7

Table 38: Mink carcasses - Stable Isotope Data

Sex	Age	Date	Weight	C	N
F	4	12/1/92	775	-18.89	14.54
F	2	9/28/93	550	-16.26	14.57
M	0	12/18/90		-19.95	13.58
M	5	12/20/91		-19.43	14.76
M	3	12/20/91		-17.64	15.05
M	1	12/20/91		-16.94	15.48
M	1	12/20/91		-19.26	14.44
M	2	12/1/92	750	-15.52	17.31
M	5	12/1/92	450	-16.43	15.7
M	2	12/1/92	510	-16.12	15.83
M	2	12/1/92	610	-15.21	17.45
M	2	12/1/92	760	-14.54	17.56
M	3	12/1/92	790	-15.18	17.71
M	5	1/15/94	1375	-15.59	17.06
M	1	1/15/94	850	-17.57	14.68
M	1	1/15/94	770	-21.16	15.01
M	0	1/15/94	1090	-18.82	14.18
M	0	1/15/94	680	-20.31	14.77
M	0	1/15/94	730	-21.8	15.24
M	5		825	-17.48	15.43

Table 39: Live Mink - Stable Isotope data

Sex	Age	Date	Weight	C	N
F	2	6/20/92	720	-19.63	15.32
F	2	6/29/92	800	-19.36	15.15
F	2	7/6/92	580	-15.44	13.68
F	2	4/16/93	600	-19.99	10.23
F	2	6/2/93	825	-14.94	13.4
F	2	6/3/93	650	-18.49	10.66
F	3	6/26/93	925	-19.99	14.64
F	2	7/6/93	675	-19.45	14.96
F	3	7/7/93	700	-19.67	15.36
F	2	7/7/93	650	-19.07	15.2
F	1	11/17/93	625	-17.8	14.21

Table 39: Live Mink - Stable Isotope data

Sex	Age	Date	Weight	C	N
M	2	6/10/92	1100	-21.48	13.89
M	2	6/17/92	1000	-22.17	13.14
M	2	6/19/92	1080	-19.62	14.84
M	3	3/31/93	1400	-19.27	15.72
M	2	4/2/93	1300	-18.98	13.4
M	3	4/6/93	1375	-19.05	15.4
M	2	4/8/93	1125	-15.23	14.44
M	2	4/8/93	1475	-14.37	14.18
M	3	4/9/93	1300	-14.61	14.1
M	5	4/11/93	975	-15.76	12.5
M	4	4/14/93	1175	-15.6	13.82
M	3	4/19/93	1525	-19.12	16.22
M	2	4/21/93	1075	-19.58	15.25
M	3	4/22/93	1625	-18.82	16.09
M	3	5/7/93	1100	-19.07	15.25
M	1	5/7/93	1175	-21.46	11.84
M	3	5/8/93	1150	-19.42	14.07
M	3	5/8/93	1125	-18.94	15.68
M	1	5/22/93	975	-18.88	15.25
M	2	5/25/93	1150	-14.25	14.05
M	5	5/27/93	1150	-14.65	13.51
M	5	6/9/93	975	-20.44	14.46
M	2	6/9/93	1050	-19.14	15.24
M	1	6/22/93	1150	-15.86	13.24
M	2	6/29/93	950	-19.99	14.09

Table 40: Amphipods - Stable Isotope Data

Date	Weight	Length	C	N
4/11/93	0.067		-20.56	13.08
4/11/93	0.079		-18.42	12.98
4/11/93	0.089		-19	12.9
4/11/93	0.092		-19.78	12.84
4/11/93	0.1		-20.73	11.7
4/11/93	0.111		-19.79	11.83

Table 40: Amphipods - Stable Isotope Data

Date	Weight	Length	C	N
4/11/93	0.333		-19.86	11.7
4/11/93	0.393		-19.31	11.27
4/11/93	0.414		-19.34	11.76
4/11/93	0.522		-20.91	13.56
4/11/93	0.592		-19.92	13.42
4/11/93	0.624		-19.76	12.16
4/11/93	0.636		-19.42	12
4/11/93	0.644		-19.66	11.82
4/11/93	0.726		-18.91	13.04
4/14/93	0.039		-20.29	10.04
4/14/93	0.234		-20.06	10.74
4/14/93	0.321		-20.5	10.69
4/14/93	0.358		-20.49	10.98
4/14/93	0.398		-18.07	11.13
4/14/93	0.429		-20.68	11.13
4/14/93	0.557		-20.08	11.91
4/14/93	0.654		-19.37	12.73
4/16/93	0.22		-17.15	13.13
4/16/93	0.37		-20.06	11.47
11/12/93	0.07		-16.33	9.79
11/12/93	0.08		-14.98	10.11
11/12/93	0.09		-16.79	9.75
11/12/93	0.09		-16.66	9.89
11/12/93	0.1		-16.33	9.43
11/12/93	0.13		-16.91	9.68
11/12/93	0.14		-15.99	10.22
11/12/93	0.14		-16.3	10.84
11/12/93	0.18		-17.9	10.92
11/12/93	0.18		-16.62	12.34
11/12/93	0.19		-16.67	11.21
11/13/93	0.329		-19.38	11.66
11/17/93	0.141		-16.9	12.14
11/17/93	0.311		-17.91	13.43
11/17/93	0.314		-17.51	14.06
11/17/93	0.315		-17.51	14.57

Table 40: Amphipods - Stable Isotope Data

Date	Weight	Length	C	N
11/17/93	0.333		-17.57	13.44
11/17/93	0.444		-17.88	13.57
11/17/93	0.541		-19.37	14.25

Table 41: Blue mussels - Stable Isotope Data

Date	Weight	Length	C	N
7/9/92		4.2	-18.49	7.7
7/9/92		4.4	-18.37	8
7/9/92		5.1	-18.99	7.87
7/20/92		3.4	-17.62	8.48
7/20/92		4.4	-18.62	8.06
7/20/92		4.8	-18.48	7.81
7/26/92		3.6	-19.43	7.91
7/26/92		4.1	-18.32	8.56
7/26/92		4.5	-19.13	7.76
7/26/92		4.7	-18.92	7.74
7/26/92		5	-19.03	7.82
4/10/93		3	-20.1	7.01
4/10/93		4.1	-20.13	7.46
4/10/93		4.4	-19.53	7.73
4/15/93		4.7	-18.51	8.09
4/15/93		4.8	-18.92	8.3
4/15/93		5.2	-18.43	8.43
4/15/93		5.6	-18.46	8.29
4/16/93		4.5	-20	7.08
4/16/93		4.6	-21.02	7.65
4/16/93		4.8	-20.08	7.6
4/16/93		5.4	-19.39	7.49
5/26/93		2	-19.68	7.08
5/26/93		4.1	-19.71	7.27
5/26/93		4.5	-19.87	7.58
5/26/93		4.6	-19.75	7.44
5/26/93		4.8	-19.93	7.03
6/4/93		3.9	-18.9	7.91

