INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

You are what you eat.

- Mom

University of Alberta

An Application of Stable Isotope Ecology to the Study of Raptor Diets

by

Jason Marshall Duxbury 

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Wildlife Ecology and Management

Department of Renewable Resources

Edmonton, Alberta
Spring 1998

Abstract

Stable isotope analysis is an important tool used by geologists and geochemists. During the last two decades, ecologists have found the predictive characteristics of stable isotope variation useful in the study of biological systems. Isotope analysis can be used to study aspects of the natural history of birds such as diet and migration patterns. Bioaccumulation of heavy nitrogen is the key to studying the diet of raptor species from multiple ecoregions. Feather tissue is a non-destructive and relatively easy tissue to collect and analyze. Significant differences in isotope ratios were not detectable among samples from multiple locations in single large feathers. Stable isotope analysis shows that within a species, prey selection can be highly variable with many individuals appearing to select prey from different trophic levels. The diets of Broad-winged Hawks were found to be eating at a lower trophic level in Alberta than what the literature would predict. Great Gray Owl were found to be eating at a higher trophic level in Alberta than what the literature predicts. Stable isotope analysis should be used in conjunction with more traditional diet study methods which help to explain stable isotope analysis values, while isotope results reduce the biases associated with traditional methods.

Acknowledgments

First, I would like to thank those providing financial support who have made it possible to conduct this study. I thank the Alberta Sport, Parks, Recreation and Wildlife Foundation and the Canadian Wildlife Service of Environment Canada. I also appreciate the warm welcome I have received from the staff at the Canadian Wildlife Service over the years.

This study could not have been conducted without feathers. I sincerely appreciate and thank the volunteers who were patient enough to collect or process feathers. I thank Jim Allen, Josh Bilyk, John Campbell, Gordon Court, Ray Cromie, Al DeGroot, Jeff Dixon, John Folinsbee, Bob Goddard, Keith Hodson, Geoff Holroyd, Jocelyn Hudon, Carol Kelly, Dave Moore, Michael Otto, Hardy Pletz, Trevor Roper, Warren Schaffer, Dave Stepnisky, Lisa Takats, Eugene Taylor, Bruce Treichel, Troy Wellicome, Mark Wendlandt, and Dan Wood.

Thanks to Jim Beck for managing university affairs on my behalf. His enthusiasm for raptors is contagious.

I am very grateful the assistance of Karlis Muehlenbachs who took a student of wildlife ecology and showed him the wonderful world of stable isotopes. Not only do I appreciate the laboratory space and equipment, but I thank him for always dropping what ever he was doing to help me.

Thanks to Joe Takats, for stepping into the fray while already having a busy schedule. I am also grateful for the laboratory space he provided.

I thank everyone at Alberta Fish and Wildlife at the O.S. Longman building for letting me rummage around in the freezer and also pluck feathers from every mount on the 7th floor.

I appreciate the assistance of Jocelyn Hudon for allowing me access to the collections at the Provincial Museum of Alberta.

I thank both Geoff Holroyd and Sandra Nydokus for the long hours of patiently reviewing my thesis and for much needed computer time.

A special thanks goes to Geoff Holroyd who has emotionally, mentally and financially supported me so much over the last 6 years. He has taught me most of what I know about ecology, management, and dangling participles. Thanks to him, I now see all road kills as potential data points.

Finally, I want to thank my parents for guiding me into the life I enjoy today.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter | Page

2.0

3.0

1.0 An Application of Stable Isotope Ecology to the Study of Raptor Diets

1.1 Introduction

Many chemical elements exist in slightly different forms termed isotopes. Within the nucleus of the atom, isotopes of the same element have the same number of protons, but differ in the number of neutrons. There are two types of isotopes: radioactive isotopes and stable isotopes. Radioactive isotopes such as carbon 14, decay over thousands of years. This property allows these isotopes to be used in applications such as carbon dating where the age of organic materials can be traced back approximately 50,000 years (Wade 1987). In contrast, stable isotopes do not decay, and can be used to investigate natural systems and biological processes using mass spectrometry.

Stable isotope ratio analysis (SIRA) of selected elements was first developed by geologists and geochemists over 60 years ago (Ehleringer and Rundel 1989). The analysis of ratios of heavy and light stable isotopes such as $^{18}O/^{16}O$ and D/H (D for deuterium or heavy hydrogen) continue to be used in contemporary research. Some examples of the uses of stable isotope ratio analysis in geochemistry are isotope hydrology, tracing geomorphological pathways and palaeoclimatology (Schiegal 1972, Kharaka and Carothers 1980, Muehlenbachs 1986, Sheppard 1986, Ehleringer and Rundel 1989, Sternberg 1989).

Geochemists were the first to realize that stable isotope ratios changed in biological systems and began to determine how and why the ratios changed (Craig 1953, Park and Epstein 1960, Wickman 1952). Naturally occurring stable isotopes are found in the elements most important to biological processes: carbon, nitrogen, hydrogen, oxygen, and sulphur. The development of SIRA helped to determine the relative amount of isotopes in organic and inorganic matter, how these ratios are altered and finally, how they could be used in the investigation of natural systems.

The usefulness of stable isotope ratios stems from a process called fractionation. Fractionation takes place when a physical or chemical reaction occurs and the relative amount of heavy isotopes is reduced or increased in the product of those reactions. The key property of isotopes which allows them to fractionate is a difference in mass between the isotopes of a given element. (Peterson and Fry 1987, Schimel 1993). Because lighter isotopes have relatively less mass, they have higher velocities during reactions and can subsequently react at a faster rate. Heavier isotopes form stronger bonds in molecules and are less reactive (Schimel 1993). Therefore, during a reaction that causes fractionation, lighter isotopes are consumed at a faster rate in the formation of new products while the heavier isotopes are left behind. Over time the relatively heavy isotopes become more concentrated in the reactants of chemical, physical or biological processes.

Based on the founding work of the geochemists, the fields of archaeology, anthropology, palaeoecolcgy, agriculture and contemporary ecology all began to use stable isotope ratios for dietary analyses of prehistoric or contemporary systems (Miyake and Wada 1967 [in Ehleringer and Rundel 1989], DeNiro and Epstein 1978, Chrisholm *et al.* 1982, Bombin and Muehlenbachs 1985, Minagawa and Wada 1984, Schoeninger and DeNiro 1984, Peterson *et al.* 1985, DeNiro 1987, Wada *et al.* 1987, Fry 1988, Hobson and Montevecchi 1991).

When one uses isotopes to study the diet of organisms, the isotope fractionation characteristics of two elements are used; carbon and nitrogen. The important isotopes of these elements are found in the ratios $^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively. The rarity of the heavier isotopes makes them ideal for tracing pathways through natural systems. Studies of nitrogen fixation using ^{15}N have been important to agricultural studies (eg. Kohl and Shearer 1980, Medina and Schmidt 1982), but ^{15}N is also a tool for stable isotope ecologists. When ^{15}N is used to study trophic relationships of organisms, the bioaccumulation effects of the isotope is key. The heavy stable nitrogen isotope bioaccumulates with each upward step in a food web due to catabolic and metabolic processes that favour the elimination of the relatively lighter isotopes which are excreted in the forms of NH_4^+ or urea (Peterson and Fry 1987, Mizutani and Wada 1988, Ehleringer and Rundel 1989). The faeces of

some animals are actually enriched in ^{15}N, but urine is depleted of the heavier isotope, with the end result being a net enrichment of the heavy isotope in the body tissue (Steele and Daniel 1978, Peterson and Fry 1987). Each consumer contains a higher concentration of heavy isotopes because with each increase in trophic level, organisms are eating prey which has bioaccumulated the heavy isotopes from the previous trophic level. The elimination of lighter isotopes by the predator continues to increase the ratio of $^{15}N/^{14}N$ with the end result that the animals at the top of a food web have higher ratio values than the animals lower in a food web.

The earliest stable isotope ecology studies dealt with how $^{13}C/^{12}C$ ratios are changed by photosynthesis (Craig 1953, Park and Epstein 1960 and 1961, Wickman 1952). The relative amount of fractionation is dependant upon the type of photosynthesis used by the plant: C_3, C_4 or Crassulacean acid metabolism (CAM). Whether the effects causing fractionation are controlled by enzymatic reactions involved in the ribulose bisphosphate step of the Calvin cycle during photosynthesis, diffusion of CO_2 through cell membranes, additional fractionation during photorespiration in C_3 plants, or efficient use of CO_2 by C_4 plants is still poorly understood (Park and Epstein 1960, Peterson and Fry 1987, Ehleringer and Rundel 1989, Schimel 1993). However, the end results of the fractionation of each type of photosynthesis is well documented. Plants using C_3 photosynthesis are significantly more depleted in heavy carbon isotopes (^{13}C) than plants using C_4 photosynthesis. Since CAM plants can use both types of photosynthesis, the isotope ratio values of CAM plants are found between the values of the C_3 and C_4 plants (Park and Epstein 1960, Rau *et al.*1983, Peterson and Fry 1987, Ehleringer and Rundel 1989, Schimel 1993). Fresh water and marine plants have different values because of different initial ratios found in different sources of carbon (the mixing or suspended particulate organic carbon from terrestrial systems, dissolved inorganic carbon or phytoplankton from the aquatic systems) (Chrisholm *et al.* 1982, Fry and Sherr 1984). The isotope ratios are represented in the tissues of the consumer and thus the type of ecosystem (marine, fresh water, C_3, or C_4 photosynthesis dominated terrestrial systems) at the base of a food web can be traced (Fry *et al.* 1978). The establishment of these facts has led to the realization that one can discern whether or not an animal (even a human) is basing its diet on C_3 plants, C_4 plants or a marine diet (Angerbjörn *et al.*

1994). SIRA of carbon has been applied in the fields of archaeology, anthropology and palaeontology where the diets of extinct animals and prehistoric humans have been determined (eg. Chrisholm *et al.* 1982, Bombin and Muehlenbachs 1985, DeNiro 1987, Stern *et al.* 1994).

One of the most recent developments in stable isotope ecology is its use in avian ecology. Physiological studies have found that different metabolic rates associated with different tissue types produce variation in the turnover rate of isotopes within a single bird (Hobson and Clark 1992). Stable isotopes have been used to determine the relative trophic level at which a bird is feeding in relation to all other organisms within a single ecosystem (Hobson 1993, Hobson *et al.* 1994). SIRA can be used to determine food web relationships by indicating which food items are being consumed by which predator (Mizutani *et al.* 1986, Mizutani and Wada 1988, Mizutani *et al.* 1990, Hobson and Sealy 1991, Alisauskas and Hobson 1993, Thompson and Furness 1995). Stable isotope analysis is also being used to create geographical "finger prints" in order to monitor bird migrations and populations (Chamberlain *et al.* 1997, Hobson and Wassenaar 1997,). Finally, since isotopes ratios can be preserved in bone collagen, all of the above methods are being used in palaeoecological studies to determine the diets of extinct species of birds (Hobson and Montevecchi 1991, Stern *et al.* 1994). However, a study which focusses on the ecology of birds of prey has not been conducted.

The use of SIRA to determine the type of ecosystem and the relative trophic level in which raptors are feeding is a new domain. While many traditional dietary studies have been conducted on some raptor species, many species lack dietary information due to remoteness of study areas, small sample sizes or rarity of the species. Valuable information on the diets of these species may be discovered using SIRA. Analysis of heavily studied species along with the more unknown species may help develop associations that can provide insights into the more unknown diets.

The first objective of this study was to establish a sampling protocol for future studies using feathers as a sampling tissue. The large feather sizes of some species, the small sample required for analysis, and problems associated with

the collection of samples required an investigation of the sampling technique. The second objective of this study was to take advantage of the founding work conducted to establish stable isotope ecology and apply it to birds of prey. SIRA was used with results from more traditional methods of studying raptor diets to form more comprehensive conclusions of what raptors are consuming at the individual, species and ecosystem levels. This study investigated, compared and contrasted the diets of most species of raptors found in a variety of ecosystems throughout Alberta, Canada, including; hawks, accipiters, falcons, eagles and owls. The determination of stable isotope ratio relationships between multiple species of raptors and their prey will allow SIRA to become a tool to assist dietary studies in the future.

1.2 LITERATURE CITED

Alisauskas, R.T. and K.A. Hobson. 1993. Determination of lesser snow goose diets and winter distribution using stable isotope analysis. Journal of Wildlife Management 57:49-54.

Angerbjörn, A., P. Hersteinsson, K. Lidén and E. Nelson. 1994. Dietary variation in arctic foxes (*Alopex lagopus*) - an analysis of stable carbon isotopes. Oecologia 99:226-232.

Bombin, M. and Muehlenbachs, K. 1985. $^{13}C/^{12}C$ ratios of Pleistocene mummified remains from Beringia. Quaternary Research 23: 123-129.

Chamberlain, C.P., J.D. Blum, R.T. Holmes, X. Feng, T.W. Sherry and G.R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. Oecologia 109:132-141.

Craig, H. 1953. The geochemistry of stable carbon isotopes. Geochimica Cosmochimica Acta 3: 53-92.

Chrisholm, B.S., D.E. Nelson and H.P. Schwarcz. 1982. Stable carbon isotope ratios as a measure of marine versus terrestrial protein in ancient diets. Science 216:1131-1132.

DeNiro, M.J. 1987. Stable Isotopy and Archaeology. American Scientist 75:182-191.

DeNiro, M.J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica Cosmochimica Acta 42:495-506.

Ehleringer, J.R. and P.W. Rundel. 1989. Stable isotopes: history, units, and instrumentation. Pages 1-15 *In* Stable Isotopes in Ecological Research. Ecological Studies V. 68. *Edited by* P.W. Rundel, J.R. Ehleringer and K.A. Nagy Springer-Verlag New York Inc., New York.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography 33: 1182-1190.

Fry, B., A. Joern and P.L. Parker. 1978. Grasshopper food web analysis: Use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. Ecology 59:498-506.

Fry, B. and E.B. Sherr. 1984. $\delta^{13}C$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions to Marine Science 27:13-47.

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series 95: 7-18.

Hobson, K.A. and L.I. Wassenaar. 1997. Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotope analysis of feathers. Oecologia 109:142-148.

Hobson, K.A., J.F. Piatt and J. Pitocchelli. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786-798.

Hobson, K.A. and Clark, R.G. 1992. Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. Condor 94:181-188.

Hobson, K.A. and W.A. Montevecchi. 1991. Stable isotope determination of trophic relationships of great auks. Oecolgia 87: 528-531.

Hobson, K.A. and S. G. Sealy. 1991. Marine protein contributions to the diet of northern saw-whet owls on the Queen Charlotte Islands: a stable-isotope approach. Auk 108: 437-440.

Kharaka, Y.K and Carothers, W.W. 1980. Oxygen and hydrogen isotope geochemistry of deep basin brines. Pages 305-360. *In* Handbook of

Environmental Isotope Geochemistry, *Edited by* P. Fritz and J.CH. Fontes, Amsterdam.

Kohl, D.H. and G, Shearer. 1980. Isotopic fractionation associated with symbiotic N_2 fixation and uptake of NO_3^- by plants. Plant Physiology 66:51-56.

Medina, R and H.L. Schmidt. 1982. Nitrogen isotope ratio variation in biological material, indicator for metabolic correlations? Pages 465-473 *In* Stable Isotopes. *Edited by* H.L. Schmidt, H. Förstel and K. Heinzinger, Elsevier Scientific Publishing Company, Amsterdam, Netherlands.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochimica Cosmochimica Acta 48:1135-1140.

Mizutani, H., M. Fukuda, Y. Kabaya and E. Wada. 1990. Carbon isotope ratio of feathers reveals feeding behaviour of cormorants. Auk 107:400-403.

Mizutani, H., H. Hasegawa and Wada, E. 1986. High nitrogen isotope ratio for soils of seabird rookeries. Biogeochemistry 2:221-247.

Mizutani, H. and E. Wada. 1988. Isotope ratios in seabird rookeries and the ecological implications. Ecology 69: 340-349.

Muehlenbachs, K. 1986. Alteration of the oceanic crust and the 18O history of seawater. Pages 425- 445 *In* Stable Isotopes in High Temperature Geological Processes. *Edited by* J.W.Valley, H.P. Taylor, Jr. and J.R. O'Neil. Mineralogical Society of America - BookCrafters, Inc., Chelsea, Michigan.

Park, R. and S. Epstein. 1960. Carbon isotope fractionation in plants. Geochimica Cosmochimica Acta 21:110-126.

Park, R. and S. Epstein. 1961. Metabolic fractionation of C^{13} and C^{12} in plants. Plant Physiology 36:133-138.

Peterson, B.J. and B. Fry. 1987. Stable isotopes in ecosystem studies. Ann. Rev. Ecol. Syst. 18:293-320.

Peterson, B.J., R.W. Howarth and R.H. Garritt. 1985. Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. Science 227:1361-1363.

Rau, G.H., A.J. Mearns, D.R. Young, R.J. Olsen, H.A. Schafer and I.R. Kaplan. 1983. Animal $^{13}C/^{12}C$ correlates with trophic level in pelagic food webs. Ecology 64:1314-1318.

Schiegal, W.E. 1972. Deuterium content of peat as a paleoclimatic recorder. Science 175:512-513.

Schimel, D.S. 1993. Distribution and fractionation of isotopes in the environment. Pages 35-113 *In* Theory and Application of Tracers. *Edited by* E.A. Paul and J.M. Melillo, Academic Press, Toronto.

Schoeninger, M.J. and M.J. DeNiro. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochimica Cosmochimica Acta 48:625-639.

Sheppard, M.F. 1986. Characterization and isotopic variations in natural waters. Pages 165-183 *In* Stable Isotopes in High Temperature Geological Processes. *Edited by* J.W.Valley, H.P. Taylor, Jr. and J.R. O'Neil. Mineralogical Society of America - BookCrafters, Inc., Chelsea, Michigan.

Steele, K.W. and R.M. Daniel. 1978. Fractionation of nitrogen isotopes by animals: A further complication to the use of variations in the natural abundance of ^{15}N for tracer studies. Journal of Agricultural Science 90:7-9.

Stern, L.A., G.D. Johnson and C.P. Chamberlain. 1994. Carbon isotope signature of environmental change found in fossil ratite eggshells from a South Asian Neogene sequence. Geology 22:419-422.

Sternberg, L. 1989. Oxygen and hydrogen isotope ratios in plant cellulose: mechanisms and applications. Pages 124-141 *In* Stable Isotopes in Ecological Research. Ecological Studies V. 68. *Edited by* P.W. Rundel, J.R. Ehleringer and K.A. Nagy Springer-Verlag New York Inc., New York.

Thompson, D.R. and R.W. Furness. 1995. Stable-isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in northern fulmars. Auk 112:493-498.

Wada, E., M. Terazaki, Y. Kabaya and T. Nemoto. 1987. ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeographical structure of the food web. Deep-Sea Research 34:829-841.

Wade, L.G., Jr. 1987. Organic Chemistry. Prentice-Hall, Inc. Englewood Cliffs, New Jersey.

Wickman, F.E. 1952. Variations in the relative abundance of the carbon isotopes in plants. Geochimica Cosmochimica Acta 2: 636-639.

2.0 Determining a sampling protocol: is there significant stable isotope ratio variation within a single raptor feather?

2.1 Introduction

The use of stable isotope ratio analysis (SIRA) in avian ecology is one of the most recent developments in the study of stable isotopes. With the growth of isotopic ecological studies, physiology experiments have become more and more important (Mizutani *et al.*1991, Hobson and Clark 1992, Hobson 1993 and 1995, Thompson and Furness 1995). Most ecosystem-scale studies using SIRA depend upon changes in isotope ratios due to a physical or chemical reaction where products of the reactions have different isotope ratios than the reactants. This process is known as fractionation. However, for any alteration of ratios found at a population scale to be meaningful, variation within single birds should first be explored. Since different organs have different metabolic rates, each organ can have different stable isotope ratios (Hobson and Clark 1992). Organs having higher metabolism will incorporate new isotope ratios from a change in diet faster than organs with lower metabolism. This means that each type of tissue can be used to determine dietary input from different time periods. Many raptor species are rare enough that collection of the organs from the birds is not an option, thus the use of an expendable tissue, such as feathers, is the most acceptable tissue type for analysis.