Table 41: Blue mussels - Stable Isotope Data

Date	Weight	Length	C	N
6/4/93		4	-18.99	7.98
6/4/93		4	-19.4	7.65
10/30/93		3.2	-19.02	8.18
10/30/93		3.5	-18.24	8.58
10/30/93		3.6	-19.01	7.79
10/30/93		3.9	-19.85	7.51
10/30/93		4.5	-18.44	7.77
10/30/93		4.8	-19.5	7.44
10/30/93		4.9	-19.08	7.19
10/30/93		4.9	-18.85	7.6
10/30/93		5.1	-18.46	7.63
11/16/93		2.2	-18.64	8.06
11/16/93		2.6	-18.4	8
11/16/93		3.6	-18.19	7.82
11/17/93		4.1	-17.69	7.8
11/17/93		4.1	-17.26	7.77
11/17/93		4.6	-18.68	7.6

Table 42: Shrimp - Stable Isotope Data

Date	Weight	Length	C	N
7/8/92	2.09		-17.39	9.79
7/9/92	3.89		-17.64	10.13
7/9/92	5.87		-17.57	10.08
7/10/92	2.09		-17.59	10.13
7/10/92	2.39		-18.04	9.79
7/11/92	3.323		-17.78	10.3
4/12/93	1.42		-17.37	10.27
6/1/93	3.51		14.57	10.43
6/1/93	3.97		-18.59	9.09
6/1/93	4.02		-18.86	10.21
6/1/93	7.65		-17.64	10.13
6/5/93	1.27		-16.36	9.63
11/17/93	1.5		-16.89	10.11
11/17/93	1.826		-17.62	9.86

Table 42: Shrimp - Stable Isotope Data

Date	Weight	Length	C	N
11/17/93	2.369		-16.38	9.75
11/17/93	3.49		-17.56	9.46
11/17/93	3.654		-18.36	9.62
11/17/93	3.696		-17.54	10.09
11/17/93	4.86		-18.36	9.93
11/17/93	6.171		-18.63	10.01
11/17/93	8.41		-18.5	10.23
11/17/93	9.18		-16.98	9.28
11/19/93	2.3		-17.03	9.62

Table 43: Crabs - Stable Isotope Data

Date	Weight	Length	C	N
7/9/92	0.04		-17.12	7.11
7/9/92	0.09		-17.03	6.95
7/9/92	0.48		13.19	6.99
7/9/92	0.97		-16.68	7.67
7/9/92	1.03		-18.45	7.69
7/11/92	0.393		-16.44	7.99
7/12/92	9.79		-20.38	8.78
7/13/92	45.26		-16.59	9.55
7/18/92	0.45		-17.49	7.77
7/18/92	0.95		-15.23	7.17
7/19/92	0.51		-14.75	7.55
7/20/92	1.998		-17.54	7.39
7/20/92	2.11		-17.19	6.995
7/22/92	0.25		-15.69	7.15
7/24/92	3.57		-16.48	8.77
5/26/93	2.15		-13.99	9.32
6/1/93	0.4		-16	7.99
6/1/93	0.99		-14.74	8.14
6/1/93	1.71		-14.79	8.5
6/1/93	3.07		-16.56	9.03
6/3/93	1.02		-17.47	7.28
6/3/93	1.35		-16.31	8.19

Table 43: Crabs - Stable Isotope Data

Date	Weight	Length	C	N
6/4/93	1.36		-13.96	8.15
6/5/93	2.46		-15.65	8.56
10/30/93	0.13		-17.09	8.58
10/30/93	0.24		-16.65	8.26
10/30/93	0.26		-16.96	8.88
10/30/93	0.28		-17.53	8.53
10/30/93	0.32		-17.96	8.39
10/30/93	0.33		-17.53	8.84
10/30/93	0.35		-17.81	9.01
10/30/93	0.37		-17.64	8.19
10/30/93	0.47		-18.72	8.54
10/30/93	0.47		-18.5	8.66
10/30/93	0.49		-16.93	8.32
10/30/93	0.57		-18.18	7.66
10/30/93	0.59		-17.91	8.25
10/30/93	0.73		-19.11	8.03
10/30/93	0.81		-16.92	7.79
10/30/93	0.84		-17.76	7.6
10/30/93	1.2		-16.45	8.82
10/30/93	1.26		-16.93	8.65
10/30/93	1.75		-16.77	8.55
11/14/93	1.98		-14.22	8.49

Table 44: Hermit Crabs - Stable Isotope Data

Date	Weight	Length	C	N
7/8/92	0.159		-17.08	6.84
7/9/92	0.081		-20.3	6.49
7/9/92	0.213		-16.03	6.85
7/9/92	0.42		-18.94	8.08
7/19/92	0.441		-16.49	8.6
7/19/92	1.275		-17.13	8.85
7/22/92	0.032		-16.02	7.22
7/22/92	0.088		-17.46	7.4
7/22/92	0.157		-16.77	8.08

Table 44: Hermit Crabs - Stable Isotope Data

Date	Weight	Length	C	N
7/22/92	0.176		-16.35	7.64
7/22/92	1.01		-16.36	8.79
7/24/92	0.805		12.35	8.88
4/10/93	0.47		-15.98	10.01
4/10/93	0.73		-15.77	9.33
4/10/93	0.91		-16.04	9.39
4/10/93	1.39		-16.04	9.09
4/11/93	0.184		-17.75	9.08
4/11/93	0.225		-15.98	8.21
4/11/93	0.337		-16.65	8.71
4/11/93	0.675		-17.45	8.64
4/11/93	0.856		-15.79	9.17
4/14/93	0.103		-17.53	9.3
4/14/93	0.434		-16.06	9.95
4/14/93	0.436		-17.02	10.15
4/14/93	0.498		-17.19	10.24
4/14/93	0.778		-17.2	9.81
4/14/93	1.069		-16.96	9.91
6/1/93	0.13		-18.94	9.18
6/1/93	0.19		-18.04	8.86
6/1/93	0.66		-17.47	9.56
6/4/93	0.93		-15.53	8.8
6/4/93	1.28		-16.47	9.19
6/5/93	0.78		-17.48	9.86
6/5/93	0.89		-16.24	9.02
6/5/93	0.95		-16.81	9.9
6/5/93	1.44		-17.15	8.95
10/30/93	0.1		-18.31	7.34
10/30/93	0.11		-18.2	8.06
10/30/93	0.15		-19.5	7.43
10/30/93	0.16		-18.17	8.65
10/30/93	0.19		-17.2	8.46
10/30/93	0.5		-16.97	9.34
10/30/93	0.5		-17.61	9.26
10/30/93	0.5		-16.58	9.21

Table 44: Hermit Crabs - Stable Isotope Data

Date	Weight	Length	C	N
10/30/93	0.55		-15.76	8.31
10/30/93	0.77		-17.59	9.97
11/12/93	0.46		-16.57	9.11
11/12/93	0.49		-15.92	8.49
11/12/93	0.69		-15.56	9
11/12/93	0.81		-15.78	9.21
11/12/93	0.97		-16.42	8.04
11/17/93	0.382		-16.06	7.44
11/17/93	0.475		-16.55	8.84
11/17/93	0.695		-16.13	9.63
11/17/93	0.764		-16.98	8.82
11/17/93	0.823		-17.29	9.69
11/17/93	3.206		-17.3	9.3
11/18/93	1.87		-16.14	9.15

Table 45: Intertidal Fish - Stable Isotope Data

Date	Weight	Length	C	N
7/8/92	23.384	10.3	-14.5	13.38
7/8/92	4.807	12.3	-17.45	12.31
7/8/92	4.599	12.7	-16.32	10.65
7/8/92	4.495	12.9	-17.18	11.03
7/8/92	11.367	13	-16.05	12.75
7/8/92	25.17	16.1	-16.02	14.2
7/10/92	1.3	6.5	-17.77	10.56
7/10/92	1.93	8	-15.14	12.26
7/10/92	1.12	8	-17.71	9.91
7/10/92	1.35	8.2	-18.12	10.21
7/10/92	4.44	12.6	-16.31	11.56
7/10/92	5.91	13.6	-17.56	11.3
7/11/92	12.098	10.7	-15.55	13.07
7/11/92	6.64	14	-16.68	12.16
7/18/92	1.94	8	-15.68	12.2
7/19/92	10.175	10	-18.56	10.89
7/19/92	14.546	10.6	-19.42	10.61

Table 45: Intertidal Fish - Stable Isotope Data

Date	Weight	Length	C	N
7/19/92	13.759	11.4	-17.72	10.48
7/19/92	13.444	11.4	-15.56	9.86
7/19/92	15.866	11.8	-18.25	10.76
7/19/92	17.679	12.2	-18.03	10.1
7/19/92	4.564	12.2	-16.88	10.99
7/19/92	19.615	12.3	-18.69	10.75
7/19/92	20.54	12.6	-21.1	11.62
7/19/92	26.794	12.9	-17.5	12.39
7/19/92	8.309	14.6	-17.58	10.89
7/19/92	10.81	15.8	-16.67	11.54
7/20/92	7.17	9.6	-19.75	10.11
7/20/92	11.21	10.6	-16.88	9.6
7/20/92	3.13	10.6	-17.71	10.55
7/20/92	11.51	11.1	-17.8	11.7
7/20/92	3.49	11.7	-17.41	10.55
7/20/92	4	12.1	-16.69	11.08
7/21/92	23.56	23.1	-17.2	11.82
7/22/92	2.619	6.7	-16.88	12.5
7/22/92	4.031	7.4	-16.55	12.42
7/23/92	1.374	5.1	-16.93	12.62
7/23/92	10.24	10.3	-15.83	12.64
7/23/92	13.069	10.8	-14.95	12.78
7/23/92	3.429	11.4	-17.11	11.23
7/23/92	3.856	12	-16.44	11.33
7/23/92	9.565	15	-16.63	11.73
7/24/92	0.69	5.9	-17.69	10.86
7/24/92	12.18	10.1	-16.17	12.74
7/24/92	38.65	30.1	-16.59	12.14
4/11/93	0.3	4.1	-12.7	12.2
4/11/93	0.51	4.6	-14.68	12.21
4/11/93	3.98	7.8	-15.59	12.79
4/11/93	6.45	8.9	-15.11	12.93
4/11/93	11.94	10.1	-15.12	12.66
4/11/93	14.64	16.8	-15.03	12.16
4/14/93	2.9	6.9	-15.44	12.43

Table 45: Intertidal Fish - Stable Isotope Data

Date	Weight	Length	C	N
4/14/93	6.38	8.2	-15.47	12.63
4/14/93	7.22	8.9	-15.75	12.93
4/14/93	9.65	9.5	-16.22	13.2
4/14/93	15.3	10.7	-15.7	13.25
4/16/93	0.19	3	-15.91	12.65
4/16/93	0.48	4.2	-14.51	12.35
4/16/93	1.39	5.4	-15.95	13.03
4/16/93	7.55	9.2	-15.3	12.76
5/26/93	0.39	3.8	-15.99	12.05
5/26/93	0.46	3.8	-15.89	12.67
5/26/93	0.87	4.6	-16.21	12.67
6/1/93	7.12	9.3	-15.29	13.26
6/1/93	10.91	10.4	-16.08	13.39
6/1/93	10.42	10.5	-15.74	13.13
6/1/93	4.2	12.4	-17.1	12.27
6/1/93	7.09	14	-16.84	11.77
6/2/93	9.42	11.1	-17.48	12.31
6/5/93	0.94	4.6	-16.53	12.4
6/5/93	3.8	8	-14.36	13.27
6/5/93	5.75	8.6	-14.63	12.26
6/5/93	5.9	8.8	-14.29	12.06
6/5/93	9.96	10.2	-15.59	12.54
6/5/93	5.36	13	-17.93	10.52
6/5/93	6.39	13.2	-17.24	10.99
6/5/93	5.78	14	-16.25	11.54
6/5/93	6.75	14.1	-15.94	11.72
6/5/93	6.99	14.1	-16.16	11.47
6/5/93	8.09	14.6	-17.32	11.74
6/5/93	12.31	15.6	-16.42	11.52
6/5/93	14.98	18.1	-15.97	11.35
6/5/93	17.17	19.5	-15.81	11.33
6/6/93	0.44	3.7	-15.09	11.72
6/6/93	2.82	6.7	-13.14	12.28
6/6/93	11.48	10.2	-14.2	12.64
6/6/93	4.25	11.6	-14.96	11.21

Table 45: Intertidal Fish - Stable Isotope Data

Date	Weight	Length	C	N
6/6/93	4.4	11.9	-15.33	11.12
6/6/93	10.06	14.5	-16.92	11.22
6/6/93	11.27	15.9	-16.78	11.21
6/6/93	14.35	16.1	-15.76	11.58
11/12/93	1.88	5.3	-15.74	11.69
11/12/93	1.25	5.5	-14.18	13.27
11/12/93	1.35	5.6	-14.25	13.09
11/12/93	2.55	6.1	-15.89	12.45
11/12/93	3.54	6.6	-14.75	12.16
11/12/93	3.77	6.8	-14.9	12.29
11/17/93	0.309	2.8	-16.13	12.38
11/17/93	1.294	5.4	-16.99	11.76
11/17/93	8.717	9.1	-16.95	11.42
11/17/93	12.63	9.3	-16.4	12.77
11/17/93	11.316	9.5	-16.23	12.08
11/17/93	14.35	10	-16.84	12.69
11/17/93	12.92	10.3	-16.32	12.28
11/18/93	3.26	8.9	-16.23	11.88
11/18/93	18.76	13.9	-17.69	12.84
11/19/93	11.28	9.7	-16.84	12.31
11/19/93	19.74	13.7	-16.8	12.73
11/19/93	19.6	15.4	-15	13.1

Appendix C - Analysis of stable isotope data using a randomization test based on the k nearest neighbors statistic.