Feather tissue is inert. Once it grows there is no documentation of subsequent changes in carbon or nitrogen ratios with all fractionation occurring during the growth of the feather. Mizutani *et al.* (1986) demonstrated that the isotope ratios of feathers analyzed in their study were closely distributed near the mean of the ratios of all organs. Therefore, the use of feathers as a sampling tissue is not only accessible and non-destructive to the subjects, but represents a good estimate of the overall isotope ratios found in whole birds. However, are there detectable differences in isotope ratios within a single feather? Stable isotope ecology of small species of birds requires the use of whole flight feathers in order to get enough for analysis. Whole bones or feathers are usually necessary, therefore, within tissue variation is of less concern. But when stable isotope ecology is applied to larger birds, a sampling bias may be introduced if the stable isotope ratio values change over the length of the feather. As discussed later,

flight feathers are superior feathers to sample. Since flight feathers are dropped and regrown in a specific sequence in most bird species, a change in their diet during feather growth can lead to different isotope ratios between the growth of the first and last feathers. Thompson and Furness (1995) discovered that variation within Northern Fulmar (*Fulmarus glacialis*) wings can occur when there is a change in the diet during the subsequent growth of feathers during moult. However, Thompson and Furness (1995) did not find significant difference between stable isotope ratios between different locations within single Northern Fulmar primary feathers. Seabird diets tend to be highly specific from a trophic point of view (Hobson *et al.* 1994), changes in isotope ratios due to changes in diet are possible but not as likely as in feathers from birds having a more variable diet such as raptors. Raptor flight feathers can range from under 10 cm long in American Kestrels (*Falco sparverius*) to over 40 cm long in Golden Eagles (*Aquila chrysaetos*). With a wingspan of just over a metre, Northern Fulmar flight feathers would be comparable to those of male Northern Goshawks. The quantity of feather tissue required for analysis by current technology is small. For carbon and nitrogen isotope analysis, only 250 µg per sample is required, which is a relatively small amount of tissue compared to a whole raptor feather. If a change in isotope ratio values is undetectable with seabird feathers, can it be detected within single large raptor feathers?

The best solution for a sampling protocol is to sample from the same type of feather and at same the location on the feather for each analysis. However, the acquisition of large samples of feathers at a provincial, state or continental scale is highly dependent upon volunteers. Thus obtaining the exact same feathers from multiple species may be unrealistic considering the volume of birds sampled and that many different people assist in the sample collection. Whole feathers which have been dropped by moulting birds may be collected or only small pieces of feather may be snipped from wild birds or museum specimens. When pieces of feathers are collected, they may be taken from anywhere along the length of a feather dependent upon the collectors opinion of where it is suitable for removing feather tissue. Tips of feathers are the easiest to sample, however the tips can be used for determining ages of birds or may be required for forensic studies (J. Hudon pers. comm.). Therefore, it is important to determine whether or not a sample taken from the tip of the feather has a significantly different ratio from an area midway down a feather or the base of a feather.

There are two main possible causes for variation within a single feather. The first could possibly be changes in diet during the growth of a long feather. The relevant elements in isotopic dietary studies are nitrogen and carbon (Mizutani and Wada 1988, Hobson and Welch 1992, Alisauskas and Hobson 1993, Hobson 1995). Since, heavy nitrogen (^{15}N) bioaccumulates through trophic levels and indicates the relative trophic level of an organism, changes in diet may cause a shift in the ratios along the length of a single feather. Where ^{13}C bioaccumulates through trophic levels (DeNiro and Epstein 1978, Schoeninger and DeNiro 1984, Mizutani et al 1986, Fry 1988, Hobson and Clark 1992), $^{13}C/^{12}C$ ratios are more useful for determining what type of ecosystem is at the base of a given food web system (Hobson and Sealy 1991, Mizutani *et al.* 1991, Fry *et al.* 1978). If a bird fed in one ecosystem and then switched to a different ecosystem during the growth of a feather, different $^{13}C/^{12}C$ ratios may be detectable along the length of the feather.

Another cause of variance within a feather may be varying growth rates in different parts of the feather. For example, it is not known if the distal portions of primary feathers grow more rapidly with the proximal growth slowing down as the feather nears completion (Figure 1). Differing speeds of growth may cause different fractionation rates and subsequently different isotope ratios. Also, the growth of a feather is a complex process that involves more than one type of keratinization: alpha (α) and beta (β) (Bell and Thathachari 1963, Kemp and Rogers 1972). Haake *et al.* (1984) found that the α-keratin is present during the initial formation of a feather, but only in the underlying skin tissue and then later in the sheath. As the growth of a feather progresses β-keratinization occurs. The β-keratin is introduced sequentially from the tip area of the feather to the base as well as from the distal areas to the proximal areas of the barbules within a feather (Haake *et al.* 1984). It is not known if one protein structure is synthesized at a different rate than the other. If they are synthesized at different rates, there may be different fractionation rates involved as well. Once again, there would be different ratios within a single feather. The present study determined if any shift in ratios within a single feather was detectable with the cause being either a diet switch during the growth of a large feather or changes in growth rates.

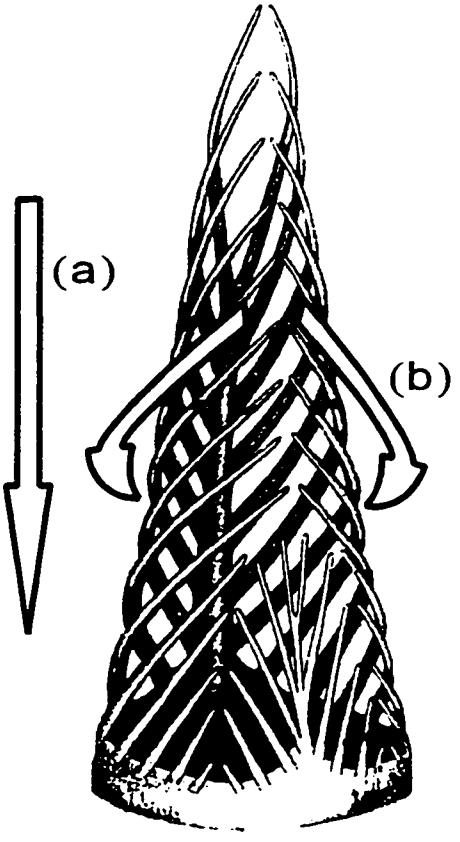


Figure 1. Feather keratinization patterns. Once α-keratinization occurs, β-keratin is laid down from the tip to the base of a feather (a) and from the distal areas to proximal areas (b). Figure adapted from King and McLelland 1985.

Four sets of raptors were selected to determine if significant variance exists within feathers: Golden Eagle (*Aquila chrysaetos*), Great Gray Owl (*Strix nebulosa*), and Peregrine Falcon (*Falco peregrinus anatum*) both wild and captive bred. The eagles and owls were chosen because of the size of their flight feathers. If the growing time of a feather is a determining variable in fractionation rates within the feather, the longer it is the more chance there is for fractionation. The eagles have a fairly consistent diet from a trophic point of view as most of their diet consists of lagamorphs and/or deer carrion, both herbivores (Knight and Erickson 1978, Collopy 1983, Steenhof and Kochert 1988). The Golden Eagle primaries were the largest feathers sampled (42-45 cm), and had the largest distance between sampling points along a feather. Thus they had the greatest possibility of having variation in isotope ratios due to factors associated with feather growth.

Great Gray Owls have consistent diets of small mammals with little variation in trophic levels (Earhart and Johnson 1970, Bull and Duncan 1993). They had relatively medium sized feathers in this study (28-30 cm).

The eagles and owls sampled were breeding in the Spirit River area of north west Alberta in 1995. Since both of their diets were expected to consist of terrestrial prey, the possibility of the introduction of different isotope ratios from multiple ecosystems should not be likely as in the case of Peregrine Falcons.

While the Peregrine Falcon feathers were the shortest (20-23 cm), the wild falcons have the potential to have the most variable diet. Although all of the samples were collected in north-eastern Alberta, a variety of prey can be taken from a variety of habitats and trophic levels: herbivorous marsh birds, piscivorous or insectivorous lake birds, or insectivorous terrestrial birds (Holroyd unpublished data). If dietary shifts occur during feather growth, the potential for changes in ratios along the feather are great in a bird with a variable diet. Therefore, if variation due to changes in diet is detectable within a feather, it should be most obvious in wild Peregrines.

The captive Peregrine Falcon feathers were the same size as the wild falcon feathers, but the captive diet consisted entirely of Japanese Quail (*Corturnix japonica*). The quail themselves were fed a grain based fowl feed (H. Trefry pers. comm.). This means that there was no variation in trophic level or ecosystem for

the captive birds. Any variation in ratios within a feather must be growth related having little or no contribution from the diet.

To test whether or not homogenizing a whole feather before sampling produces less variable results than sampling from specific areas along a feather, aliquots of homogenized feathers from a Red-tailed Hawk (*Buteo jamaicensis*) and a Whooping Crane (*Grus americana*) used in an unpublished experiment were compared. Such a comparison was used to determine whether or not a homogenized feather should be sampled, or if a single sample from an intact feather will suffice.

If a variable diet produces feathers that contain different isotope ratios in different areas of the feathers, variable isotope ratios are more likely to occur in the wild Peregrine Falcon feathers than any other set. If variable tissue growth rates are more significant than variable diets to changes of isotope ratio values within a feather, the largest of the feathers should have most variable SIRA values. If all feathers go through a consistent biochemical process that is independent of the length, all species should have a consistent amount of variability in isotope ratios within their feathers. The less stressful lifestyle of a captive bred bird could possibly produce the lowest variability of ratios within a feather. The last possibility is that there is no significant variation within raptor feathers and sampling techniques for subsequent studies need not be location specific.

2.1 Methods

Three primary flight feathers from each species were collected for testing. Primary feathers were sampled to ensure all feathers were grown during a similar period of the life cycle for each bird. These feathers would have been grown after the pre-basic moult, subsequent to breeding. The Golden Eagle and Great Gray Owl feathers were obtained from dead birds sent to Alberta Fish and Wildlife, Edmonton, Alberta for forensic examination after the 1995 breeding season. Their origins were all from the Spirit River region in north-western Alberta. The wild Peregrine Falcon feathers were collected from eyries near Fort Chipewyan in north-eastern Alberta, during the summer of 1995. The captive Peregrine Falcon feathers were provided from the Canadian Wildlife Service's

Peregrine Falcon breeding facility near Wainwright, Alberta in April, 1995. Feathers collected were all approximately the same size within each species with an attempt to obtain the same feather (eg. primary 7 or primary 8) from each bird (Figure 2).

Whole feathers were first washed with soap and distilled water to remove debris and external contaminants. Each of the 12 feathers was sampled three times from three locations along it's length: the tip, the exact middle of the feather (relative to the two ends), and from the calamus, just above the inferior umbilicus (Figure 3), for a total of 108 samples. To ensure complete combustion of the sample tissue, each feather sample was cut into very fine fragments with stainless steel scissors. Incomplete combustion leads to undesirable fractionation resulting in altered ratios (Owens 1987). All feathers were then washed with diethyl ether to remove contaminants and lipid tissue since fractionation effects of lipid tissues can severely alter the final isotope ratios (Tieszen *et al.* 1983). Using an electronic scale, 0.230-0.280 µg of sample was placed into tin combustion cups. A mass spectrometer needs a minimum amount of sample gas, so the amount of the sample was dependent upon the predicted amount of nitrogen and carbon of the sample tissue: approximately 15% nitrogen and 50% carbon (Kemp and Rogers 1972, Reed and Woods 1964). The samples were then combusted at 1021 °C in a Fisons NA1500 NC that was interfaced with an Finnigan Mat 252 mass spectrometer in a continuous flow mode (Appendix 1). A standard of atropine powder was sampled and the accuracy of the mass spectrometer was found to have an standard analytical error of ±0.174‰ for nitrogen and ±0.073‰ for carbon.

An isotope ratio value is the amount of heavy isotope within a tissue relative to that found in the standard. Stable isotope ratios are expressed in δ (delta) notation according to the following formula:

$$\delta X = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

where: X is the isotope in question (in this case either ^{15}N or ^{13}C) and R is the isotopic ratio of the sample or standard (eg. $^{13}C/^{12}C$ - always heavy over light). The ratio for **R**standard for carbon derived from the standard PDB (Pee-Dee

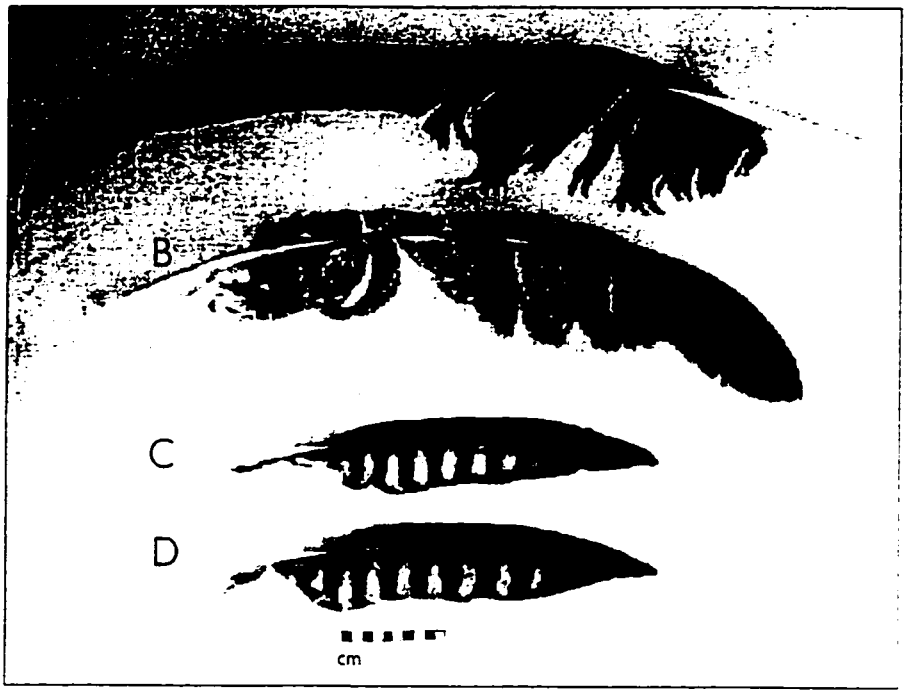


Figure 2. Relative size of feathers from which samples were taken. Feathers were from Golden Eagle (a), Great Gray Owl (b), wild (c) and captive (d) Peregrine Falcons.

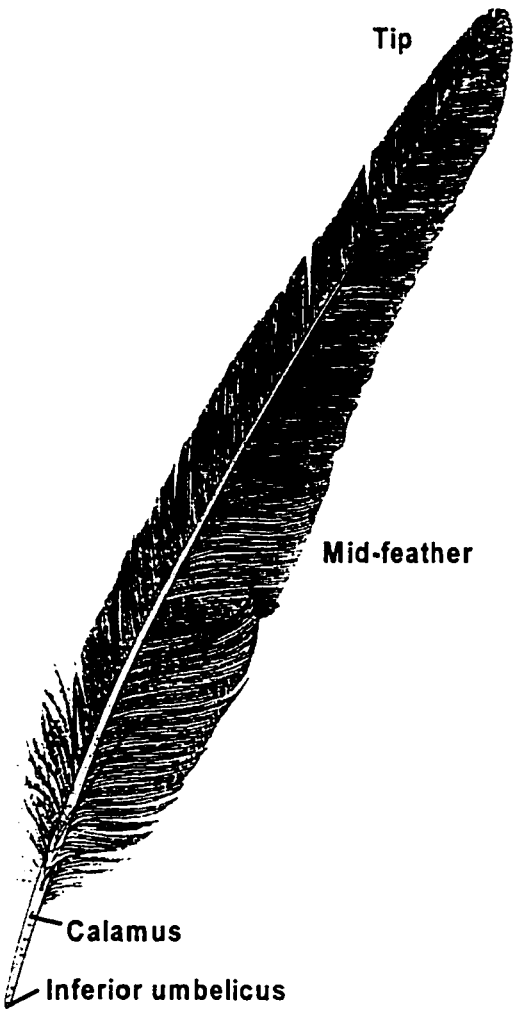


Figure 3. Sampling areas on a flight feather. Adapted from Proctor and Lynch 1993.

Belamnite, carbonate from the Cretaceous marine fossil *Belemnitella americana*, from the Pee-Dee Formation in South Carolina). The standard for nitrogen was atmospheric air. **R**sample is the ratio found in the sample tissue. The relative amount of naturally occurring heavy isotopes is less than 1%. Therefore, final numbers are always multiplied by 1000 and presented in the per mil (‰) notation.

An analysis of variance (GLM) was conducted using SAS© for analysis of variance between feather locations for both nitrogen and carbon values (Appendix 2). Sources of variance in isotope values considered included:

- variance between species
- variance between feathers within species
- variance between locations within a feather
- variance between locations across species
- variance between locations across feathers within species

To see if there was any relationship between the variability in isotope ratios and the length of a feather, simple correlations were calculated between individuals and between whole species.

To test whether or not a single sample of a feather produces better, worse or similar results than an aliquot of homogenized feather tissue, four samples each of homogenized Red-tailed Hawk and Whooping Crane feathers were analyzed. F-tests were used to compare the variances between homogenized and non-homogenized isotope values.

2.3 Results

The resulting stable isotope ratio values were compared between the 4 species (the captive Peregrine Falcons were considered a species)(Table 1, Figure 4), among feathers from individuals within a species (Figure 5), and within single feathers (Figures 6-13).

The $\delta^{15}N$ values were found to increase in order of Golden Eagle, Great Gray Owl, captive Peregrine Falcon and wild Peregrine Falcon (Table 1, Figure 4a).

Table 1. $\delta^{15}N$ results for various groupings used in the analysis of variance. Numbers are means and plus/minus one standard deviation (‰)(Cal=calamus).

Species (n=27)	Individuals (n=9)	Locations (n=3)
		Tip = 5.527±0.108
	#1 = 5.308±0.206	Mid = 5.160±0.035
		Cal = 5.237±0.211
		Tip = 5.777±0.176
Golden Eagles = 5.929±0.598	#2 = 5.938±0.442	Mid = 6.493±0.095
		Cal = 5.543±0.085
		Tip = 6.750±0.056
	#3 = 6.541±0.265	Mid = 6.203±0.065
		Cal = 6.670±0.106
		Tip = 7.893±0.065
	#1 = 8.273±0.786	Mid = 7.633±0.228
		Cal = 9.29±0.160
		Tip = 6.567±0.015
Great Gray Owls = 7.662±0.895	#2 = 6.878±0.737	Mid = 6.233±0.029
		Cal = 7.833±0.185
		Tip = 7.123±0.041
	#3 = 7.834±0.545	Mid = 8.103±0.115
		Cal = 8.277±0.106
		Tip = 11.277±0.148
	#1 = 11.103±0.588	Mid = 11.677±0.163
		Cal = 10.367±0.035
		Tip = 10.237±0.133
Wild Peregrine Falcons = 10.774±0.532	#2 = 10.397±0.281	Mid = 10.207±0.093
		Cal = 10.747±0.119
		Tip = 11.227±0.092
	#3 = 10.822±0.457	Mid = 10.537±0.591
		Cal = 10.703±0.301
		Tip = 8.210±0.538
	#1 = 7.981±0.347	Mid = 7.963±0.197
		Cal = 7.770±0.085
		Tip = 8.523±0.35
Captive Peregrine Falcons = 8.389±0.507	#2 = 8.682±0.417	Mid = 9.120±0.197
		Cal = 8.403±0.300
		Tip = 9.010±0.442
	#3 = 8.504±0.491	Mid = 8.460±0.114
		Cal = 8.043±0.228

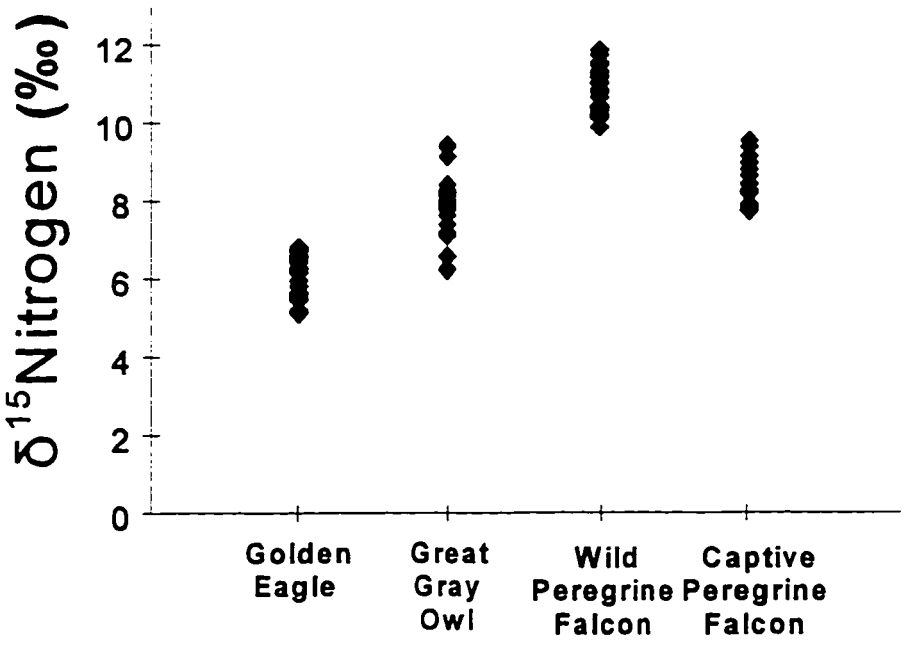


Figure 4a. $\delta^{15}N$ values grouped by species (n=27 per species).