Michael N.Rosing, Merav Ben-David, and Ron P. Barry

Abstract

The use of stable isotope analysis in ecological studies is rapidly increasing in recent years. Studies range from evaluating flow of nutrients in ecosystems, to studying dietary composition of individual animals. Several mixing models have been developed to evaluate the relative contribution of different foods to the diet of consumers. All these mixing models, require that all prey types will be bivariately, significantly different from each other. This requirement usually poses a problem in analyzing data of stable isotope ratios because sample sizes in most studies are small and usually not normally distributed. We propose a randomization test, based on the k-nearest neighbor approach. The k nearest-neighbor test is consistent compared with other general alternatives and is also resistant to outliers compared with other test statistics such as Hotelling T^2 or MRPP. Results from our simulations of power revealed that the K nearest neighbor test appears to have a high power even with small sample sizes and comparatively low displacement, which makes it a powerful tool for analyzing stable isotope data. In evaluating the test performance on data collected from martens and their prey on Chichagof Island, Southeast Alaska we were able to reject our null hypothesis that at least two samples of prey were drawn from identical populations, at the 0.05 significance level. A program to evaluate the k nearest neighbor statistic for several groups, written in Pascal or S-Plus is available from the authors.

Introduction

The use of stable isotope analysis in ecological studies is rapidly increasing in recent years. Studies range from evaluating flow of nutrients in ecosystems (Ehleringer and Rundel, 1988; Gearing, 1991; Keegan and Deniro, 1988; kline et al., 1993; Smith et al., 1976), to studying dietary composition of individual animals (Bada et al., 1990; Ben-David and Flynn, in press; Ben-David et al., in review *a*; Ben-David et al., in review *b*; Hobson, 1991; Ramsay and Hobson, 1991; Schell et al., 1988; Schoninger and DeNiro, 1984; Welch and Parsons, 1993). In nature carbon and nitrogen each occur as two stable isotopes: ^{12}C and ^{13}C ;^{14}N and ^{15}N. Ratios of the two isotopes as compared with standards are noted as ^{13}C for carbon, and ^{15}N for nitrogen, and are measured in parts per thousand (‰).The analysis of food webs using natural abundance of stable isotope ratios compares the ^{13}C and ^{15}N values of predator and prey tissues. Values of ^{13}C differ between terrestrial and marine food sources due to differential assimilation of ^{13}C by primary producers in these ecosystems, and enable tracing food webs (Fry and Sherr, 1988; Tieszen and Button, 1988). Values of ^{15}N increase with transfer between trophic levels and therefore reflect both diet and trophic levels (DeNiro and Epstein, 1981). The specific combination of values of ^{13}C and ^{15}N result from the dietary interaction of species or individuals (Ambrose and DeNiro, 1986; Gearing, 1991; Hobson, 1991; Schell et al., 1988; Schoninger and DeNiro, 1984). Kline et al. (1993) developed a dual-isotope multiple-source mixing model to determine the relative contribution of each food item to the diet of an individual consumer. Ben-David et al. (in review *a*) modified the model and Ben-David and Swingley (in prep.) have changed the model from a deterministic to a stochastic one. This modeling approach enables researchers to establish the importance of different foods (Ben-David et al., in review), which is especially important for species like marine mammals and birds for which other techniques for the assessment of diets are difficult (Ramsay and Hobson, 1991; Schell et al., 1988, A. Hirons, Unpublished data). All the mixing models developed so far, require that

all prey types will be bivariately, significantly different from each other (Ben-David et al., in review *a; b*). This requirement usually poses a problem in analyzing stable isotope ratio data because sample sizes in most studies are small (due to the high cost of mass-spectrometry), and usually not normally distributed (see Appendix B). Therefore, parametric techniques, such as Hotelling $T^{2,}$ that have been used on isotope data before (Welch and Parsons, 1993) are not appropriate.

In this paper we propose a randomization test, based on the k-nearest neighbor approach proposed by Schilling (1986), and Henze (1988), which treats the two dimensional stable isotope data as spatial data. Although stable isotope ratios data are not truly in the form of spatial data, the unit of measurement in both variables (^{13}C and ^{15}N) is equal and stable which allows treating them as such (Cressie, 1993). We developed programs (Pascal and S-Plus) to perform this test. Simulation studies were used to assess its power under various alternatives, and the test was later applied to data collected by M. Ben-David on martens (*Martes americana*) in Southeast Alaska (Ben-David and Flynn, in press; Ben-David et al., in review *a; b*) in order to evaluate the test performance on real data.

The K Nearest Neighbor Test

The test statistic is the k nearest neighbor statistic as described by Schilling (1986) and Henze (1988). Consider two bivariate (and possibly multivariate) samples of sizes m and n, and an integer k. For each point ($x = {}^{13}C, {}^{15}N$) in the data set , find the k nearest neighbors (Euclidean distance), that are of the same type as x (see example in Figure 31 where $n = 9$, $m = 11$, and $k = 4$). The cumulative count of these nearest neighbors for each x in the combined samples provides the test statistic Q*. To test whether the two samples (m and n) are from different populations the resulting test statistic is compared with a frequency distribution of the statistic Q under the null hypothesis that both samples are random samples from the same population. We used the randomization approach (Schilling, 1986) to get the frequency distribution under the null hypothesis: m of the points are randomly assigned to one group, the other n points to the second group and then Q is re-computed (see an example inFigure 32). If the number of simulations is large enough (at least 1000) the proportion of simulated Qs that exceed Q* can be used as the p-value of the test. To compare several groups, the p-values from each pairwise comparisons are added to result in an overall p-value for this test. This addition, based on the Bonferroni method, produces an upper-bound probability and tends to be conservative.

The k nearest-neighbor test is consistent compared with other general alternatives in that if one sample is drawn from a population with continuos density f and the other is drawn from a population with continuos density g, and if $f(x)$ is not equal to $g(x)$ on some set with positive measure (i.e., mean, variance, shape, distribution, etc.), as long as$n \to \infty$, $m \to \infty$, and $n/m \to \tau$ for τ between 0 and 1, then the test will detect the difference between the two populations.