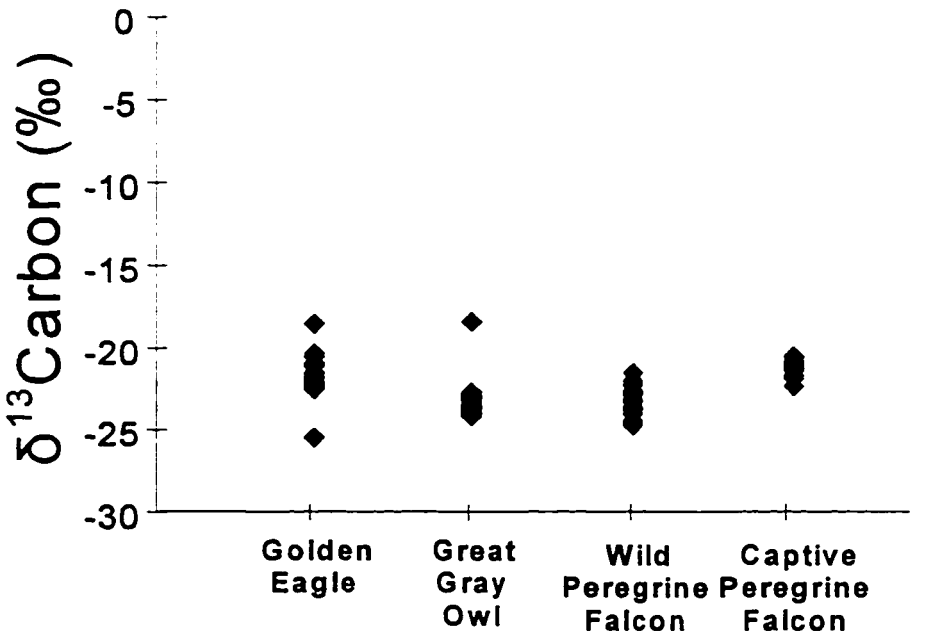


Figure 4b. $\delta^{13}C$ values grouped by species (n=27 per species).

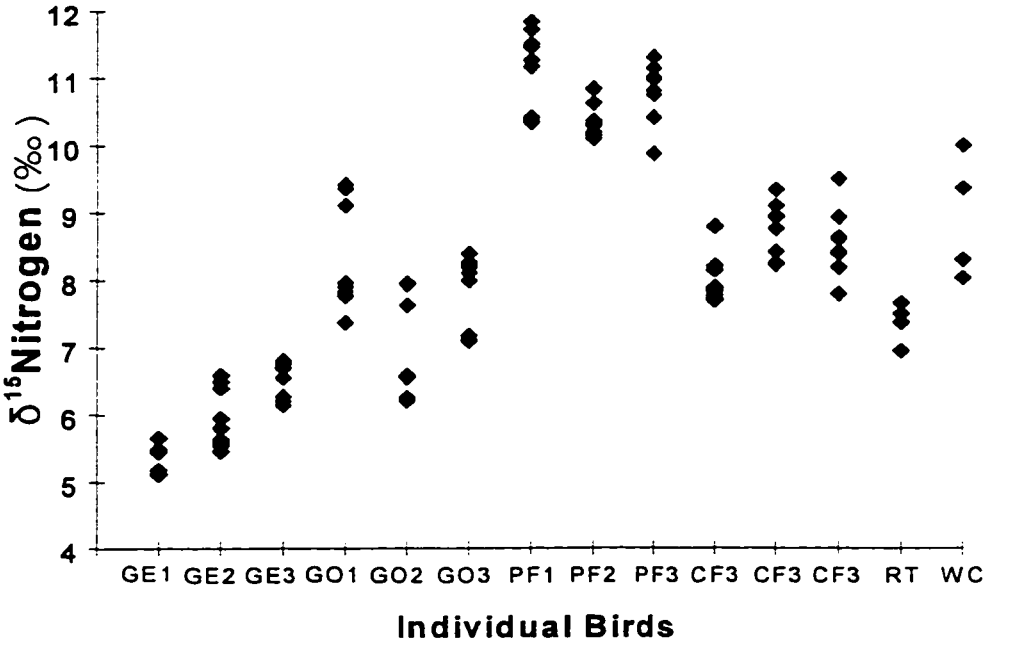


Figure 5a. $\delta^{15}N$ values grouped by individuals. GE1-3 = 3 Golden Eagles (n=9 each), GO1-3 = 3 Great Gray Owls (n=9 each), PF1-3 = 3 Wild Peregrine Falcons (n=9 each), CF1-3 = 3 Captive Peregrine Falcons (n=9 each), RT = Red-tailed Hawk (n=4), WC = Whooping Crane (n=4).

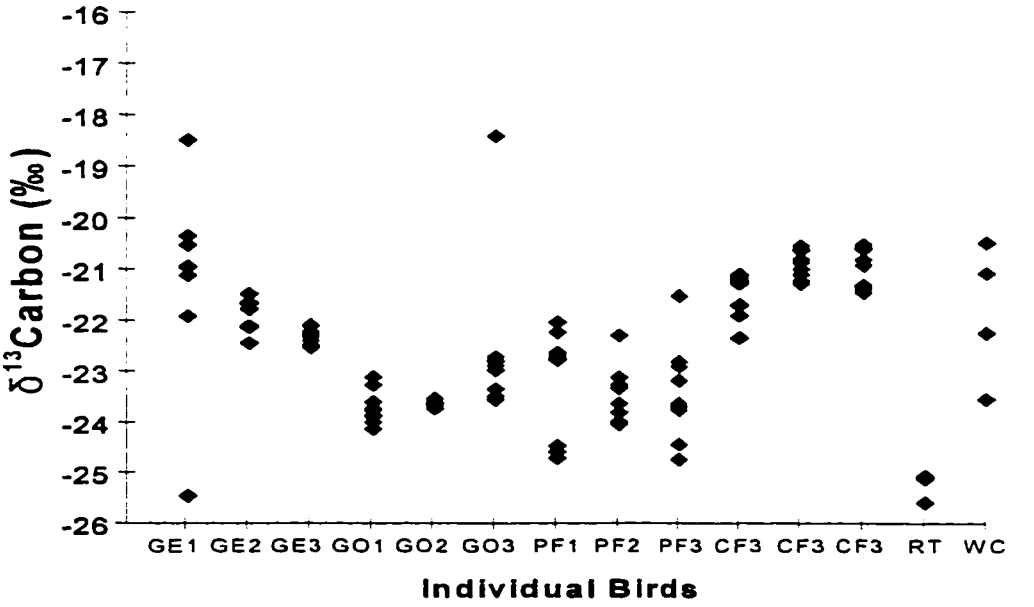


Figure 5b. $\delta^{13}C$ values grouped by individuals. GE1-3 = 3 Golden Eagles (n=9 each), GO1-3 = 3 Great Gray Owls (n=9 each), PF1-3 = 3 Wild Peregrine Falcons (n=9 each), CF1-3 = 3 Captive Peregrine Falcons (n=9 each), RT = Red-tailed Hawk (n=4), WC = Whooping Crane (n=4).

Figure 6a.

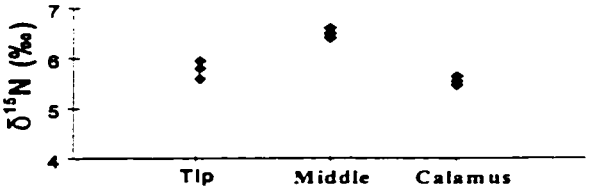


Figure 6b.

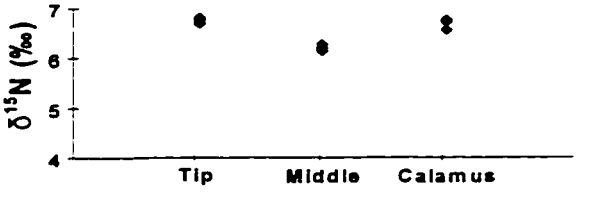


Figure 6c.

Figure 6. δ^{15}Nitrogen values from three locations on a feather from each of three Golden Eagles (a, b, c). Three samples were analyzed from each location per eagle feather. Values are given in per mil notation.

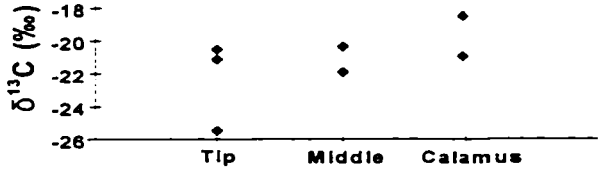


Figure 7a.

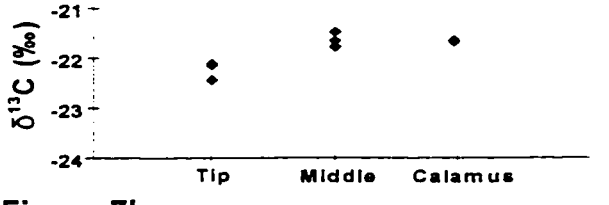


Figure 7b.

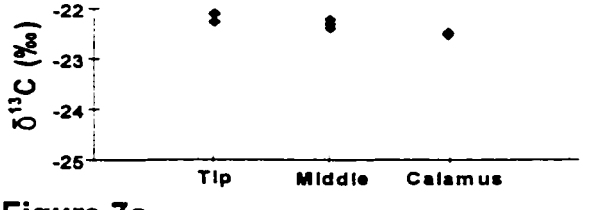


Figure 7c.

Figure 7. δ^{13}Carbon values from three locations on a feather from each of three Golden Eagles (a, b, c). Three samples were analyzed from each location per eagle feather. Values are given in per mil notation.

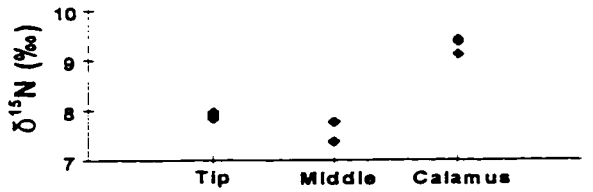


Figure 8a.

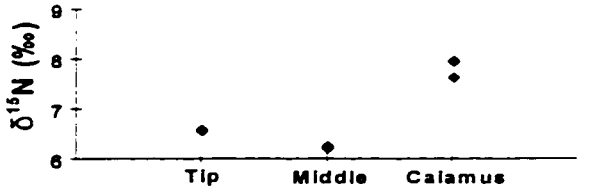


Figure 8b.

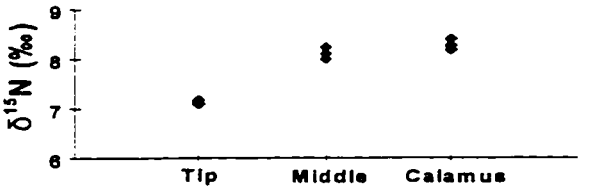


Figure 8c.

Figure 8. δ^{15}Nitrogen values from three locations on a feather from each of three Great Gray Owls (a, b, c). Three samples were analyzed from each location per owl feather. Values are given in per mil notation.

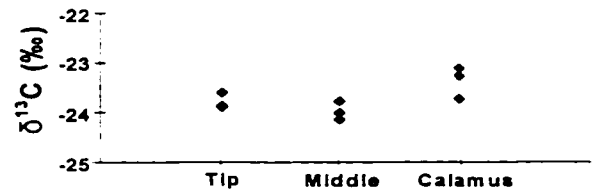


Figure 9a.

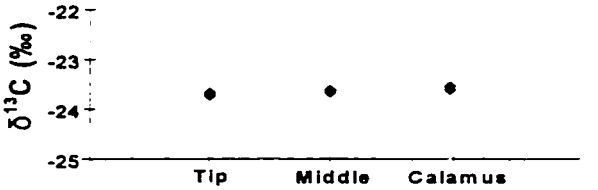


Figure 9b.

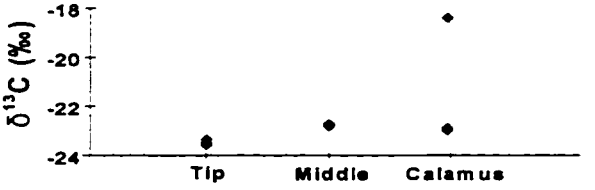


Figure 9c.

Figure 9. δ^{13}Carbon values from three locations on a feather from each of three Great Gray Owls (a, b, c). Three samples were analyzed from each location per owl feather. Values are given in per mil notation.

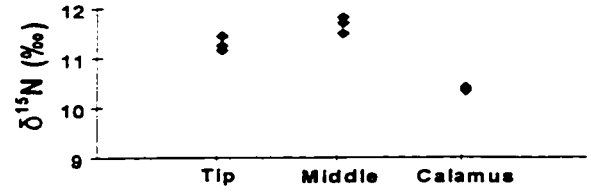


Figure 10a.

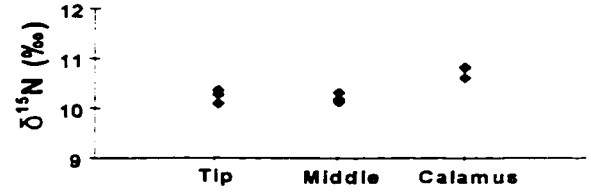


Figure 10b.

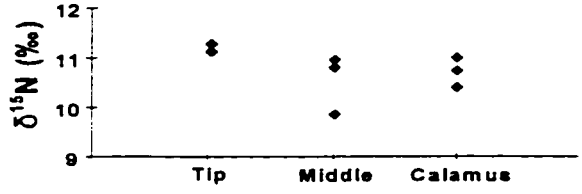


Figure 10c.

Figure 10. δ^{15}Nitrogen values from three locations on a feather from each of three wild Peregrine Falcons (a, b, c). Three samples were analyzed from each location per falcon feather. Values are given in per mil notation.

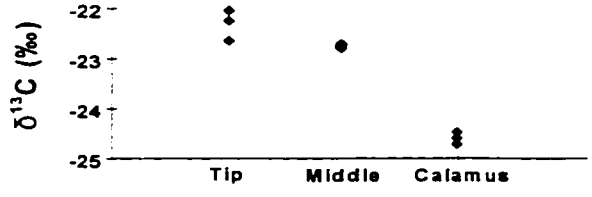


Figure 11a.

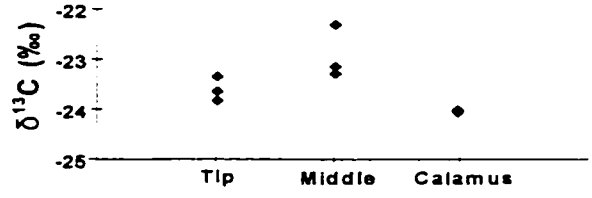


Figure 11b.

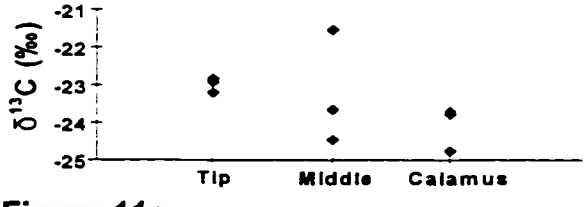


Figure 11c.

Figure 11. δ^{13}Carbon values from three locations on a feather from each of three wild Peregrine Falcons (a, b, c). Three samples were analyzed from each location per falcon feather. Values are given in per mil notation.

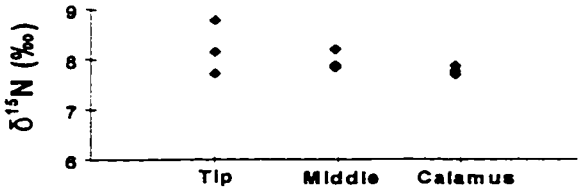


Figure 12a.

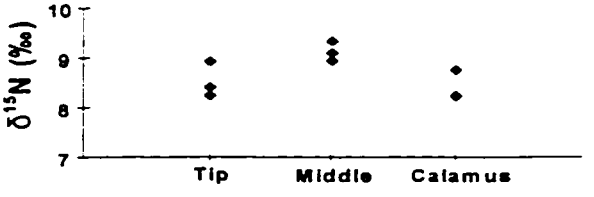


Figure 12b.

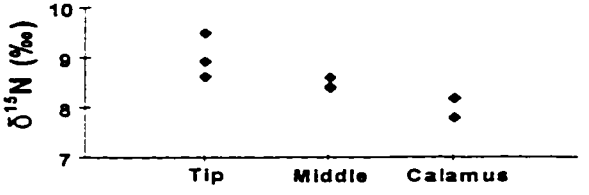


Figure 12c.

Figure 12. δ^{15}Nitrogen values from three locations on a feather from each of three captive Peregrine Falcons (a, b, c). Three samples were analyzed from each location per falcon feather.

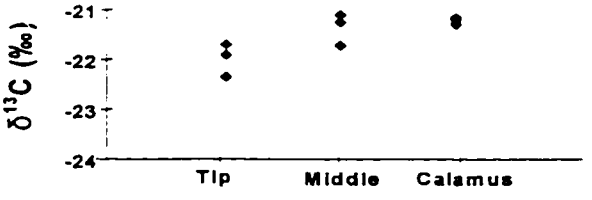


Figure 13a.

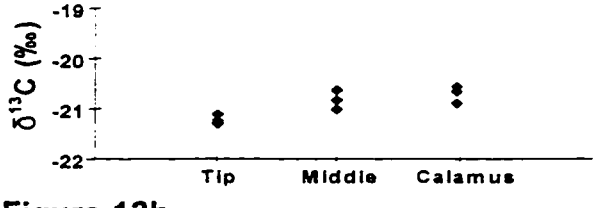


Figure 13b.

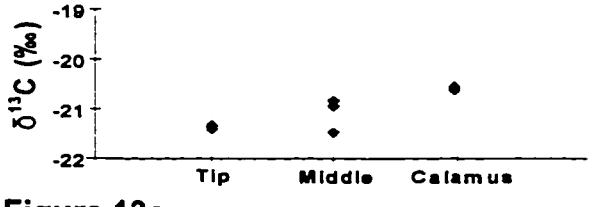


Figure 13c.

Figure 13. δ^{13}Carbon values from three locations on a feather from each of three captive Peregrine Falcons (a, b, c). Three samples were analyzed from each location per falcon feather.

This result was not surprising since the eagles eat at a relatively low trophic level while falcons eat at a relatively high trophic level. Also not surprising is the fact that there was a significant difference in $\delta^{15}N$ values between species, since the different species are feeding at various trophic levels ($F = 2369.90$, $p < 0.0001$). A comparison between individuals of a species also produced significant variance ($F = 56.22$, $p < 0.0001$)(Figure 5a). In fact, all groupings that were tested had a significant effect on the variation in $\delta^{15}N$ values except locations within a feather ($F = 1.75$, $p = 0.1816$). This means that there is no significant difference between $\delta^{15}N$ values from samples taken from the tip, mid-feather or calamus of a *single* feather.

Values for the carbon isotopes ranged from a high of -18.43 to a low of -25.47 with a mean of -22.42. Unlike the nitrogen results, the $\delta^{13}C$ values for each species was similar (Table 2, Figure 4b). However, the results of the analysis of variance show that there is still a significant difference between species ($F = 57.73$, $p < 0.0001$). Similar to the nitrogen results, the differences between individuals within a species was again significant ($F = 3.17$, $p < 0.0039$). In the case of carbon, there were two partitionings of data which were found not to have significant effects; among locations among all of the feathers ($F = 1.57$, $p < 0.2150$), and among locations of feathers within a species ($F = 1.30$, $p < 0.2218$). Once again, the results of the ANOVA indicate that there is no significant difference in $\delta^{13}C$ values in samples from anywhere along a feather.

Although some variability was detected within samples taken within locations on a single feather (Figures 4-11, Tables 1 and 2), generally, the results were found to be highly repeatable indicating that the mean square for this category may not have been a suitable error term which to measure the variance of the other categories in the ANOVA. Therefore, the variances were tested again using different error terms. The error term used to test for significant causes of variance within species was the mean square of the group; feather within species (Appendix 2). To test for significant causes of variation within all other measurements, the mean square of the second smallest group of measurements was used; the locations across feathers within species. Once again, the results were similar to the original ANOVA in that variance caused by measurements among locations within a single feather were insignificant for both nitrogen ($F = 0.14$, $p = 0.8724$) and carbon ($F = 1.21$, $p = 0.3245$).

Table 2. $\delta^{13}C$ results for various groupings used in the analysis of variance. Numbers are means and plus/minus one standard deviation(‰)(Cal=calamus).

Species (n=27)	Individuals (n=9)	Locations (n=3)
Golden Eagles = -21.644±1.467	#1 = -20.758±2.326	Tip = -22.377±2.695
		Mid = -19.757±2.520
		Cal = -20.140±1.420
	#2 = -21.844±0.312	Tip = -22.230±0.182
		Mid = -21.643±0.146
		Cal = -21.660±0.017
	#3 = -22.331±0.165	Tip = -22.163±0.093
		Mid = -22.317±0.085
		Cal = -22.513±0.025
Great Gray Owls = -23.308±1.046	#1 = -23.718±0.337	Tip = -23.793±0.159
		Mid = -23.983±0.188
		Cal = -23.377±0.323
	#2 = -23.640±0.063	Tip = -23.700±0.035
		Mid = -23.647±0.031
		Cal = -23.573±0.040
	#3 = -22.567±1.583	Tip = -23.477±0.107
		Mid = -22.783±0.047
		Cal = -21.440±2.607
Wild Peregrine Falcons = -23.390±0.863	#1 = 23.223±1.063	Tip = -22.317±0.306
		Mid = -22.753±0.040
		Cal = -24.600±0.120
	#2 = -23.519±0.570	Tip = -23.610±0.242
		Mid = -22.913±0.528
		Cal = -24.033±0.023
	#3 = -23.428±0.957	Tip = -22.983±0.193
		Mid = -23.220±1.509
		Cal = -24.080±0.590
Captive Peregrine Falcons = -21.155 ±0.444	#1 = -21.532±0.423	Tip = -21.997±0.332
		Mid = -21.370±0.320
		Cal = -21.230±0.066
	#2 = -20.920±0.271	Tip = -21.223±0.093
		Mid = -20.827±0.195
		Cal = -20.710±0.171
	#3 = -21.013±0.379	Tip = -21.363±0.042
		Mid = -21.083±0.339
		Cal = -20.593±0.040

Correlation calculations to test whether or not there was a relationship between length of a feather and the variance of isotope ratio values within a feather were insignificant; r^2=-0.195 for nitrogen and r^2=0.179 for carbon. Correlations between the length of feathers for each species and the variability in $\delta^{15}N$ values for each species was insignificant for nitrogen (r^2=0.316), but significant for carbon (r^2=0.914).

In the comparisons for differences in variance between sampling homogenized samples and sampling specific areas of a feather using the F-test, the homogenized Red-tail Hawk and Whooping Crane samples had more variability than some of the other samples, and less variability than others (Table 3 and 4, Figure 5). Significant differences were found in 15 of the 48 comparisons. In 10 of the 15 times where occurrences of significant differences were found, the homogenous samples were found to have the greater variance as compared to samples taken from the specific locations on the feathers.

2.4 Discussion

The focus of the study was to determine the relative variation in isotope ratios in feather samples within and between species and locations within a feather. The stable isotope ratio values in the Golden Eagle, Great Gray Owl, captive and wild Peregrine Falcon feathers in this study were found to be similar along a given feather for each group. The lack of significant differences in isotope ratio values between the tip, mid-feather and calamus locations supports similar findings of Thompson and Furness (1995) in seabirds. It can be assumed that a single sample can be taken from anywhere along a single feather, with the resulting SIRA values representing those found anywhere within that feather.

As to be expected, the most variance was found in comparisons across species. Since each species eats at different trophic levels, their isotope ratios were bound to be dissimilar. Wild Peregrine Falcons eating at the top of the food chain had relatively high $\delta^{15}N$ values compared to those of the Golden Eagles and Great Gray Owls feeding at a lower trophic level. Even the $\delta^{13}C$ values were significantly different between species. Since heavy carbon isotopes bioaccumulate at a slower rate than heavy nitrogen, and ecosystems where the birds in this study grew their feathers would have very little input of C_4

Table 3. F-test results for comparisons of $\delta^{15}N$ values from samples taken from specific areas of feathers from Golden Eagles (GOEA), Great Gray Owls (GGOW), wild Peregrine Falcons (PEFA) and captive Peregrine Falcons (WAIN) to aliquots of homogenized feather samples from Red-tailed Hawks (RTHA) and Whooping Cranes (WHCR). An asterisk denotes significant differences (≤ 0.05) in variance between the two sampling techniques.

	GOEA 1	GOEA2	GOEA3	GGOW1	GGOW2	GGOW3
RTHA	F=2.182 p<0.281	F=2.116 p<0.290	F=1.321 p<0.451	F=6.688 p<0.073	F=5.875 p<0.086	F=3.208 p<0.183
WHCR	F=20.025 p<0.016*	F=4.337 p<0.127	F=12.119 p<0.032*	F=1.372 p<0.437	F=1.562 p<0.390	F=2.860 p<0.209

	PEFA 1	PEFA 2	PEFA 3	WAIN 1	WAIN 2	WAIN 3
RTHA	F=3.744 p<0.153	F=1.168 p<0.498	F=2.263 p<0.271	F=1.303 p<0.456	F=1.882 p<0.327	F=0.232 p<0.232
WHCR	F=2.451 p<0.248	F=10.716 p<0.038*	F=4.055 p<0.138	F=7.040 p<0.068	F=4.875 p<0.110	F=3.515 p<0.165

Table 4. F-test results for comparisons of $\delta^{13}C$ values from samples taken from specific areas of feathers from Golden Eagles (GOEA), Great Gray Owls (GGOW), wild Peregrine Falcons (PEFA) and captive Peregrine Falcons (WAIN) to aliquots of homogenized feather samples from Red-tailed Hawks (RTHA) and Whooping Cranes (WHCR). An asterisk denotes significant differences (≤ 0.05) in variance between the two sampling techniques. Two asterisks denotes where homogeneous samples had less variance than samples from specific locations on a feather.

	GOEA 1	GOEA2	GOEA3	GGOW1	GGOW2	GGOW3
RTHA	F=86.826 p<0.002**	F=1.563 p<0.390	F=2.289 p<0.267	F=1.823 p<0.337	F=15.671 p<0.022*	F=40.244 p<0.006**
WHCR	F=2.954 p<0.202	F=18.801 p<0.017*	F=67.280 p<0.003*	F=16.124 p<0.022*	F=460.57 p<0.001*	F=1.369 p<0.438

	PEFA 1	PEFA 2	PEFA 3	WAIN 1	WAIN 2	WAIN 3
RTHA	F=18.127 p<0.018**	F=5.207 p<0.101	F=14.692 p<0.025**	F=2.875 p<0.208	F=1.176 p<0.496	F=2.302 p<0.266
WHCR	F=1.968 p<0.311	F=5.644 p<0.091	F=2.000 p<0.307	F=10.221 p<0.041*	F=24.993 p<0.011*	F=12.765 p<0.030*

photosynthezing plants, one would predict even less variance between birds. Yet it appears that either each species' catabolic, metabolic and/or excretory - isotope fractionation rates differ (which would be magnified if all their respective prey have different fractionation rates throughout a food chain), or that variations in heavy carbon isotopes in their respective ecosystems are indeed significantly different. If a subsequent study was to analyze isotope ratio values of carbon within the plant communities where the raptor samples were collected, it could be determined if the resulting variance in the raptor feathers is due to catabolism, metabolism and or excretion, or if the variance is due to the values in the plants forming the base of each food chain.

It was not surprising that variance caused by comparing isotope ratio values among individuals within a species was significant, since each individual would have feeding preferences which may involve prey taken from various trophic levels and habitats. Therefore, the captive bred falcon feathers should have had the least variation since the prey and ecosystem are always the same. The results of this experiment reflect this prediction (Tables 1 and 2). An interesting result was the amount of variation among individuals in terms of heavy carbon. One would predict that variable diets would cause greater variance in terms of trophic levels and heavy nitrogen, but as shown in tables 1 and 2, $\delta^{13}C$ values were more variable than the $\delta^{15}N$ values. The fact that the captive bred falcon feathers had variation, indicates that the catabolic, metabolic and or excretory fractionation of each individual was playing some role in providing variability in the isotope ratio values. However, as discussed below, either variability in carbon isotopes throughout a given ecosystem or technical errors could also provide variability in the carbon isotopes in the birds' feathers.

When the analysis of variance of isotope ratios between locations on feathers was conducted between multiple species, significant differences were detected within both nitrogen and carbon values. Testing for differences between locations within feathers between individuals should have produced insignificant results due to different individuals having potentially different diets. This was the case for heavy nitrogen, however, in the case of heavy carbon, the variation of isotope ratio values within feathers among individuals was not significantly different. This may indicate that the specimens from each species came from the same type of ecosystem and that the effects of catabolism, metabolism and or excretion are not as strong as suspected.

Even though the variation within a feather was found to be insignificant, there was still noticeable deviations from the means. These results then still beg the question of what may be the possible cause for such variation. To answer this question, one must look at which species have the most variability in isotope values in their feathers and then determine if the cause is more likely diet related, growth related or some combination. All groupings of data had relatively small standard deviations in $\delta^{15}N$ values (Table 1, Figures 4a). However, the Great Gray Owl and Golden Eagle feathers had more variation in values compared to the wild and captive Peregrine Falcons feathers. The greatest standard deviations in carbon values were also in the owl and eagle feathers (Table 2, Figure 4b), while the captive bred falcon feathers had the smallest deviations. The fact that the feathers from the wild Peregrine Falcons (which should have potentially the most variable diets), have smaller $\delta^{15}N$ standard deviations than those of the owls and eagles (whose diets should have less variability from a trophic point of view), reduces the possibility that a variable diet can be detected in the nitrogen isotopes within a feather.

The greater variability in isotope ratios in the larger feathers of the eagles and owls indicated a possible relationship between the size of feather and the amount of variability. When the feathers were considered individually they were found to have an insignificant correlation between the length of the feathers and variability in stable isotope ratio values. However, when the feathers were grouped and compared between species, the relationship between increased variation in $\delta^{15}N$ values in the larger species became pronounced. The correlation between increasing variability in carbon isotope ratio values and increasing size of species was very significant. Generally, fractionation occurred more in the longer feathers. These results can be interpreted in a number of ways. They could indicate that fractionation which occurs during different growth periods of a feather may play the most important role in changing isotope ratio values in a feather. However, figures 6-13 indicate that there is no predictable pattern in which the values change through the length of a feather. One would assume that if all feathers grow the same way, fractionation would mirror those growth events on each feather sampled, but this is not the case. Another interpretation could be that the longer the feather the more chance there is for changes in diet to be detected. Even though, trophically speaking, the eagles and owls probably had a less variable diet, any differences in diet selection that occurred would change the isotope ratios since their feathers grow during a

longer period of time. The smaller wild Peregrine Falcon feathers may simply grow too quickly to use too many sources of isotopes from multiple prey items. Also, the fact that the captive Peregrine Falcons also had a small amount of variability, may indicate that kinetic events during keratinization have some role in fractionation of isotopes during feather growth. Therefore, the most realistic conclusion of the cause of variability of stable isotope ratio values in feathers would be a combination of a variable diet during the time it takes to grow a feather, and fractionation during the growth of the feather itself. A study that entailed the switching of the diets of captive eagles, owls and falcons should be conducted to determine if the variability in longer feathers is due more to dietary or growth effects.

Finally, one cannot discount technical and/or machine error. The application of techniques used in this study to feathers is still relatively new and may still introduce biases not yet detected. Mass spectrometry is dependent upon streams of particles only ions in width and small detection devices. Fine tuned machines and trustworthy standards are always required but inconsistencies may occur. It seems unlikely that natural causes can lead to isotope ratio differences of as much as 5‰ in samples taken only millimeters apart. Problems with the technology or sample contamination might have produced sets of erroneous data in the carbon isotope ratio values in the Golden Eagle feathers, Great Gray Owl feathers and wild Peregrine Falcon feathers (Figures 7a, 9c, 11c). Without knowing the exact cause of the variation in these samples, the data was included in the analysis of variance. However, if the erroneous data is not included in the statistical analysis, the final conclusion regarding the lack of significant variation within a feather would be strengthened.

There were no differences in analyzing aliquots from homogenous samples and analyzing samples from specific locations on a feather. In choosing a sampling technique however, there are some factors to consider. Since this type of analysis can make use of museum specimens, it is highly probable that whole feathers will not be attainable, and therefore homogenous samples would not be an option. Also, in terms of sample preparation, snipping a very small piece off a feather leaves the whole structure otherwise intact. An intact feather can be used for other uses such as anatomical or colour phase comparisons or forensic studies since the mode of death of some birds can be determined by markings

along a feather tip or calamus (J. Hudon pers. comm.). Therefore, homogenized samples do not appear to be necessary.

2.5 Conclusion

With an increase in use of feathers for avian isotope research comes an increase in the need to determine a foundation on which sampling protocols can be based. Analyzing stable isotopes in large raptor feathers requires the knowledge of whether or not whole feathers must be used, and if not, will it matter where samples are taken from along a single feather? Results of this study indicate that there is no significant difference in where samples are taken from along the length of the raptor feathers. As well, a whole feather does not have to be homogenized to get a number that genuinely reflects stable isotope ratio values found anywhere within that single raptor feather. These findings will permit research to be conducted on museum specimens where the preservation of intact feathers is very desirable. Volunteers collecting samples will have the choice of where they want to collect wing feather samples and the amount of feather tissue removed from live birds can be minimized. Such freedom will help encourage volunteers to participate and will allow for greater sample sizes for future research. These results will also save time during sample preparation since 20-50 cm feathers will not have to be completely cut up and homogenized to obtain a single 250 µg sample.

2.6 Literature Cited

Alisauskas, R.T. and K.A. Hobson. 1993. Determination of lesser snow goose diets and winter distribution using stable isotope analysis. Journal of Wildlife Management 57:49-54.

Bell, E. and Thathachari, Y.T. 1963. Development of feather keratin during embryo genesis of the chick. Journal of Cellular Biology 16: 215-223.

Bull, E.L. and J.R. Duncan. 1993. Great gray owl (*Strix nebulosa*) *in* Birds of North America, No. 42 (A. Poole and F.Gill Eds.) Philadelphia: The Academy of Natural Sciences, Washington D.C.The American Ornithologists' Union.

Collopy, M.W. 1983. A comparison of direct observation and collections of prey remains in determining the diet of golden eagles. Journal of Wildlife Management 47:360-368.

DeNiro, M.J. and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42: 495-506.

Earhart, C.M. and N.K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72:251-264.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic Compositions. Limnology and Oceanography 33: 1182-1190.

Fry, B., Joern, A, and Parker, P.L. 1978. Grasshopper food web analysis: use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. Ecology 59:498-506.

Haake, A.R., Konig, G. and Sawyer, R.H. 1984. Avian feather development: relationships between morphogenesis and keratinization. Developmental Biology 106:406-413.

Hobson, K.A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. Condor 97:752-762.

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series 95: 7-18.

Hobson, K.A., J.F. Piatt and J. Pitocchelli. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786-798.

Hobson, K.A. and R.G. Clark. 1992. Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. Condor 94:181-188.

Hobson, K.A. and H.E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series 84:9-18.

Hobson, K.A. and S.G. Sealy. 1991. Marine protein contributions to the diet of Northern Saw-whet Owls on the Queen Charlotte Islands: a stable isotope approach. Auk 108: 437-440.

Kemp, D.J. and G.E. Rogers. 1972. Differentiation of avian keratocytes. Characterization and relationships of the keratin proteins of adult and embryonic feathers and scales. Biochemistry 11: 969-975.

King, A.S. and J.McLelland (Editors) 1985. Form and Function in Birds, Vol.3. Academic Press, Toronto.

Knight, R.L. and A.W. Erickson. 1978. Marmots as a food source of golden eagles along the Columbia River. Murrelet 59:28-30.

Mizutani, H. and E. Wada. 1988. Isotope ratios in seabird rookeries and their ecological implications. Ecology 69:340-349.

Mizutani, H., H. Hasegawa and Wada, E. 1986. High nitrogen isotope ratio for soils of seabird rookeries. Biogeochemistry 2:221-247.

Mizutani, H., Y. Kabaya and E. Wada. 1991. Nitrogen and carbon isotope compositions relate linearly in cormorant tissues and its diet. Isotopenpraxis 4: 166-168.

Owens, N.J.P. 1987. Natural variations in the ^{15}N in the marine environment. Advances in Marine Biology 24:389-451.

Proctor, N.S. and P.L. Lynch. 1993. Manual of Ornithology: avian structure and form. Yale University Press, New Haven, Connecticut.

Reed, H.A. and E.F. Woods. 1964. Heterogeneity of feather proteins. Biochemical Journal 92:12-18.

Schoeninger, M.J. and M.J. DeNiro. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochimica Cosmochimica Acta 48:625-639.

Steenhof, K. and M.N. Kochert. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. Journal of Animal Ecology 57:37-48.

Thompson, D.R. and R.W. Furness. 1995. Stable-isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in northern fulmars. Auk 112:493-498.

Tieszen, L.L., T.W. Boutton, K.G. Tesdahl, and N.A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for ^{13}C analysis of diet. Oecologia 57:32-37.

3.0 Determining the Hierarchy of Raptor Trophic Levels Using Stable Isotope Ratio Analysis

3.1 Introduction

Researchers may use multiple methods to establish what birds of prey are consuming. The most widely used traditional techniques to determine the diets of raptors are; pellet analysis (Errington 1932, Marti 1974), crop/stomach content analysis (Duncan 1966, Errington 1933, Sherrod 1978), prey remains analysis (Craighead and Craighead 1956, Hunt 1993, Meng 1959), and direct observation (Quinn 1991, Bielefeldt *et al.* 1992, Hunt 1993). These techniques all have their advantages, but also have biases that can lead to problematic conclusions (Thomsen 1971, Marti 1987, Quinn 1991, Bielefeldt *et al.* 1992, Mermann *et al.* 1992, Hunt 1993). The selection of a technique to study the diet preferences of the raptors is dependent upon the species being studied, and must be chosen carefully as not to produce biased results. Raptors have been seen eating different prey than what was found at the nest in the form of remains (Errington 1932, Bond 1936, Collopy 1983, Bielefeldt 1992, Mermann *et al.* 1992). Also, prey found in pellets has differed from stomach contents (Reynolds and Meslow 1984). Biases may also be introduced due to the relatively digestibility of prey or respective parts of the prey (Longhurst 1942, Fitch *et al.*1946, Balgooyen 1971, Bradstreet 1980).

Pellets are indigestible prey remains that are regurgitated by raptors. The species of prey items can be identified through analysis of the contents of the pellets. Species of mammals can be distinguished from bone morphology, skull sizes, and teeth patterns. Bird prey can be identified from hollow bones, feathers and feet. The chitinous insect remains in pellets can be used to identify insect prey (Errington 1932, Marti 1974). Unfortunately, some prey are more easily digested and leave few traces in pellets, while other prey will have many indigestible components and will be easily detectable in the pellets (Bradsteet 1980, Marti 1987, Brown and Ewins 1996). Captive owls, fed both mammals and birds, were found to pluck the birds and consume mostly breast meat, while the small mammals were swallowed whole (Brooks 1929a). The hair and bones of the mammals would be regurgitated, but there is no need to form a pellet when owls consume wholly digestible tissue from birds. Pellet analysis used to study raptors in the wild could lead to a false conclusion biased towards mammalian prey. Prey items which can be digested will be under represented in pellets.