The K nearest-neighbor is also resistant to outliers compared with other test statistics that are based on distances such as Hotelling T^2 or MRPP. These latter test are sensitive to relocation of points at greater distances, whereas the K

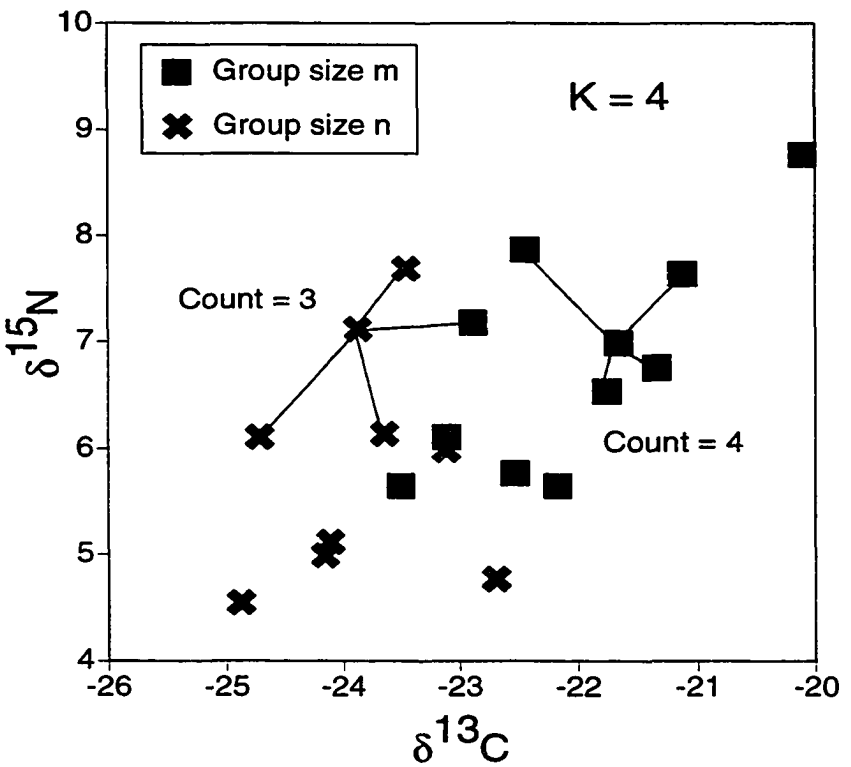

Figure 31. Example of distribution of data points from two groups: one of size m and the other of size n. K = 4 nearest neighbors are plotted for two data points, one from each group, and an example of the counts of same type is given.

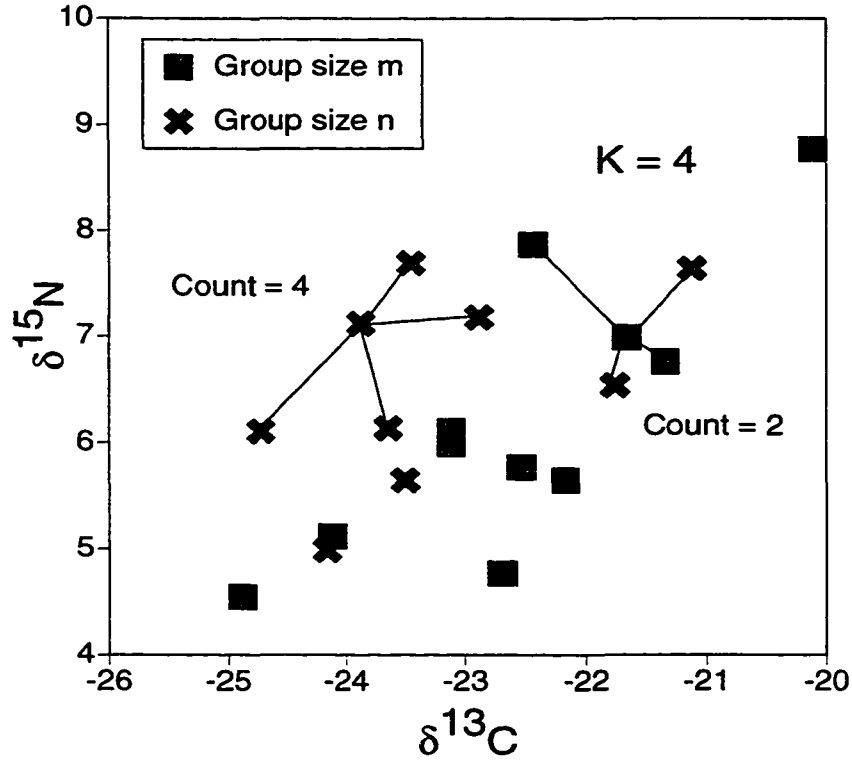

Figure 32. Example of distribution of the data points from Figure 31 after one randomization procedure in which the assignment to group of size m and group of size *n* was done randomly. K = 4 nearest neighbors are plotted for two data points, one from each group, and an example of the counts of same type is given.

nearest-neighbor test can change at most by $n + m$, and can be considered a test on ranks.

Power Evaluation

Schilling (1986) investigated the power of the K nearest-neighbor permutation test using simulations for large data sets ($n = m = 100$) and low k values (1, 2, 3). This power estimation, however, are not applicable to stable isotope analysis, which usually results in small sample sizes. Therefore, we estimated the power of the test for $n = m = 10$ and $k = 1$ to 10 at $\alpha = 0.1$ and 0.01. We considered the case where two samples were each drawn from populations that were uniformly distributed in a square. The amount of overlap between the two populations was varied (see example in Figure 33). The displacement of the two groups (() was varied between 0.0 to 1.5. Our results suggest that the power of this test depends on, k, and the locations (i.e. amount of displacement) of the two populations (Figure 34 and Figure 35). Power increased to values above 0.7 at $\Delta = 0.7$ even at $\alpha = 0.01$. Therefore, the K nearest neighbor test appears to have a high power even with small sample sizes and comparatively low displacement, which makes it a powerful tool for analyzing stable isotope data. From repeated simulations we found that, in general, the optimal k is Min(m,n).

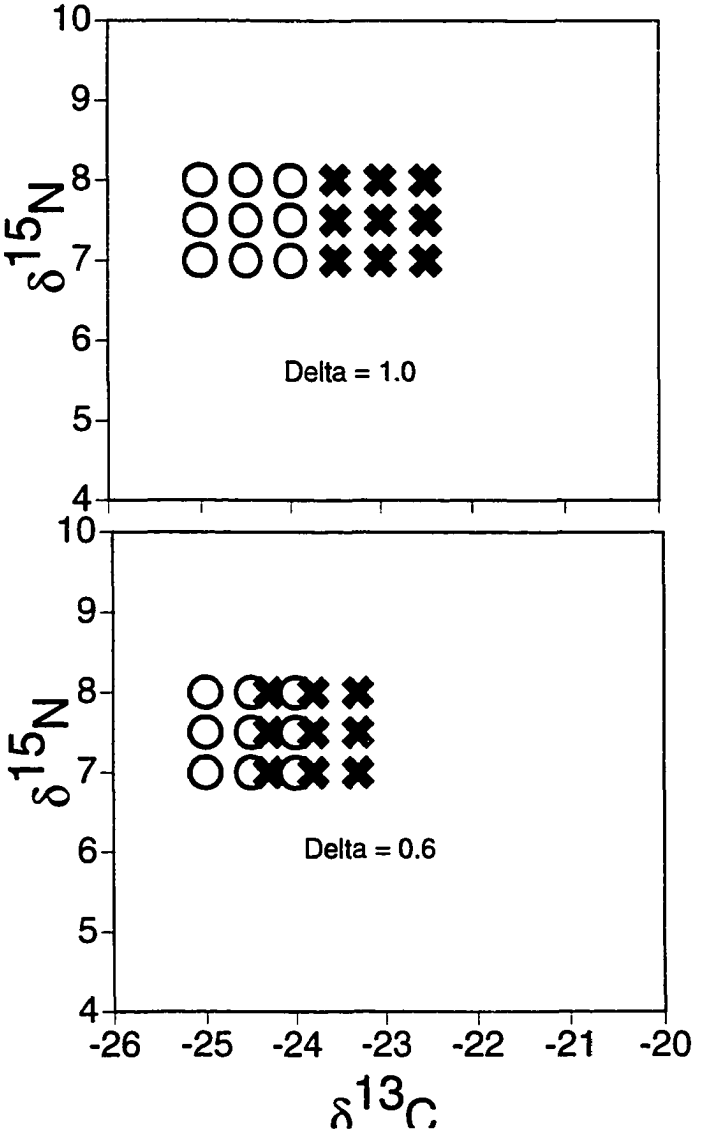

Figure 33. Graphical representation of data distribution for the power test. Data uniformly distributed in a square were tested using different levels of displacement (Δ).

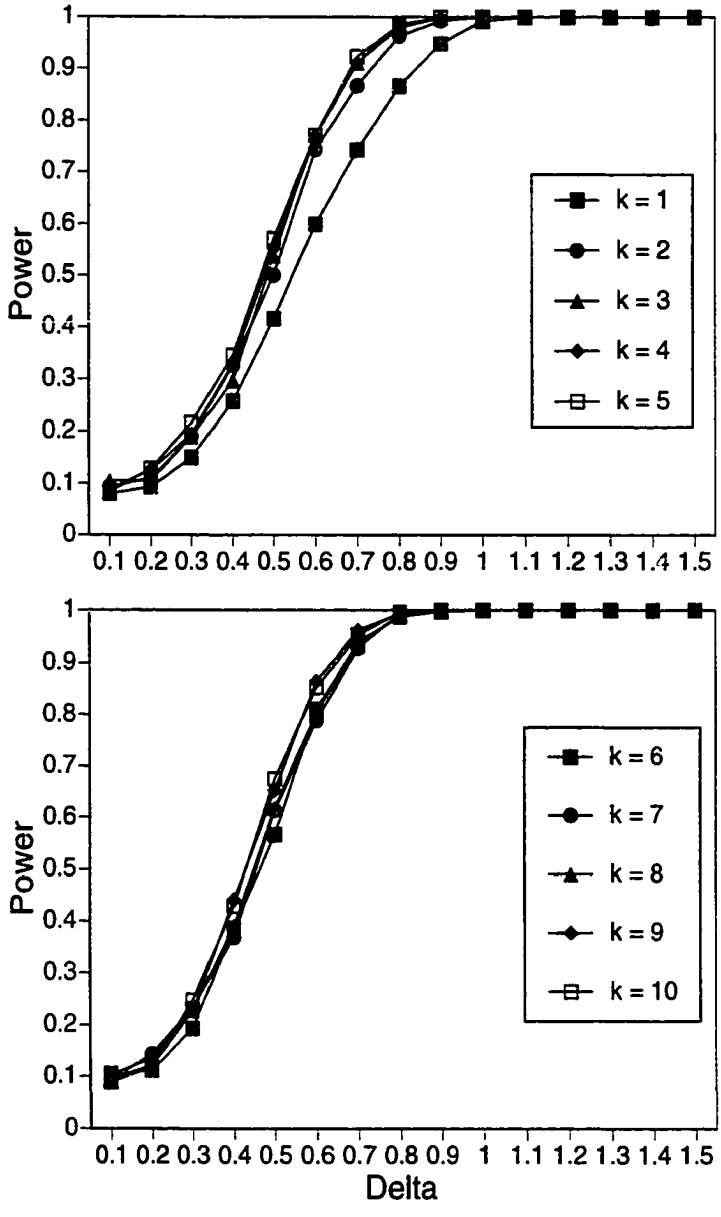

Figure 34. Values of power plotted against displacement (Δ) for *k* 1 to 5 (top), and 6 to 10 (bottom), at $\alpha = 0.1$