Also, the number of prey items is hard to determine since large prey items may be found in more than one pellet and small prey items may be combined into a single pellet (Brooks 1929a, Mermann *et al.* 1992). Raptors may also cache prey, consuming the remainder in a subsequent feeding and forming multiple pellets from single prey items (Thomsen 1971). Another problem with analyzing pellets is they are comprised mostly of calcareous bones and hair keratin which does not decay quickly and therefore, will not easily weather away. Thus, pellets from nesting birds may remain from the previous year (Brooks 1929b). Since some species of raptors eject pellets over wide areas, pellets collected at or near nests may not fully represent prey selection (Southern 1969, Ziesemer 1981 [in Marti 1987]). Finally, owls do not have the digestive capabilities of the other diurnal raptors thus forming more complete pellets. Raptors other than owls can have crops with very acidic digestive conditions (pH 0.2 - 1.2) or peptic enzymes that can dissolve bone in hours (Gill 1989). Therefore, comparisons of diet of owls and other birds of prey from pellet analysis can be biased.

Stomach or crop content analysis is an excellent way to determine exactly what a raptor has eaten. If the prey is still undigested, it can be accurately identified. However, this technique requires the use of emetics to encourage birds to regurgitate the last prey consumed and can be very stressful on the study birds. The regurgitation also means the loss of the meal to the bird. To analyze the contents of the stomach, dissection is required and unfortunately requires dead birds. This hinders studies on most raptors since many are on endangered, threatened or vulnerable conservation lists. Unless a great number of dead raptors are found, sample sizes are limited. The bias associated with this method is that contents of the stomach or crop only represent a single instance of feeding (Errington 1932). Unless this method is repeated daily (which is not possible or should not be encouraged since the raptors need to either be dead or forced to repeatedly regurgitate their food), it only provides a brief glimpse of what may be a highly variable diet. Making broad assumptions based on a few feedings presents strong biases in making any conclusions on the seasonal dietary habits of a raptor.

Body parts, feathers and/or fur left at food preparation sites, such as plucking posts, provide evidence of prey captures. A list of prey species, their relative abundance and relative contribution to biomass of diet can be determined from prey remains at the nest (Bosakowski *et al.*1992). But once again, this method is

not without it's imperfections. Colourful feathers are far more conspicuous than fur and have a much greater chance of being detected and collected over cryptic brown fur and small dark chitinous parts from insects (Errington 1932, Bielefeldt *et al.* 1992). Feathers are also structurally durable and can weather harsh conditions and remain detectable for multiple years. Also, scavengers will remove edible remains which raptors do not consume, leaving behind inedible parts such as feathers (Ziesemer 1981 [in Marti 1987). A raptor's prey list based on prey remain analysis alone may have biased results leading to a potentially wrong conclusion: a diet concentrating on relatively more avian prey than what is actually consumed (Tyler 1923, Quinn 1991, Bielefeldt *et al.* 1992). Some raptors may pluck and/or consume small prey far from the nest and only return to the nesting area with prey large enough that it would be worth the energy expended (Newton 1979). Other problems with this technique are counting errors associated with piecing prey back together during tallies (eg. multiple counts of the same prey item), making sure all possible kill sites or plucking posts were found, and observer biases associated with species identification of the remains if more than one person is conducting a study. Also, the carcasses of both birds and mammals are often removed by adult raptors and leave no trace for researchers to find. (Fitch *et al.* 1946, Quinn 1991, Bielefeldt *et al.* 1992, Hunt 1993).

While casual observations of hunting raptors have the same temporal limitations as stomach content analysis, constant observation of prey deliveries at nests can provide a more complete picture of the prey that is important to individual raptors. A limitation to this technique is that if the prey delivery observations are not conducted with high standardization, great dedication and exceptional concentration, then temporal biases are again introduced (Errington 1932). Observer bias is also a problem if more than one researcher conducts the watches, since different people have different abilities to identify the prey items upon delivery. Finally, observations at a multitude of nests in a season is time consuming, thus, sample sizes are usually limited. Therefore, this technique leads to conclusions that are specific to only a few nests and does not allow for broad generalization of the species as a whole (Bielefeldt *et al.* 1992, Hunt 1993).

Combining the above techniques removes some of the biases (Brooks 1929a, Thomsen 1971, Collopy 1983, Mermann *et al.* 1992, Hunt 1993), but may not

always be temporally, physically or financially possible. Stable isotope ecology can be applied in conjunction to the above methods to enhance these techniques and help reduce or remove their associated biases.

Dietary analysis studies using stable isotope ratio analysis (SIRA), utilizes the fractionation properties associated with the isotopes of nitrogen and carbon. Fractionation is the change in isotope ratios (heavy over light) due to a chemical or physical reaction. The most important characteristic of the heavy isotope of nitrogen (^{15}N) in its application to diet studies, is that it bioaccumulates through food web systems. The relative amount of the heavier stable isotopes increase with each upward step in a food web due to catabolic and metabolic processes that favour the elimination of the relatively lighter isotopes which are excreted (Peterson and Fry 1987, Mizutani and Wada 1988, Ehleringer and Rundel 1989). Bird studies using SIRA demonstrated that the ratio of $^{15}N/^{14}N$ usually increases by 2 to 4‰ (parts per mil) with each increase in trophic level (Owens 1987, Wada et al 1987, Fry 1988, Hobson 1993), but can range from 1.3 to 5.3‰ (Minagawa and Wada 1984). The ratio of $^{13}C/^{12}C$ can also increase due to bioaccumulation, although not to the degree as the ratio of $^{15}N/^{14}N$. Heavy carbon usually increases by 1 to 2‰ with each trophic level (Schoeninger and DeNiro 1984, Fry 1988), although, values of as much as 3 to 5.3‰ have been found (DeNiro and Epstein 1978, Mizutani et al 1986, Hobson and Clark 1992). The higher a bird feeds in a food web system the greater the amount of bioaccumulation of the heavier isotopes and the higher the isotope ratio values. Also, the higher a bird feeds in a food web system, the greater chance of it consuming prey with isotope ratios already increased from being a predator itself. Therefore, raptors consuming prey which are carnivorous, piscivorous or insectivorous (consuming insects who are predators themselves), will have higher ratio values than those consuming herbivorous prey.

However, caution must be used when comparing animals across different systems. Northern plants using different types of mycorrhizal fungi tap into different sources of nitrogen (Schulze *et al.* 1994, Michelsen *et al.*1996) which means the isotope ratios at the bottom of multiple food webs could also be different. Trophic level increases in heavy carbon are useful when studying a single system (Peterson *et al.* 1985, Mizutani and Wada 1988, Hobson and Welch 1992, 1995, Alisauskas and Hobson 1993, Hobson 1995). However, when a study encompasses more than one ecosystem, trophic level variation

may not be as important as variation due to the photosynthetic pathways of the plants forming the base of food webs. Terrestrial, fresh water and marine plants utilize different photosynthetic pathways and different sources of carbon which results in different plants with different $^{13}C/^{12}C$ ratios (-24 to -3‰ in marine systems, -45 to-23‰ in fresh water lake systems surrounded by C_3 photosynthesizing plants, and -21 to -37‰ in terrestrial areas containing C_3 photosynthesizing plants, -16 to -9‰ in terrestrial areas containing C_4 plants (Fry *et al.* 1978, Fry and Sherr 1984, Bombin and Muehlenbachs 1985, DeNiro 1987, Peterson and Fry 1987). These large differences in ratios are passed on to the consumers in each ecosystem. The consumers can be traced back to the ecosystems in which they were feeding during the growth of their tissues (Hobson and Sealy 1991, Mizutani *et al.* 1991, Fry *et al.* 1978.).

There are two key properties of stable isotopes that makes SIRA useful for studying the diets of animals. First, stable isotope ratio analysis is an indirect measure of the food that was assimilated into the consumer's tissues and not just ingested (Hobson and Clark 1992). Therefore, any conclusions about the importance of certain prey items is based on the amount of biomass of the respective prey not the total number of individuals consumed. The second property is the averaging effect that accompanies the assimilation of tissue in a consumer. Isotopic ratios differ in each organism, and different organ tissues within an organism have different cellular turnover rates. Assuming that wild consumers will have some variability in their diet, and that the ratios found in each tissue will change at different rates, a whole range of isotope ratios can be consumed by a predator (Hobson and Clark 1992). Stable isotope ratios found within a predator represent the average of all isotopes ingested and subsequently used in building the consumer's tissue. The fact that a raptor's ratios are the combination of the individual ratios from different prey items means the consumption of a large number prey having low ratios results in the predator also having a low ratio. The reverse occurs when a raptor consumes mostly prey with relatively high ratios. Consumption of equal amounts of prey having high ratios or low ratios, results in a raptor having a ratio with a value midway between the high and low ratios of the prey. However, without the use traditional methods to assist in explaining the isotope values, it is impossible to determine whether raptors with mid-range $\delta^{15}N$ values are feeding on a mix of prey with high or low isotope values or if they are concentrating on prey with mid-range isotope values.

Stable isotope ratio analysis by itself can provide insight to the diets of birds. SIRA of animal tissue has been used in dietary studies ranging from differentiating prey selection preferences (Alisauskas and Hobson 1993) to determining whole food web relationships (Fry and Sherr 1984, Minagawa and Wada 1984, Owens 1987, Fry 1988, Goering *et al.* 1990, Hobson 1992, 1993). However, SIRA used in conjunction with more traditional diet study methods provides a more complete picture of diet than when using traditional methods alone, by reducing the biases associated with those more traditional methods or confirming unique prey selection (Sydeman *et al.* 1997). Conversely, SIRA results cannot be explained without using traditional methods to determine what species the isotope values represent.

The objective of this study was to determine the relative trophic level at which each raptor species are feeding by comparing the different ratios of nitrogen isotopes of each species. Raptors feeding at high trophic levels in a food web will have relatively higher ratios, enriched with more of the heavier isotopes.

Feathers were chosen as the tissue to sample. Feather tissue is inert keratin protein. Once it grows there are no subsequent changes in nitrogen ratios with all the processes which could cause fractionation during the growth of the feather. Mizutani *et al.* (1986) demonstrated that the isotope ratios of feathers analyzed in their study were closely distributed near the mean of the ratios of all organs considered together except lipid tissue which produces isotope values distinct from all other tissue types (Tieszen *et al.* 1983). Therefore, the use of feathers as a sampling tissue is not only the most accessible and non-destructive to the subjects, but represents a good estimate of the overall ratios found in their respective bodies.

One might assume that the results describe the diet only during feather growth. Nutrients from the food are supplied to cells of growing feather by blood. The nutrients found in the blood may come directly from the food most recently consumed. However, it is also possible that the ratios incorporated into the feathers do not simply come directly from what is eaten during the growth of the feather. One potential assumption would be that the digestion of prey tissue and the subsequent catabolic processes of feather growth are more complex. The tissues of prey consumed over many weeks would be pooled into the tissues of

the predator, and all isotope ratio values of prey ingested during those weeks would be averaged into the predator's reserve resources. The isotopes incorporated in feather tissue during their growth could come from the pooled source in a predator's system. The end result is that the isotope ratios in the feathers would represent the diet during a period longer than the growth of a single feather. This latter assumption may be reflected in the results of chapter two where no significant change in ratios within a single feather was found. Thompson and Furness (1995) discovered that variation within Northern Fulmar (*Fulmarus glacialis*) wings can exist if there is a diet shift during the subsequent growth of feathers during moult. Since flight feathers are dropped and regrown singularly or in pairs in a specific sequence in most bird species, a change in the diet of the fulmars during moult produced different ratios between the first and last feathers. Since a complete moult takes weeks to complete, this seems to indicate that the isotope values are an indication of a diet regime over a period of weeks. Such a period is long enough to determine, for example, the diet that nestlings are being provided by parental birds before fledgling. Also, if the diet of adults shifts during moult after their brood has fledged, then their isotope ratios will differ from those of the fledglings. Such findings would take hours of direct observations and prey remains analyses at the nest and would almost be impossible after fledgling. Stable isotope analysis provides averages of weeks of diet incorporated in the tissue of a consumer and requires only 250 µg of feather tissue. Feather samples can be collected when any raptor is trapped.

3.2 Methods

To demonstrate the bioaccumulation of heavy nitrogen and carbon isotopes in a known food chain, feathers from Peregrine Falcons, Japanese Quail (*Coturnix japonica*) and samples of quail feed from the Canadian Wildlife Service Peregrine Falcon Breeding Facility in Wainwright, Alberta, Canada were analyzed.

Feathers from the 27 species of wild raptors were collected by permit-holding raptor banders around the province of Alberta at the time of banding. Feathers from wild raptors were also collected at nests, found on the ground or were collected at museums. Whole feathers were first washed with soap and distilled water to remove debris and external contaminants. To ensure complete

combustion of the feather tissue, each sample was cut into very fine fragments. Incomplete combustion causes fractionation and results in undesirable altered ratios (Owens 1987). All tissues were then washed with diethyl ether to remove contaminants and lipid tissue since stable isotope ratios are highly fractionated during the formation of lipid tissues (Tieszen *et al.* 1983). Between 0.230-0.280 µg of sample were placed into tin combustion cups. A mass spectrometer needs a minimum amount of sample gas, so the amount of the sample was dependent upon the predicted amount of nitrogen and carbon of the sample tissue: approximately 15% nitrogen and 50% carbon (Kemp and Rogers 1972, Reed and Woods 1964). The samples were then combusted at 1021°C in a Fisons NA1500 NC that was interfaced with an Finnigan Mat 252 mass spectrometer in a continuous flow mode (Appendix 1). A standard of atropine powder was sampled (n=15) and the accuracy of the mass spectrometer was found to have a standard analytical error of ±0.174‰ for nitrogen and ±0.073‰ for carbon.

Stable isotope ratios of samples are expressed in δ (delta) notation according to the following formula:

$$\delta X = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

where: X is the isotope in question (in this case either ^{15}N or ^{13}C) and R is the isotopic ratio of the sample or standard (i.e. $^{15}N/^{14}N$ and $^{13}C/^{12}C$ - always heavy over light). The ratio for **R**standard for carbon is derived from the standard PDB (Pee-Dee Belamnite), carbonate from the Cretaceous marine fossil *Belemnitella americana*, from the Pee-Dee Formation in South Carolina, and from atmospheric air for nitrogen. **R**sample is the ratio found in the sample tissue. The result is the amount of heavy isotope within a tissue relative to that found in the standard. The relative amount of naturally occurring heavy isotopes is less than 1%. Therefore, final numbers are always presented in the per mil (‰) notation.

To assist in the comparison of the relative trophic placements of different raptor species, each species had a trophic level index number calculated using the formula developed by Hobson (1993). A trophic index number can be

determined by subtracting a basal isotope ratio value from a raptor's isotope ratio value and dividing the remaining number by an enrichment value per trophic level. The basal isotope ratio value is the value of the food source at the bottom of a food chain, and the enrichment value is derived from the average increase per trophic level in a food chain. The trophic level index number is the number of times the enrichment value can be divided into relative increase of the heavy isotope from the base of the food chain to the consumer in question. The trophic level index number (TL) can be represented by:

$$TL = 1 + (R_f - R_b)/R_e \qquad (1)$$

Where R_f is the isotope ratio value in the feather of a raptor, R_b is the basal isotope value and R_e is the enrichment value per trophic level. It is assumed that the consumer is one trophic level above it's prey, and therefore the amount of isotopic enrichment is added to 1.

To determine a basal isotope value, the ^{15}N values of samples of grass from northern Alberta were averaged (Holroyd and Duxbury unpublished data). To determine the enrichment value for a trophic level increase, the mean differences between each of the three levels of the captive food chain were averaged to determine an approximate increase per trophic level. Different animals in different food webs will have higher or lower increases per trophic level, but a standard value is required to form an index with which to compare many raptor individuals feeding in multiple food webs. The captive food chain was used because wild raptor isotope values can be caused by a mixture of isotope values from high and low trophic level feeding prey. Therefore, the differences between the $\delta^{15}N$ values of wild raptors and herbivorous prey would not be representative of a single trophic level increase in $\delta^{15}N$ values. For this study the formula was determined to be:

$$TL = 1 + (R_f - 0.61) / 3.18 \qquad (2)$$

Non-parametric statistics were used for statistical analysis since the distributions of some of the results were not normally distributed and sample sizes varied greatly. The Mann-Whitney U test was used in all tests to keep the analyses standardized (Zar 1984).

3.3 Results

The average of the stable isotope ratio values for nitrogen from the feathers from the birds in the captive food chain indicated an relatively small increase from the feed to the quail (1.03‰), but a marked increase between the quail and the Peregrine Falcons (5.34‰)(Figure 1). The averaged $\delta^{13}C$ values also increased with each trophic level, although not as much as the nitrogen (1.95‰ between the feed and quail and 2.51‰ between the quail and the Peregrine Falcons).

Feather samples from wild raptors were collected from 27 different species (Table 1). Plotting the nitrogen and carbon isotope ratio data for the wild raptors in the same manner as the captive birds did not produce the same patterns as in the captive situation (Figure 2). While the captive food chain showed an increase in $\delta^{15}N$ and $\delta^{13}C$ isotopes with increasing trophic level, there is no discernible relationship between increasing $\delta^{15}N$ and $\delta^{13}C$ in the wild samples. Some species were found to have relatively high $\delta^{15}N$ values while having relatively low $\delta^{13}C$ values with the reverse also occurring. The bioaccumulation rate of heavy nitrogen is a better indicator of increasing trophic levels than the bioaccumulation rate of ^{13}C (Rau *et al.* 1983, Fry 1988). The ecosystem in which carbon is introduced into food webs more strongly influences carbon isotope ratio values (DeNiro and Epstein 1978). Therefore, to best demonstrate the trophic positioning of the wild raptor species sampled, only nitrogen was plotted for each species (Figures 3a and b).

Averaged $\delta^{15}N$ values ranged from a low of 4.05‰ for Snowy Owls to a high of 11.91‰ for Ospreys, with 22 out of 27 raptor species having an averaged value between 6.00‰ and 9.99‰ (Table 1). Using the trophic level (TL) index numbering system, it was found that the species were separated into six different relative trophic levels ranging from TL2 to TL4.5 (Table 1). As most species were found to have $\delta^{15}N$ values between 6.00‰ and 9.99‰, most were also found to have a TL number of TL3 or TL3.5.

Artificial Enrichment

The relative trophic levels of the 27 species of raptors as determined by their mean $\delta^{15}N$ values, contrasts with what traditional diet study methods have determined. More than one species seemed misplaced. Species known to

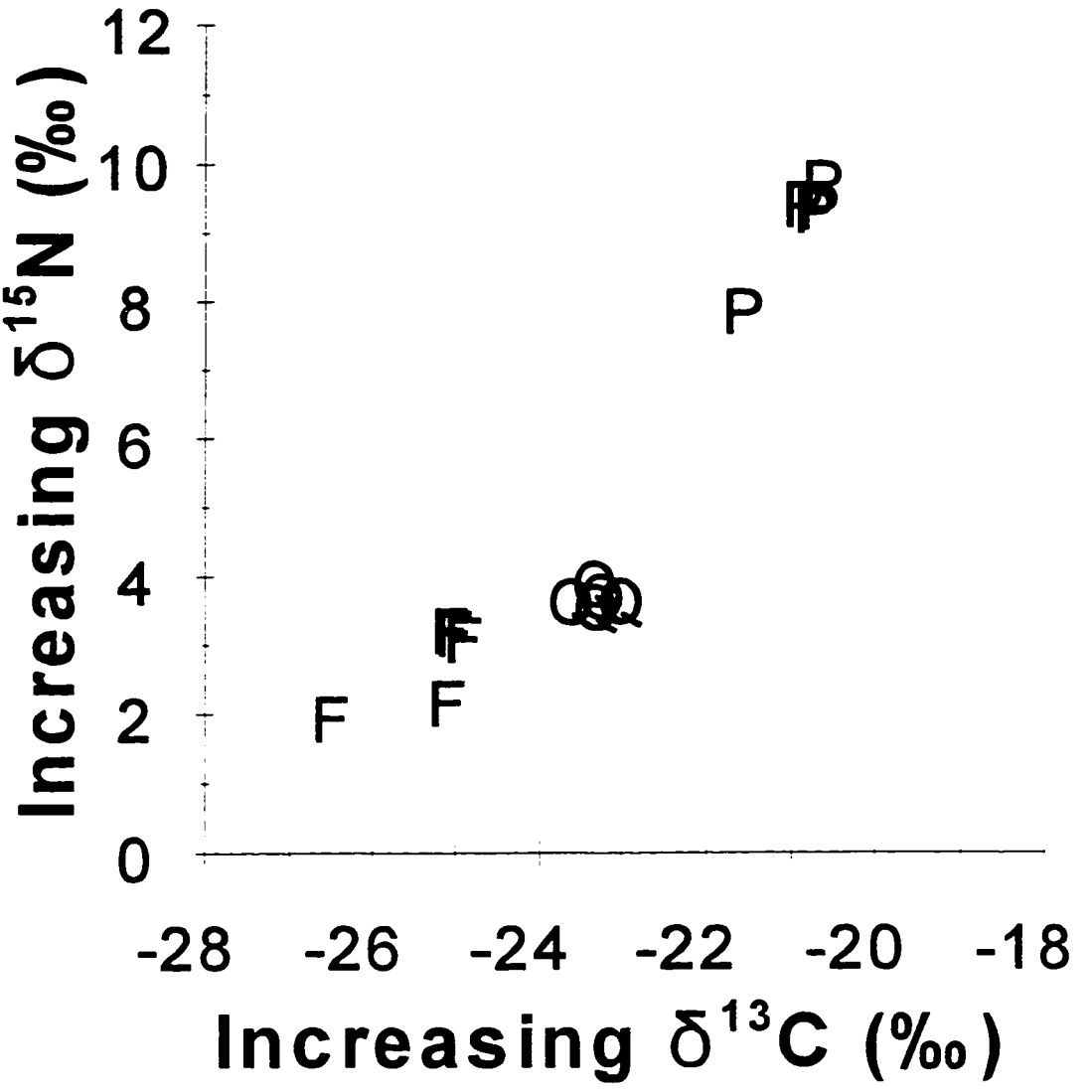


Figure 1. Bioaccumulation of heavy nitrogen and carbon isotopes in a controlled food chain. F= Quail Feed, Q = Quail, P = Peregrine Falcon.

Table 1. $\delta^{15}N$ value means, standard deviations and TL index numbers of samples from all 27 raptor species.

Species (in order of decreasing trophic level)	n	Mean $\delta^{15}N$(‰) ± 1 S.D.	Trophic Level Index Number*
Osprey (*Pandion haliaetus*)	20	11.91±1.64	4.55 (4.5)
Bald Eagle (*Haliaeetus leucocephalus*)	18	11.89±1.55	4.55 (4.5)
Burrowing Owl (*Athene cunicularia*)	24	10.64±1.91	4.03 (4)
Peregrine Falcon (*Falco peregrinus*)	24	9.48±1.36	3.79 (4)
Ferrouginous Hawk (*Buteo regalis*)	22	9.35±1.18	3.75 (4)
Merlin (*Falco columbarius*)	26	9.01±2.00	3.64 (3.5)
Prairie Falcon (*Falco mexicanus*)	19	8.92±1.86	3.61 (3.5)
Great Horned Owl (*Bubo virginianus*)	56	8.70±1.90	3.54 (3.5)
Short-eared Owl (*Asio flammeus*)	16	8.62±1.76	3.52 (3.5)
American Kestrel (*Falco sparverius*)	22	8.04±2.18	3.34 (3.5)
Swainson's Hawk (*Buteo swainsoni*)	27	8.01±1.84	3.33 (3.5)
Long-eared Owl (*Asio otus*)	17	7.97±1.34	3.31 (3.5)
Great Gray Owl (*Strix nebulosa*)	21	7.95±1.21	3.31 (3.5)
Northern Harrier (*Circus cyaneus*)	15	7.84±2.05	3.27 (3.5)
Boreal Owl (*Aegolius funereus*)	12	7.67±1.49	3.22 (3)
Northern Saw-whet Owl (*Aegolius acadicus*)	17	7.65±1.75	3.21 (3)
Cooper's Hawk (*Accipiter cooperii*)	25	7.56±1.95	3.19 (3)
Northern Hawk Owl (*Surnia ulula*)	15	7.14±1.07	3.05 (3)
Red-tailed Hawk (*Buteo jamaicensis*)	46	7.05±1.72	3.03 (3)
Sharp-shinned Hawk (*Accipiter striatus*)	20	6.96±2.07	3.00 (3)
Golden Eagle (*Aquila chrysaetos*)	12	6.92±1.40	2.98 (3)
Barred Owl (*Strix varia*)	21	6.89±1.15	2.98 (3)
Broad-winged Hawk (*Buteo platypterus*)	11	6.86±1.56	2.96 (3)
Northern Goshawk (*Accipiter gentilis*)	20	6.84±1.65	2.96 (3)
Northern Pygmy Owl (*Glaucidium gnoma*)	7	6.19±1.21	2.75 (3)
Rough-legged Hawk (*Buteo lagopus*)	20	5.96±1.64	2.68 (2.5)
Snowy Owl (*Nyctea scandiaca*)	20	4.05±1.31	2.08 (2)

*Numbers in parentheses are the index number rounded to the nearest half.

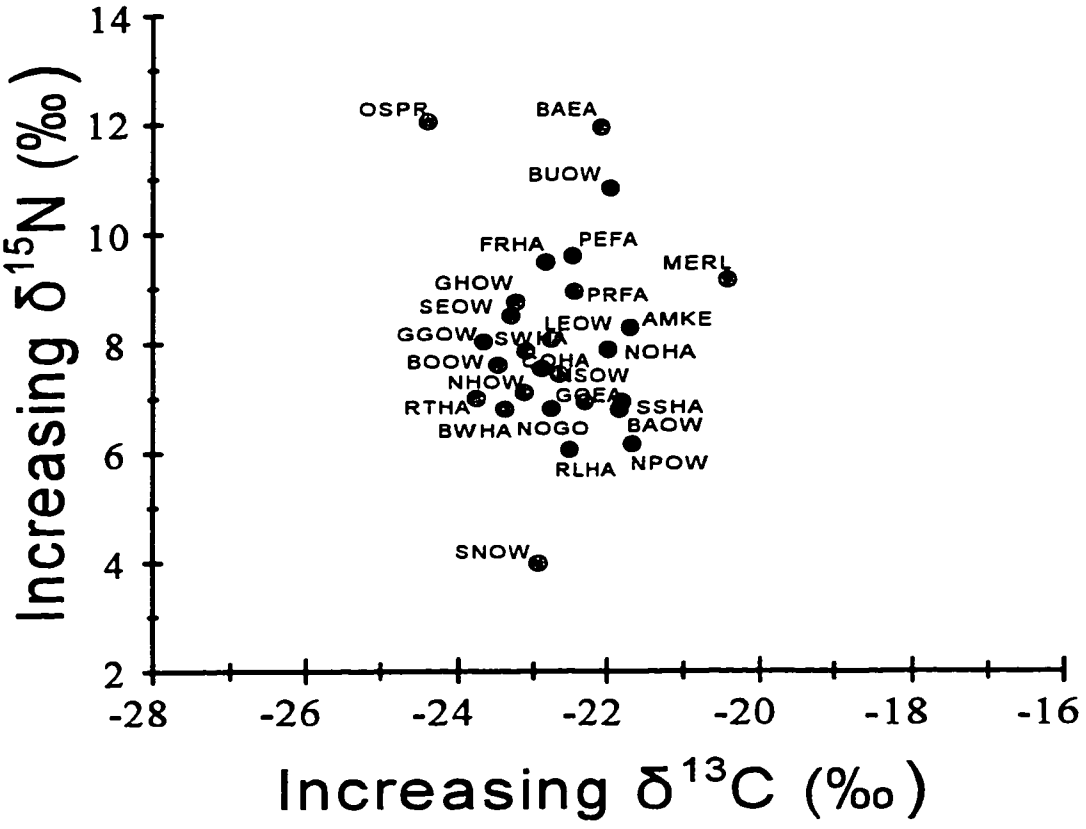


Figure 2. The result of plotting each species' heavy nitrogen mean values against their respective heavy carbon mean values. This graph indicates no relationship between increasing heavy nitrogen and increasing heavy carbon among multiple species from multiple habitats.

SNOW=Snowy Owl, RLHA=Rough-legged Hawk, NPOW=Northern Pygmy Owl, NOGO=Northern Goshawk, BAOW=Barred Owl, BWHA=Broad-winged Hawk, GOEA=Golden Eagle, SSHA=Sharp-shinned Hawk, RTHA= Red-tailed Hawk, NHOW=Northern Hawk Owl, COHA=Cooper's Hawk, NSOW= Northern Saw-whet Owl, BOOW= Boreal Owl, NOHA=Northern Harrier, GGOW=Great Gray Owl, SWHA= Swainson's Hawk, LEOW=Long-eared Owl, AMKE=American Kestrel, SEOW=Short-eared Owl, GHOW=Great Horned Owl, PRFA=Prairie Falcon, MERL=Merlin, FEHA=Ferruginous Hawk, PEFA= Peregrine Falcon, BUOW=Burrowing Owl, BAEA=Bald Eagle, OSPR=Osprey

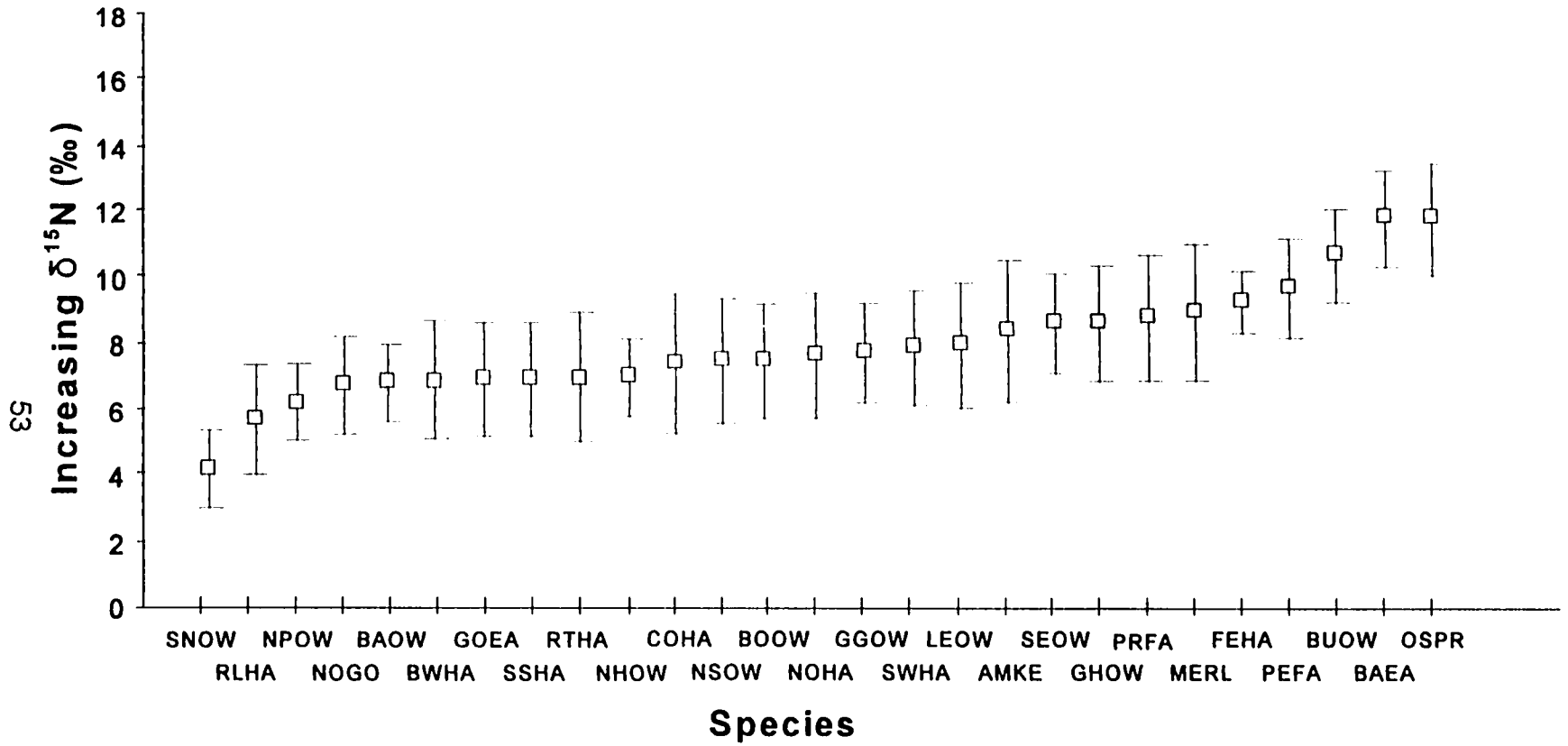


Figure 3a. Means and one standard deviation of $\delta^{15}N$ values from individuals of 27 raptor species. Species are ordered from lowest mean value to highest mean value. Abbreviations are defined in figure 2.

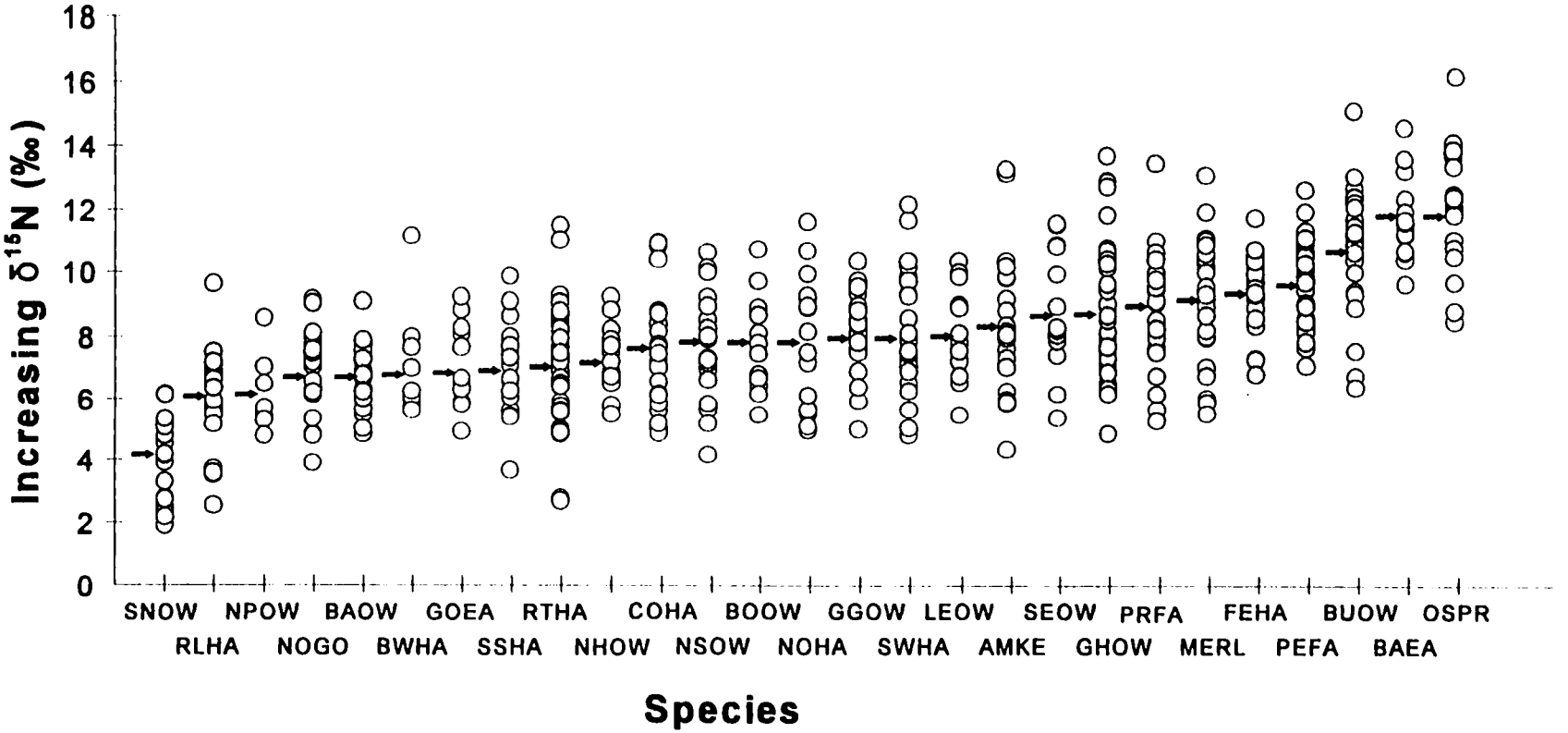


Figure 3b. Means and distributions of $\delta^{15}N$ values from individuals of 27 raptor species. Species are ordered from lowest mean value to highest mean value. Each dot represents a single individual. Small arrows indicate means. Abbreviations are defined in figure 2.

consume mostly herbivorous mammals like Prairie Falcons and Ferruginous Hawks had high $\delta^{15}N$ values which were comparable to species known to eat insectivorous birds such as Merlins and Peregrine Falcons. In fact, a great many of the species with relatively enriched isotope values either had some or all of their samples collected from birds on prairie regions where agriculture would be present.

To test whether or not the samples from agricultural areas were artificially enriched with heavy nitrogen, $\delta^{15}N$ values of feathers from Great Horned Owls and Red-tailed Hawks that were collected in both boreal forest and agricultural areas were compared. Boreal forest was assumed to include the boreal mixed-wood, foothills, and montane regions. Agriculture was assumed to be both in the prairie and parkland regions (Figures 4 and 5).

A difference of 2.06‰ between the $\delta^{15}N$ value means of Red-tailed Hawk samples collected from the boreal montane and northern Alberta regions and those samples collected in the parkland area in central and north-west, Alberta was found to be very significant ($U_{(2),\,37,8} = 245$, $Z_{0.05\,(2)} = 2.75$, $p<0.006$)(Figure 6).

The isotope values of boreal Great Horned Owls sampled in west-central Alberta were tested against the isotope values from samples collected from the parkland regions in central and north-west Alberta, and the prairies around Lethbridge, Alberta (Figure 4). The 0.49‰ difference between the $\delta^{15}N$ values of the boreal and agricultural areas was not significant ($U_{(2),33,16} = 287$, $Z_{0.05\,(2)} = 0.48$, $p=0.6312$), although the mean of the $\delta^{15}N$ values in the agricultural area was numerically higher than the mean of the boreal samples.

Feathers were also obtained from Burrowing Owls breeding in areas of intensive cultivation south and west of Regina, Saskatchewan, and areas of native prairie near Hanna, in southern Alberta. A difference of 1.22‰ between the $\delta^{15}N$ values in native prairie and areas of intense agriculture for nitrogen was not significant ($U_{(2),\,18,6} = 68$, $Z_{0.05\,(2)} = 0.90$, $p=0.3682$). But, similar to the Great Horned Owl results, there was a slight difference in nitrogen values with agricultural areas again having slightly higher isotope ratios (Figure 7).