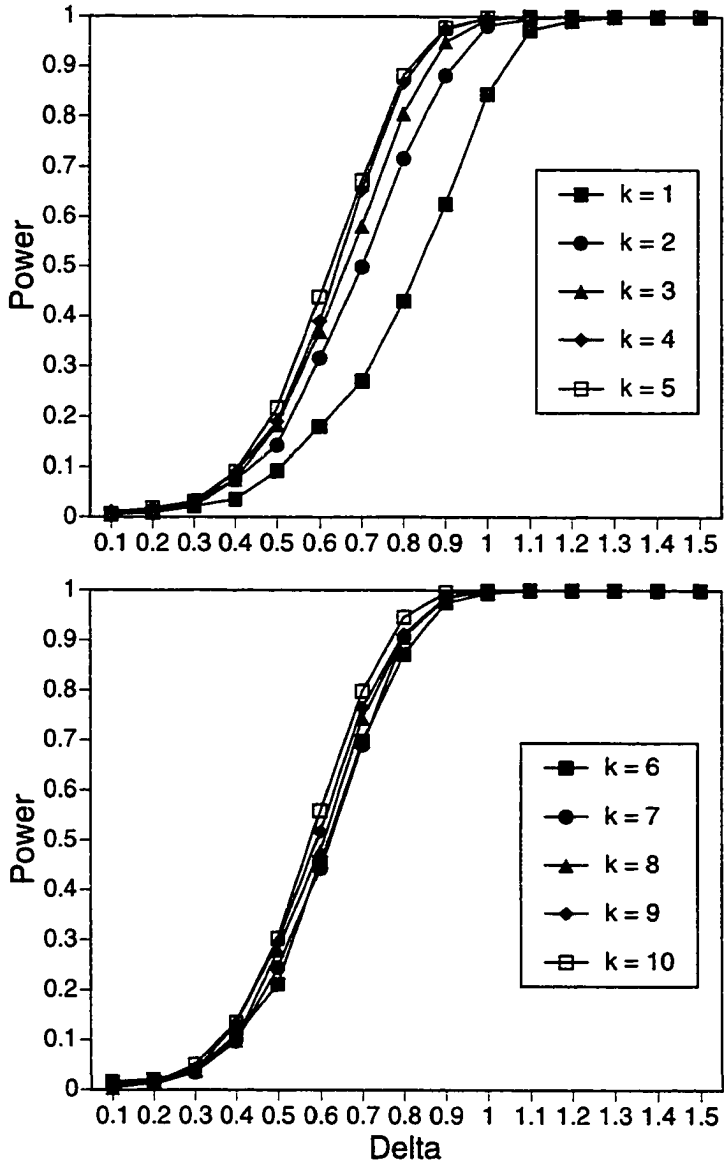

Figure 35. Values of power plotted against displacement (Δ) for *k* 1 to 5 (top), and 6 to 10 (bottom), at $\alpha = 0.01$

Test Performance on Real Data

Samples were collected on Chichagof Island in Southeast Alaska, USA (Figure 1). The island is one of the three large northern islands of the Alexander Archipelago (Tenakee Springs at 57° 52' N 135° 18' W), and is part of the Tongass National Forest (Ben-David and Flynn, in press; Ben-David et al., in review *a*). Prey of martens (*Martes americana*), as well as blood samples obtained from 75 live caught martens were collected in three different seasons (summer, autumn and spring) in order to investigate dietary composition for these animals. The ^{13}C and ^{15}N obtained from marten blood samples were later compared with the ^{13}C and ^{15}N of their possible prey (Ben-David and Flynn, in press; Ben-David et al., in review *a*). A muscle sample from Keen's deer-mice (*Peromyscus keeni*), long-tailed voles (*Microtus longicaudas*), and red squirrels (*Tamiasciurus hudsonicus*), were collected from small mammal trapping grids, as well as from a companion study by T. A Hanley (USFS, Pacific Northwest Research Station), for stable isotope analysis. The rest of each carcass was prepared as a museum specimen (including frozen tissues) and deposited at the University of Alaska Museum. Tissue samples from adult salmon carcasses (*Onchorhynchus gorbuscha*, *O. keta*, and *O. kisutch*), deer carcasses (*Odocoileus hemionus sitkensis*), song birds (winter wrens (*Troglodytes troglodytes*), dark-eye junco (*Junco hyemalis*), robin (*Turdus migratorius*), varied thrush (*Ixoreus naevius*), hermit thrush (*Catharus guttatus*), and Swainson's thrush (*Catharus ustulatus*) were collected when encountered (permit ADFG 90-16) or obtained from hunters. Eleven vegetation transacts (500 m long) were set perpendicular to the river from the riparian to the upland habitats and berry samples (blueberries (*Vaccinium* spp.), salmon berries (*Rubus spectabilis*), cloudberries (*Rubus chamaemorus*), stink current (*Ribes bracteosum*), Pacific crab apple (*Malus fusca*) and devil club berries (*Oplopanax horridus*)) were collected at 100 m intervals. Additional berry samples were collected at higher elevations and at beach fringe habitats. Tissues (clotted blood-cell, muscle samples, and vegetation samples) were kept frozen between collection and preparation for

determination of stable isotope ratios. Samples were dried at 60° to 70° C for 48 hours and then ground to powder using a Wig - L - Bug grinder. Subsequently, a sub-sample (1-1.5 mg for animal tissues and 8-10 mg for plant tissues) was weighed into a miniature tin cup (4 x 6 mm) for combustion. We used a Europa C/N continuous flow mass-spectrometer to obtain the stable isotope ratios. Each sample was analyzed in duplicates and results were accepted only if the variance between the duplicates did not exceed that of the peptone standard.

We tested the hypothesis that all possible prey samples came from distinct populations vs. The alternative hypothesis, that at least two of the samples came from identical populations. The k-nearest neighbor randomization test revealed that in each season (Figures 36 - 38) the stable isotope ratios of prey were significantly different from each other (Table 46)., except for deer-mice and voles in summer and autumn (Table 46), and voles and berries in summer (Table 46). This agrees with visual examination of the data (Figures 36 - 38). Therefore, the overall statistic in summer and autumn was not significant. When voles and deer-mice were regarded as one diet group, which we termed small rodents, the overall test statistic was highly significant for each season (Table 47), and we were able to reject our null hypothesis that at least two samples were drawn from identical populations, at the 0.05 significance level.

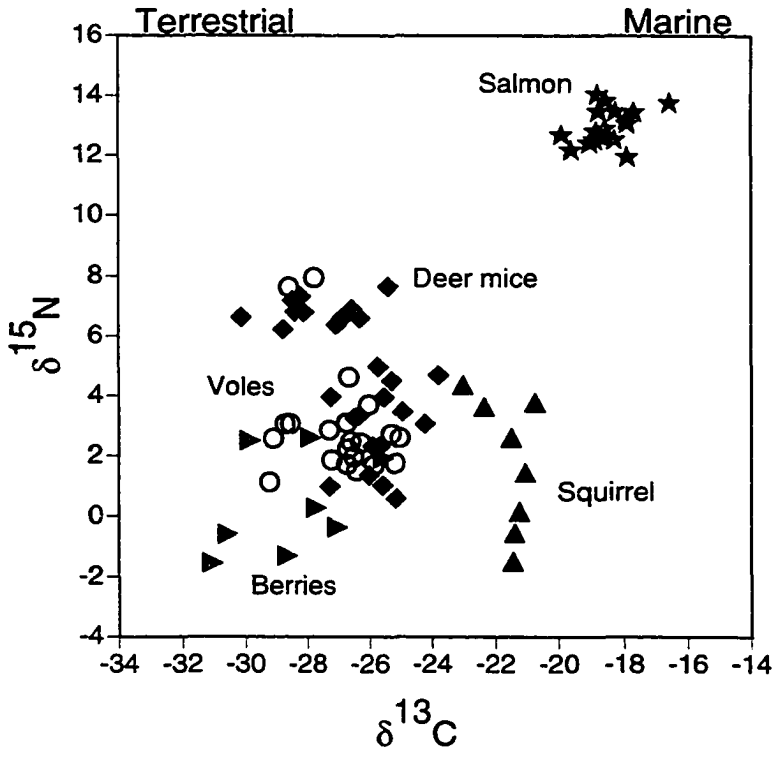

Figure 36. ^{13}C and ^{15}N values for prey of martens in autumn collected on Chichagof Island, Southeast Alaska during 1992 and 1993. Sample sizes are: berries 8, squirrels 8, deermice 26 voles 23, and salmon 18.