Most of the individual species' Trophic Level Index numbers also show an increase between boreal regions and agricultural regions (Table 2). Eleven of

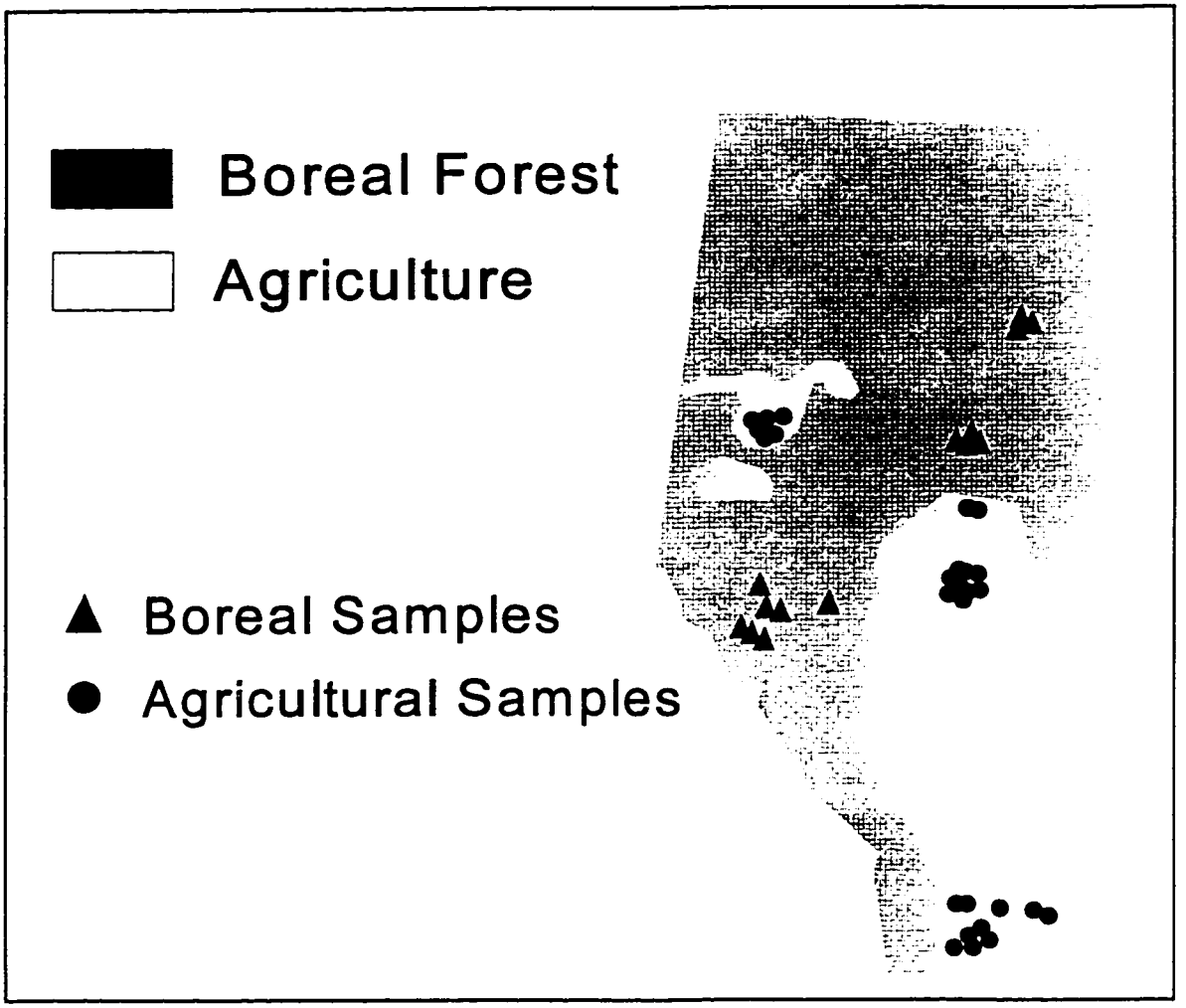


Figure 4. Locations of Great Horned Owl sample collections for comparison of $\delta^{15}N$ values between boreal and agricultural regions of Alberta.

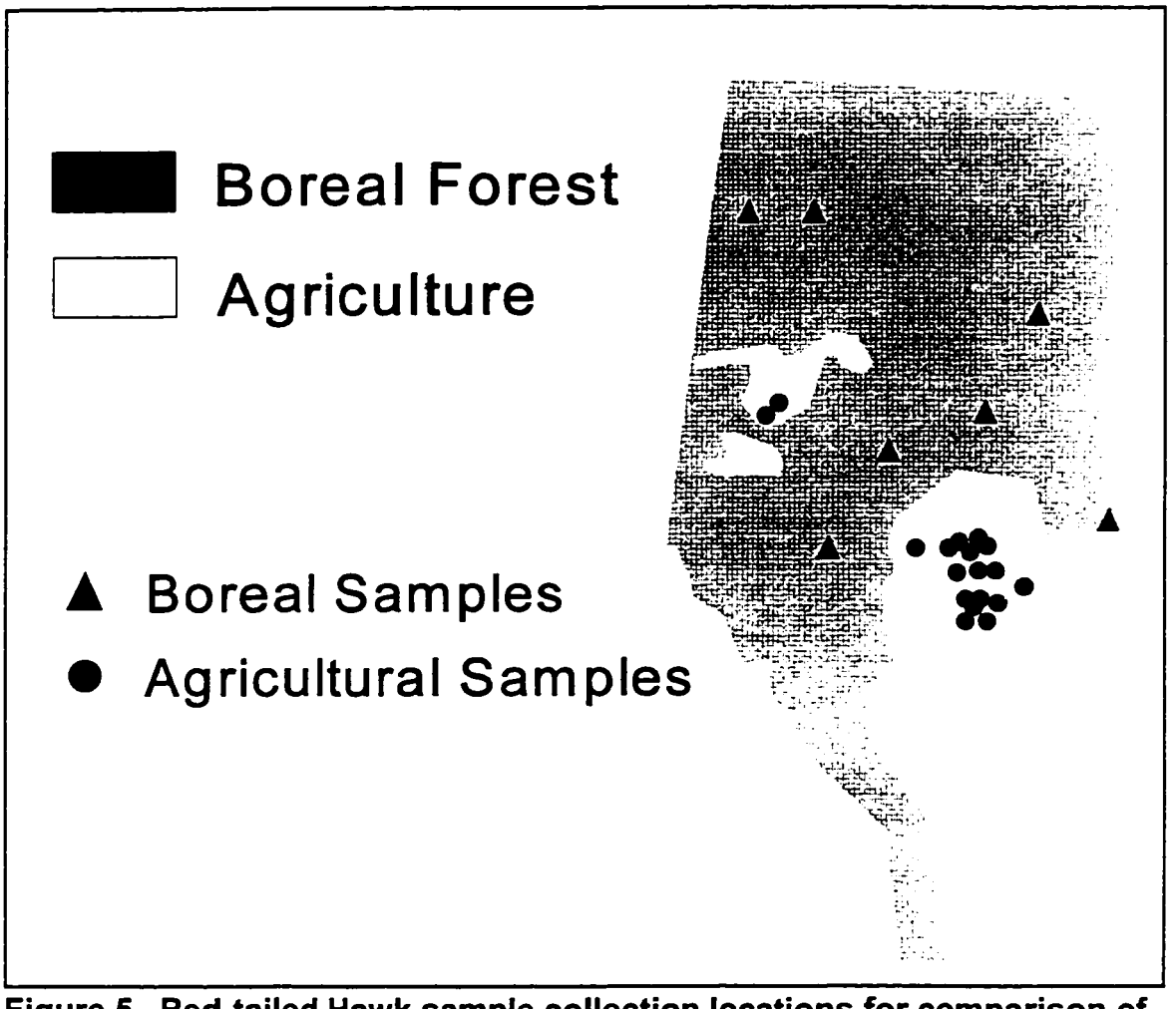


Figure 5. Red-tailed Hawk sample collection locations for comparison of $\delta^{15}N$ values between boreal and agricultural regions of Alberta.

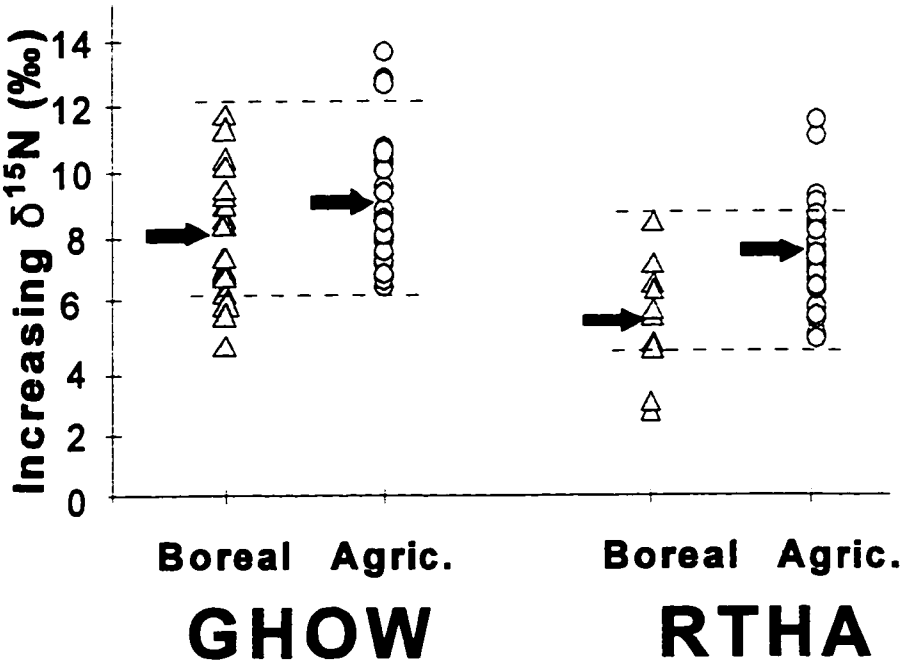


Figure 6. Great Horned Owl and Red-tailed Hawk $\delta^{15}N$ values plotted according to the landscape type where the samples were collected. Arrows indicate means and dotted lines indicate area where values overlap.

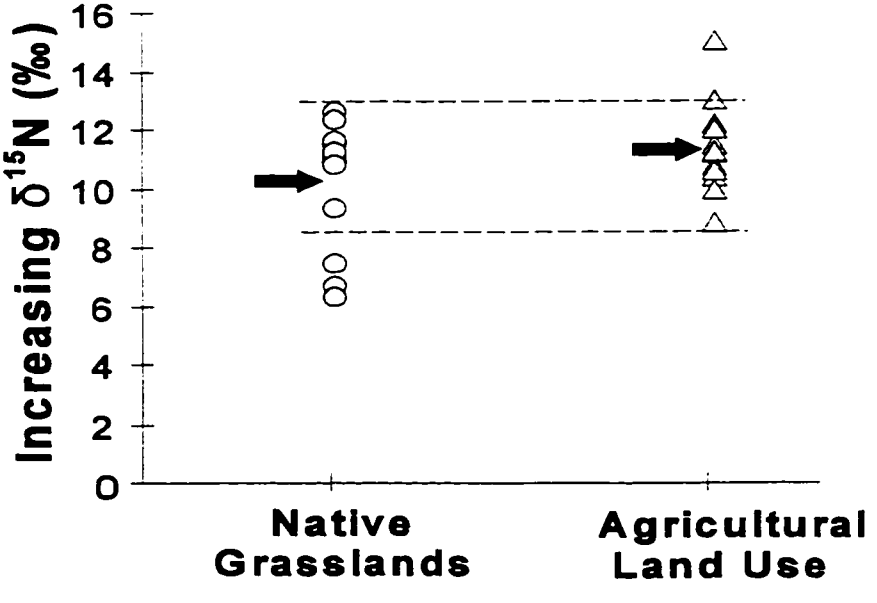


Figure 7. Burrowing Owl $\delta^{15}N$ values plotted according to the landscape type where the samples were collected.

Table 2. Trophic level index numbers separated by ecoregion. Species were only included if samples were available from more than one ecoregion.

Species	Boreal	Parkland	Prairie
Osprey	4.64	4.97	
Bald Eagle	4.29	4.25	4.87
Northern Saw-whet Owl	3.36	4.14	
Short-eared Owl	3.19	3.27	4.17
Great Horned Owl	3.35	3.36	4.03
Peregrine Falcon	3.75	3.95	
Swainson's Hawk		2.99	3.87
Merlin	3.17	3.89	3.23*
American Kestrel	3.35	3.57	
Long-eared Owl	3.24	3.31	
Red-tailed Hawk	2.38	3.17	3.09*
Golden Eagle	3.16		2.86*
Sharp-shinned Hawk	2.92	2.99	2.99
Broad-winged Hawk	2.74	2.81	

*** Species where TL index number for the prairie ecoregion was not the highest value**

the 14 species having samples collected in more than one ecoregion had the highest TL number in agricultural areas (parkland or prairie). If the parkland and prairie TL numbers are averaged together into a single agricultural region, only the Golden Eagle has a higher TL number in the boreal region than in the agricultural region.

The theory of an agricultural enrichment factor is supported by the following facts: 1) The isotope ratio values for Prairie Falcons, Ferruginous Hawks and Burrowing Owls do not correspond with results using traditional methods. 2) The differences between agricultural and boreal sample isotope ratio means of Red-tailed Hawks are significant. 3) The isotope ratio value means of the agricultural samples for both Great Horned Owls and Burrowing Owls were numerically higher than the non-agricultural samples indicating the same trend which is significant in the Red-tailed Hawk samples. And 4) Where samples from multiple ecoregions were collected for a species, 13 of 14 species had higher TL numbers in the agricultural regions than in the boreal region.

The significance of a possible enrichment effect meant that samples from all raptor species coming from different regions of Alberta should be grouped and plotted separately (Tables 3-6, Figures 8a to 11b). Sub-samples were grouped into general areas such as prairie (Table 3, Figure 8a and b), parkland (Table 4, Figure 9a and b), boreal forest (Table 5, Figure 10a and b) and the arctic (Table 6, Figure 11a and b). Although some of the sample sizes are small, the result of analyzing sub-sets of the $\delta^{15}N$ values provided a more accurate demonstration of the relative trophic positioning of each species within an ecoregion.

Prairie Ecoregion

When the $\delta^{15}N$ values of samples which came from birds known to be breeding in the prairies of Alberta, the relative placement of the raptors closely resembles what the literature predicts (Figures 8a and b). The relative placement of Ferruginous Hawks and Prairie Falcons was changed from high amongst bird eating species, to a more average level amongst species known to have diets with high mammalian content (Table 3). Piscivorous Bald Eagles were the most enriched (12.93‰[n=4]), and Golden Eagles had the lowest $\delta^{15}N$ value mean (6.51‰[n=2]). Merlins, Great Horned Owls and Bald Eagles had relatively high standard deviations than the other raptors in the prairie regions (±2.93‰[n=3], ±2.61‰[n=11] and ±2.54‰[n=4]). Golden Eagles and Swainson's Hawks had

Table 3. $\delta^{15}N$ value means, standard deviations and TL index numbers of raptor samples from the prairie ecoregion.

Species (in order of decreasing Trophic Level)	n	Mean $\delta^{15}N$ (‰) ± 1 Standard Deviation	Trophic Level Index Number*
Bald Eagle	4	12.93±2.54	4.87 (5)
Burrowing Owl	24	10.64±1.91	4.15 (4)
Short-eared Owl	4	10.38±1.36	4.17 (4)
Great Horned Owl	11	10.23±2.61	4.03 (4)
Swainson's Hawk	6	9.75±1.10	3.87 (4)
Ferruginous Hawk	22	9.35±1.18	3.75 (4)
Prairie Falcon	19	8.92±1.86	3.61 (3.5)
Merlin	3	7.71±2.93	3.23 (3)
Red-tailed Hawk	5	7.26±1.24	3.09 (3)
Sharp-shinned Hawk	8	6.94±1.35	2.99 (3)
Golden Eagle	2	6.51±0.28	2.86 (3)

*** Numbers in parentheses are TL numbers rounded to the nearest half number**

Table 4. $\delta^{15}N$ value means, standard deviations and TL index numbers of raptor samples from the parkland ecoregion.

Species (in order of decreasing Trophic Level)	n	Mean $\delta^{15}N$ (‰) ± 1 Standard Deviation	Trophic Level Index Number*
Osprey	4	13.24±1.01	4.97 (5)
Bald Eagle	3	10.94±1.22	4.25 (4)
Northern Saw-Whet Owl	1	10.58	4.14 (4)
Peregrine Falcon	2	9.99±0.89	3.95 (4)
Merlin	10	9.82±3.03	3.89 (4)
American Kestrel	7	8.77±2.31	3.57 (3.5)
Great Horned Owl	16	8.11±1.04	3.36 (3.5)
Northern Harrier	9	8.06±2.07	3.34 (3)
Long-eared Owl	12	7.97±1.25	3.31 (3)
Short-eared Owl	5	7.82±1.63	3.27 (3)
Cooper's Hawk	20	7.67±1.96	3.22 (3)
Red-tailed Hawk	31	7.52±1.52	3.17 (3)
Swainson's Hawk	10	6.96±1.66	3.00 (3)
Sharp-shinned Hawk	5	6.94±1.92	2.99 (3)
Broad-winged Hawk	6	6.36±0.83	2.81 (3)

*** Numbers in parentheses are TL numbers rounded to the nearest half number**

Table 5. $\delta^{15}N$ value means, standard deviations and TL index numbers of raptor feathers collected in the boreal forest.

Species (in order of decreasing Trophic Level)	n	Mean $\delta^{15}N$ (‰) ± 1 Standard Deviation	Trophic Level Index Number*
Osprey	11	12.17±1.54	4.64 (4.5)
Bald Eagle	5	11.07±0.41	4.29 (4)
Peregrine Falcon	20	9.36±1.45	3.75 (4)
Northern Saw-whet Owl	3	8.12±2.27	3.36 (3.5)
Great Horned Owl	21	8.10±1.83	3.35 (3.5)
American Kestrel	3	8.09±2.09	3.35 (3.5)
Great Gray Owl	21	7.95±1.30	3.31 (3.5)
Long-eared Owl	4	7.74±1.67	3.24 (3)
Boreal Owl	4	7.60±0.78	3.20 (3)
Short-eared Owl	2	7.57±0.31	3.19 (3)
Merlin	4	7.51±1.37	3.17 (3)
Golden Eagle	4	7.47±1.08	3.16 (3)
Northern Hawk Owl	15	7.14±1.07	3.05 (3)
Barred Owl	21	6.89±1.15	2.98 (3)
Northern Pygmy Owl	3	6.80±1.92	2.95 (3)
Sharp-shinned Hawk	4	6.73±1.15	2.92 (3)
Northern Goshawk	12	6.60± 1.56	2.88 (3)
Broad-winged Hawk	3	6.15± 0.75	2.74 (2.5)
Red-tailed Hawk	10	5.01± 1.81	2.38 (2.5)

*** Numbers in parentheses are TL numbers rounded to the nearest half number**

Table 6. $\delta^{15}N$ value means, standard deviations and TL index numbers of raptor samples from the arctic ecoregion.

Species (in order of decreasing Trophic Level)	n	Mean $\delta^{15}N$ (‰) ± 1 Standard Deviation	Trophic Level Index Number*
Rough-legged Hawk	13	6.12±1.31	2.73 (2.5)
Snowy Owl	20	4.05±1.31	2.08 (2)

*** Numbers in parentheses are TL numbers rounded to the nearest half number**

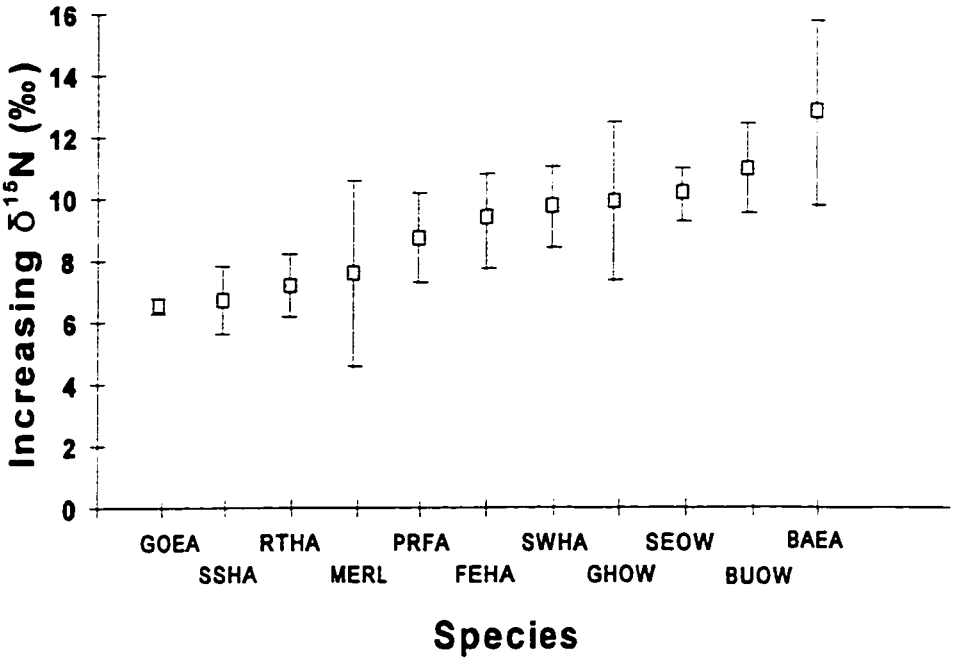


Figure 8a. Means and standard deviations of $\delta^{15}N$ values of prairie raptors. Means are represented by squares and one standard deviation is represented by bars. Abbreviations are defined in figure 2.