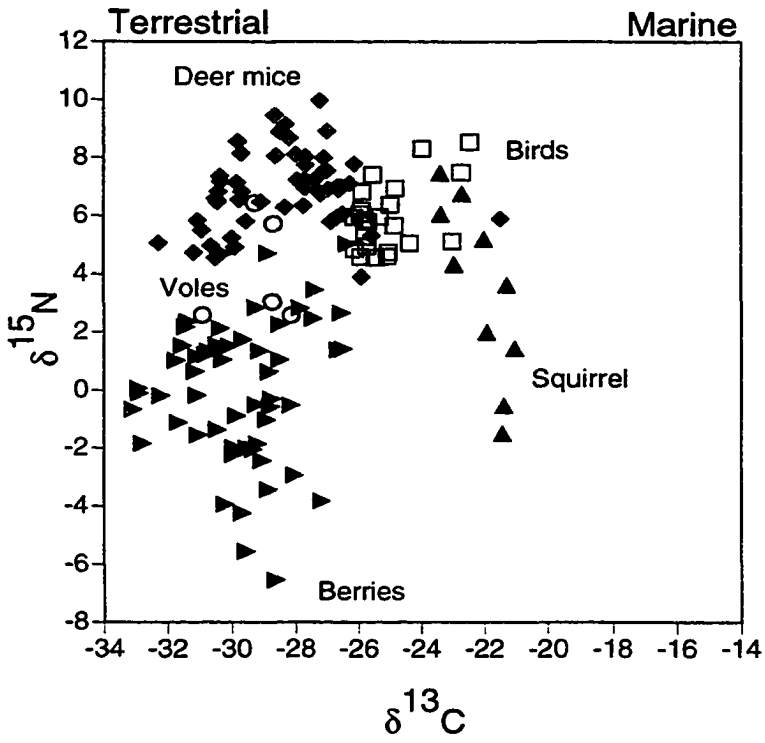

Figure 37. ^{13}C and ^{15}N values for prey of martens in summer collected on Chichagof Island, Southeast Alaska during 1992 and 1993. Sample sizes are: berries 57, squirrels 10, deermice 55, birds 24, and voles 5.

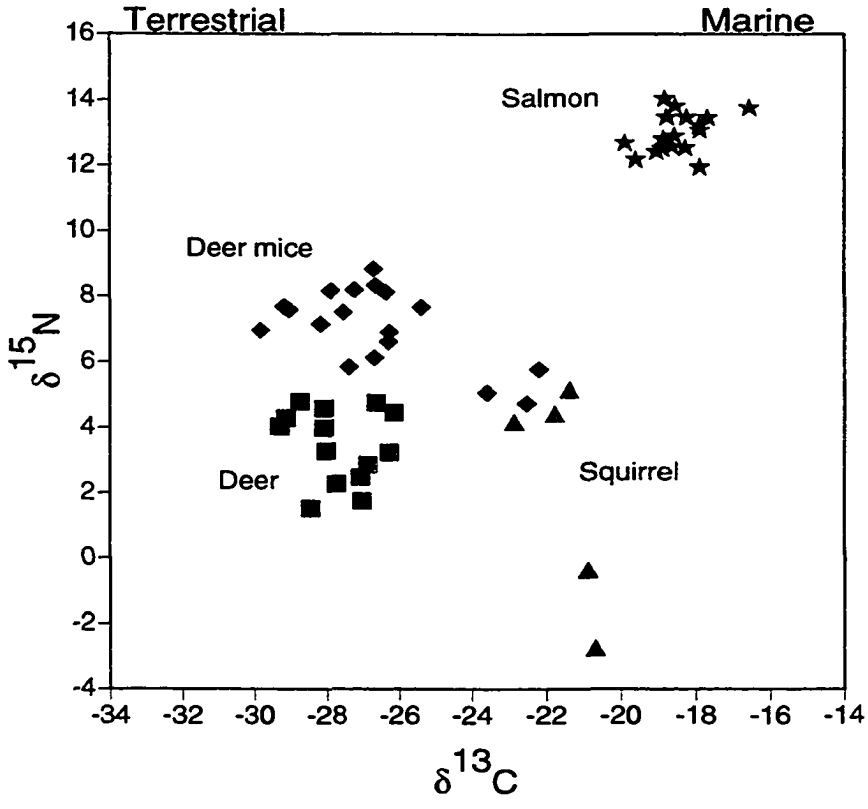

Figure 38. ^{13}C and ^{15}N values for prey of martens in spring collected on Chichagof Island, Southeast Alaska during 1992 and 1993. Sample sizes are: deer 14, squirrels 5, deermice 18, and salmon 18.

Table 46. *P* - values from K-nearest neighbor randomization test for all prey items martens collected on Chichagof Island Southeast Alaska

Summer	Berries	Deer mice	Voles	Birds	Overall
Deer mice	0.0021				
Voles	0.4301	0.1643			
Birds	<0.0001	<0.0001	<0.0001		
Squirrel	<0.0001	<0.0001	<0.0001	<0.0001	0.5965

Autumn	Berries	Deer mice	Voles	Salmon	Overall
Deer mice	<0.0001				
Voles	0.0208	0.2606			
Salmon	<0.0001	<0.0001	<0.0001		
Squirrel	0.0001	<0.0001	<0.0001	<0.0001	0.2814

Spring	Deer	Deer mice	Salmon		Overall
Deer mice	0.0001				
Salmon	<0.0001	<0.0001			
Squirrel	0.0003	0.0004	<0.0001		<0.001

Table 47. *P* - values from K-nearest neighbor randomization test for all prey items of martens collected on Chichagof Island Southeast Alaska, after small rodents were treated as one group.

Summer	Berries	Rodents	Birds	Overall
Rodents	<0.0001			
Birds	<0.0001	<0.0001		
Squirrel	<0.0001	<0.0001	<0.0001	<0.001

Autumn	Berries	Rodents	Salmon	Overall
Rodents	0.028			
Salmon	<0.0001	<0.0001		
Squirrel	0.0001	<0.0001	<0.0001	<0.05

Spring	deer	Rodents	Salmon	Overall
Rodents	0.0001			
Salmon	<0.0001	<0.0001		
Squirrel	0.0003	0.0004	<0.0001	<0.001

The Program

A program to evaluate the k nearest neighbor statistic for several groups, written in Pascal (also available in VAX Pascal and Unix Pascal) and S-Plus is available from the authors and can be obtained by writing to rosing@cqs.washington.edu (Pascal) or ffrpb@aurora.alaska.edu (S-Plus). These program can be easily modified to several dimensions and therefore will be useful in cases in which stable isotope analysis includes more than two isotopes (for example, sulfur, oxygen or hydrogen). A Pascal simulation program used to estimate power of the test is available from M. N. Rosing at rosing@cqs.washington.edu.

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