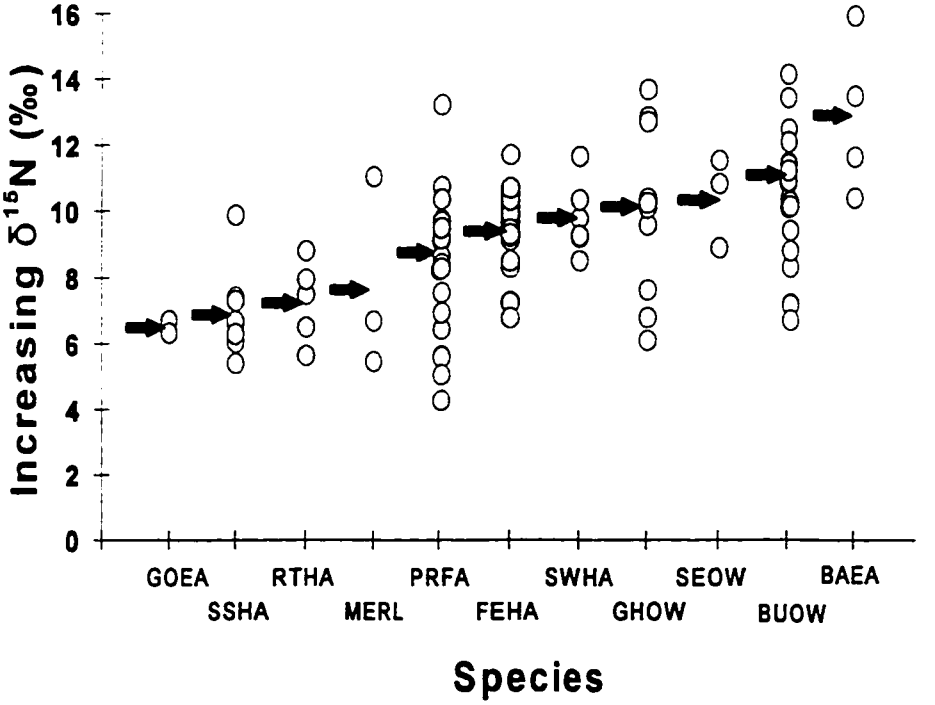


Figure 8b. Means and distributions of $\delta^{15}N$ values of prairie raptors. Means are indicated by arrows and each dot represents a single raptor.

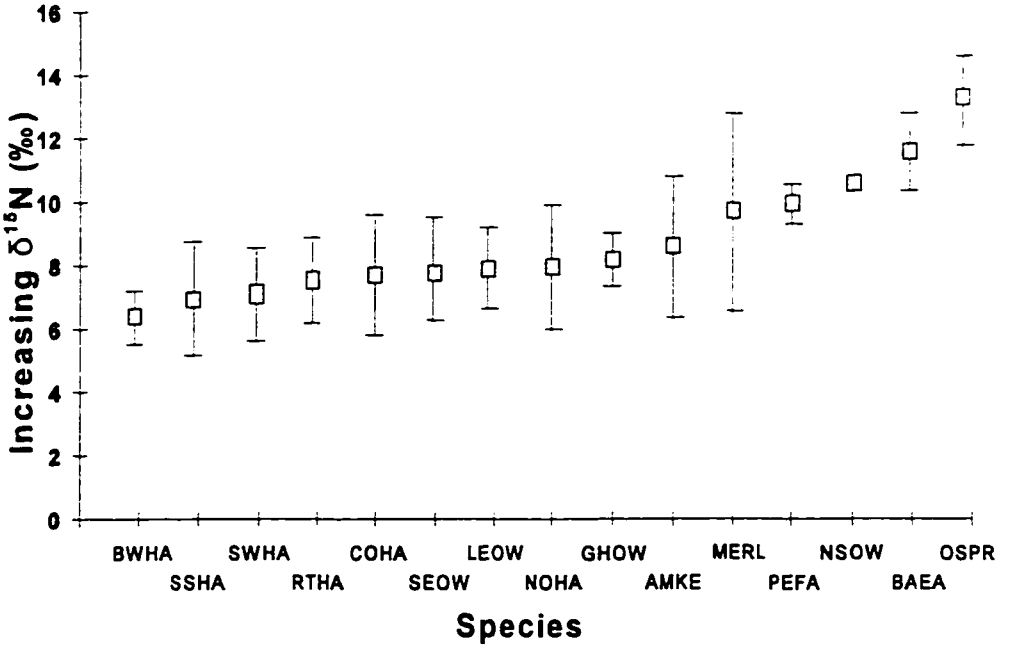


Figure 9a. Means and standard deviations of $\delta^{15}N$ values of parkland raptors.

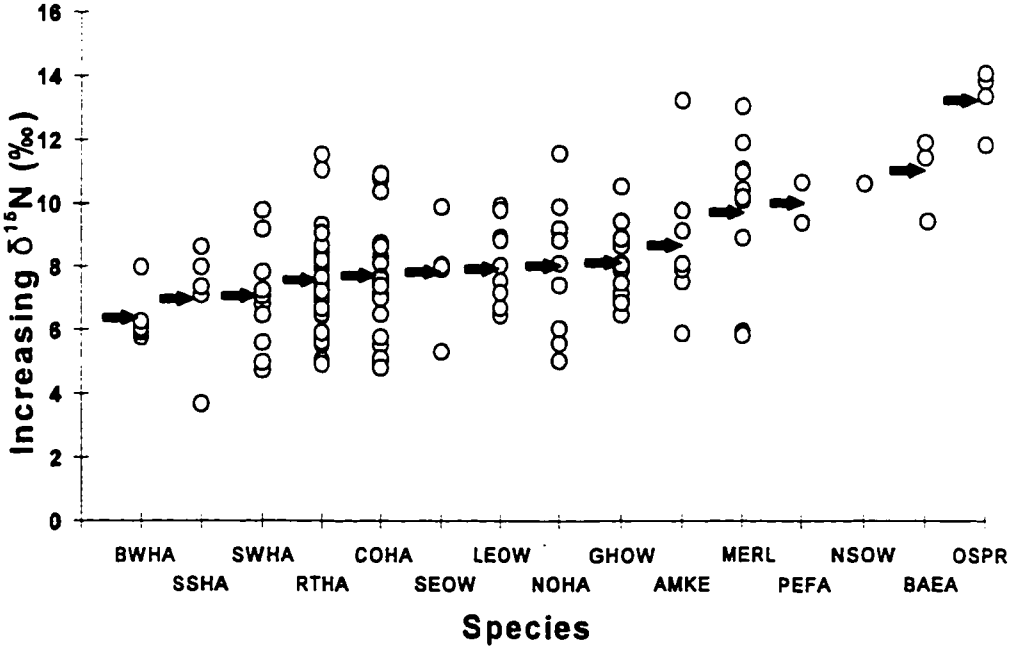


Figure 9b. Means and distributions of $\delta^{15}N$ values of parkland raptors.

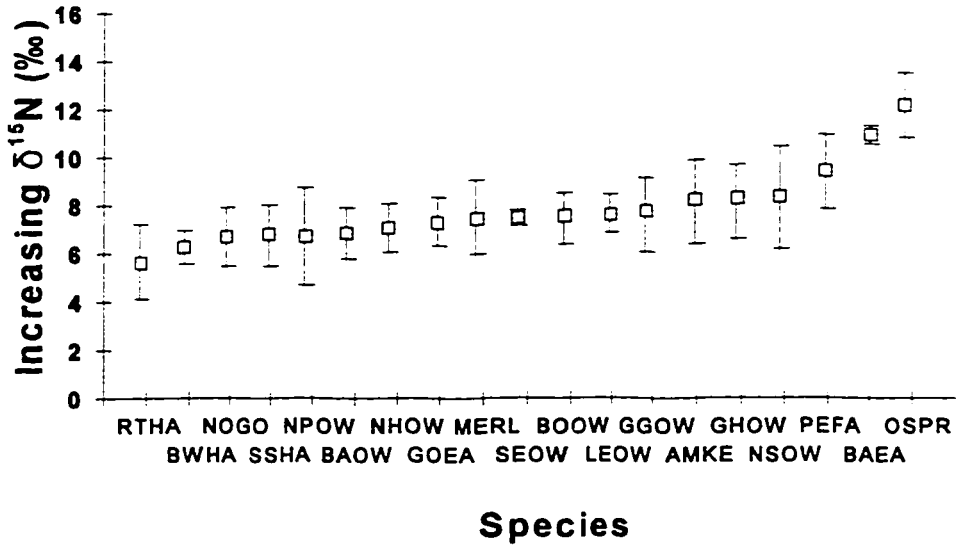


Figure 10a. Means and standard deviations of $\delta^{15}N$ values of boreal raptors.

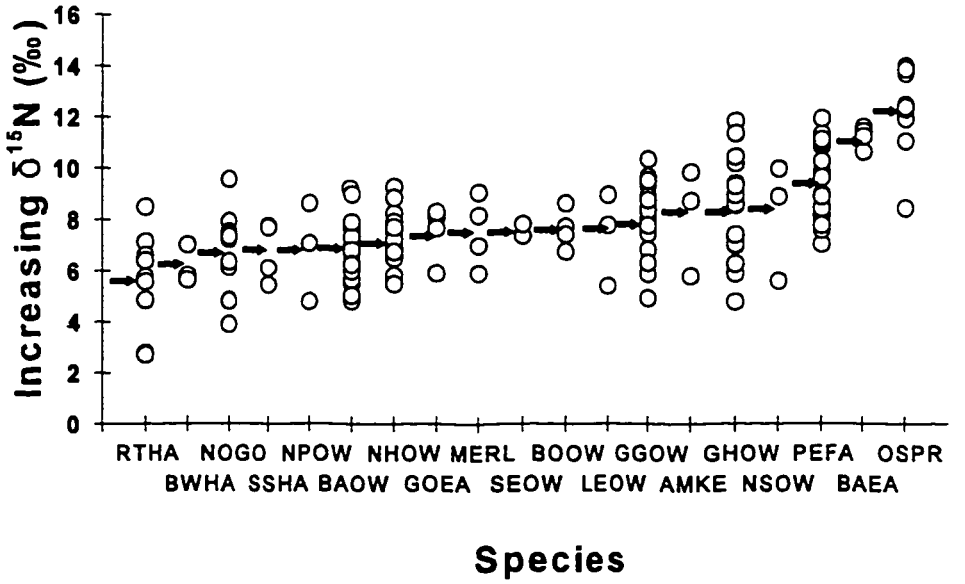


Figure 10b. Means and distributions of $\delta^{15}N$ values of boreal raptors.

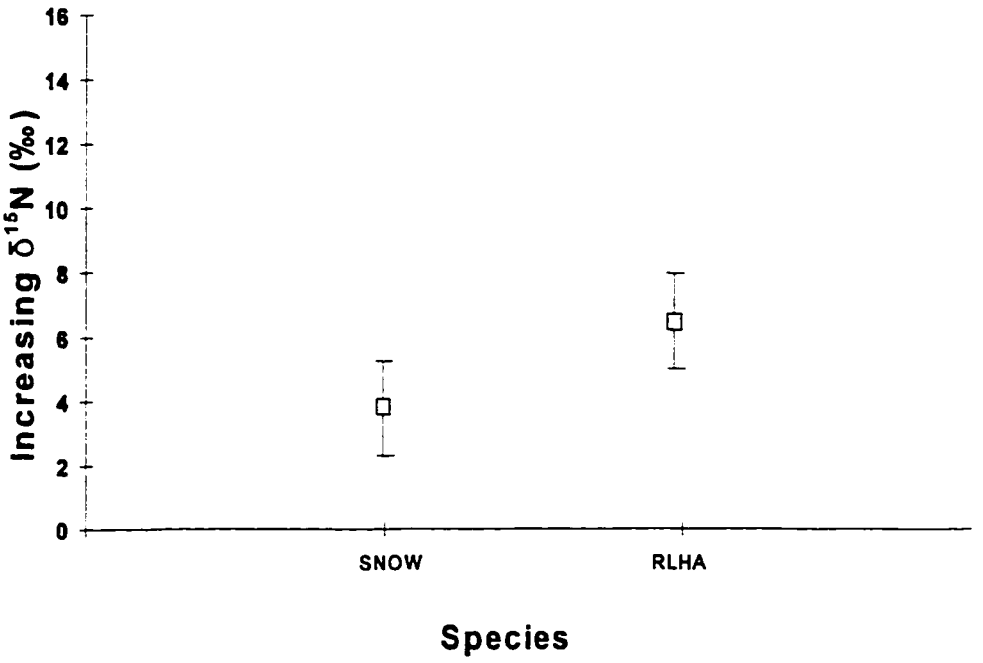


Figure 11a. Means and standard deviations of $\delta^{15}N$ values of arctic raptors.

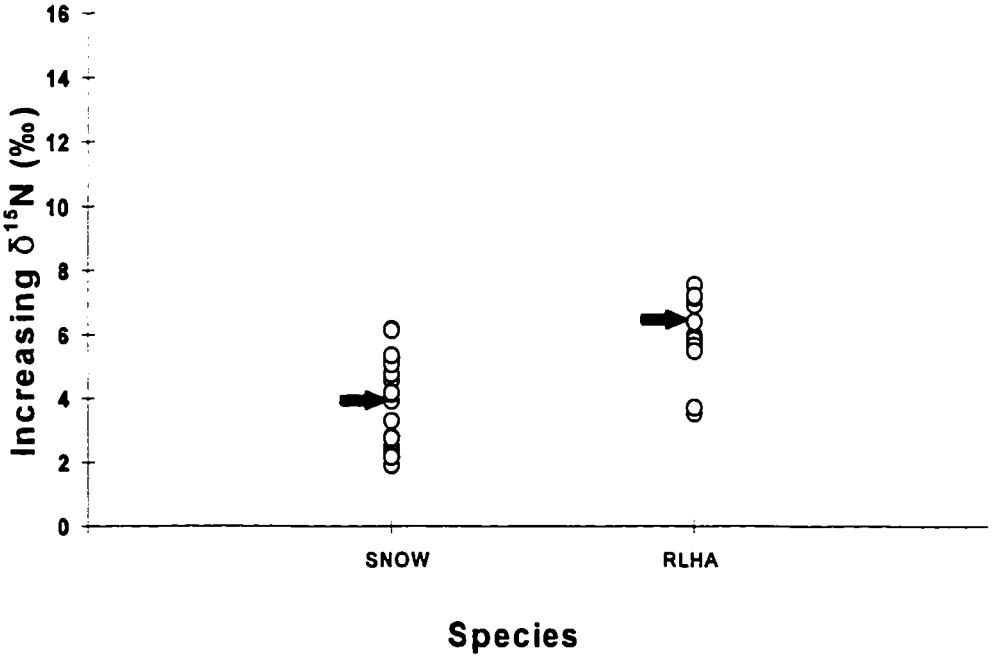


Figure 11b. Means and distributions of $\delta^{15}N$ values of arctic raptors.

the smallest standard deviations (±0.28‰[n=2] and ±1.10‰[n=6])(Table 2, Figure 8a). Most of the trophic level index numbers of the prairie raptors were in the TL3 to 4 range (Table 3, Figure 12).

Parkland Ecoregion

Most raptors in the parkland ecoregion had the TL number of 3 (Table 4, Figure 13). Piscivorous Ospreys and Bald Eagles had the highest ratio means in the parkland region (13.24‰[n=4] and 10.94‰[n=3])(Table 4, Figures 9a and b), and Broad-winged Hawks had the lowest isotope ratio mean (6.36‰[n=6]). Merlins had a relatively high standard deviation compared to all the other raptors in the parkland region (±3.03‰[n=10]). Broad-winged Hawks had the smallest standard deviation (±0.83‰[n=6])(Table 4, Figure 9a).

Boreal Forest Ecoregion

The raptors of the boreal forest ecoregion had more raptor species with relatively low trophic index number than high trophic index numbers (Table 5, Figure 14). The piscivorous raptors had the highest isotope means (Osprey 12.17‰[n=11] and Bald Eagles 11.07‰[n=5])(Table 5, Figures 10a and b). Red-tailed Hawks and Broad-winged Hawks had the lowest $\delta^{15}N$ value means (5.01‰[n=10] and 6.15‰[n=3]). American Kestrels had the largest standard deviation of all boreal raptors (±2.09‰[n=3]), while Short-eared Owls, Bald Eagles and Boreal Owls had the smallest standard deviations (±0.31‰[n=2], ±0.41‰[n=5] and ±0.78‰[n=4])(Table 5, Figure 10a).

Arctic Ecoregion

Snowy Owls and Rough-legged Hawks are the only two raptors sampled which would have grown their feathers in the Arctic. Their $\delta^{15}N$ values were low (4.05‰ and 6.12‰)(Table 6, Figures 11a and b) which translated into low TL numbers (TL2 and TL2.5)(Table 6, Figure 15).

Enrichment Factor

The detection of distinct differences in $\delta^{15}N$ values is not as clear as when contrasting the trophic level index numbers. The comparison of the means of trophic index numbers from the different ecoregions indicates that the prairies had the highest overall enrichment and the arctic had the least (prairie $\bar{x}$TL = 3.69, parkland $\bar{x}$TL = 3.56, boreal $\bar{x}$TL = 3.40, and arctic $\bar{x}$TL = 2.41). While the means of the trophic level index numbers indicate the greatest heavy nitrogen

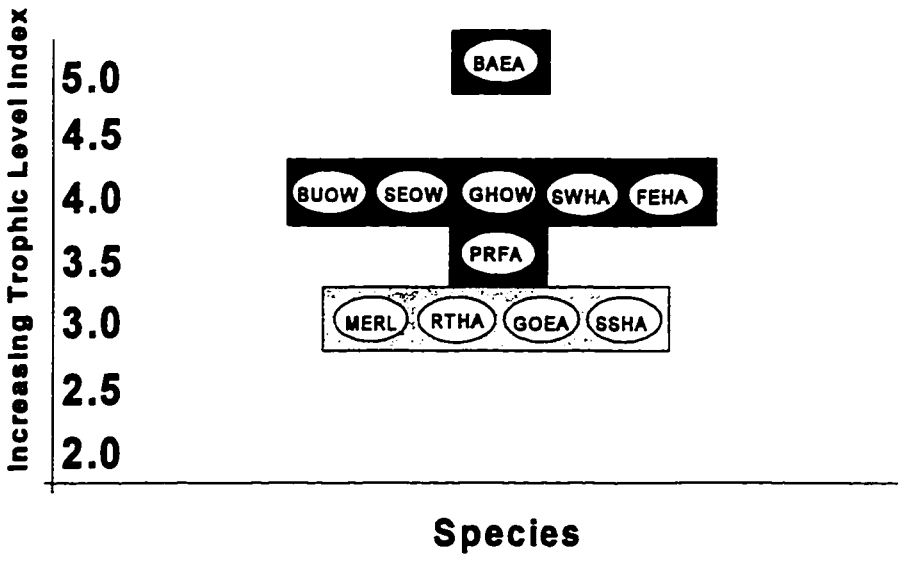


Figure 12. Trophic hierarchy of prairie raptors according to stable isotope ratio analysis. Trophic level index numbers calculated using formula 2. Abbreviations are defined in figure 2.

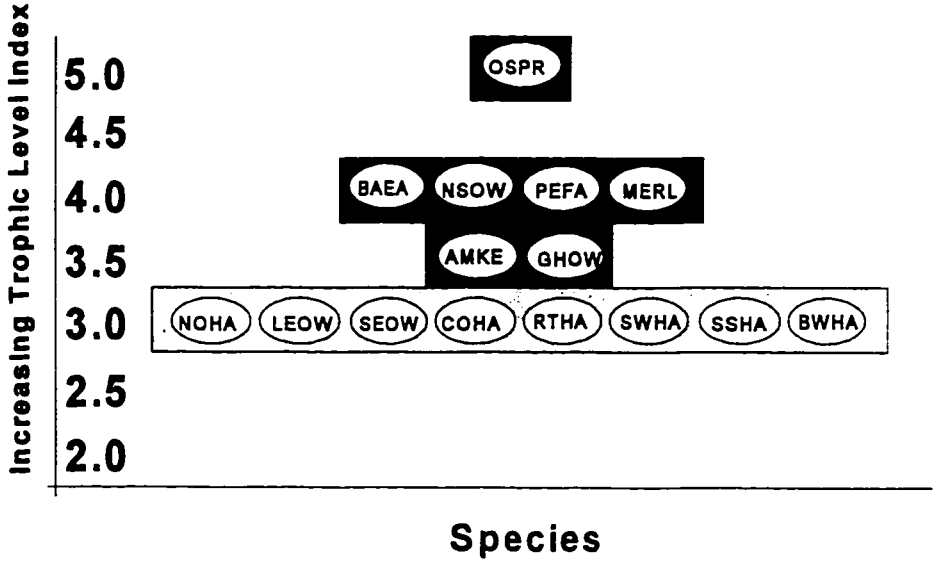


Figure 13. Trophic hierarchy of parkland raptors according to stable isotope ratio analysis.

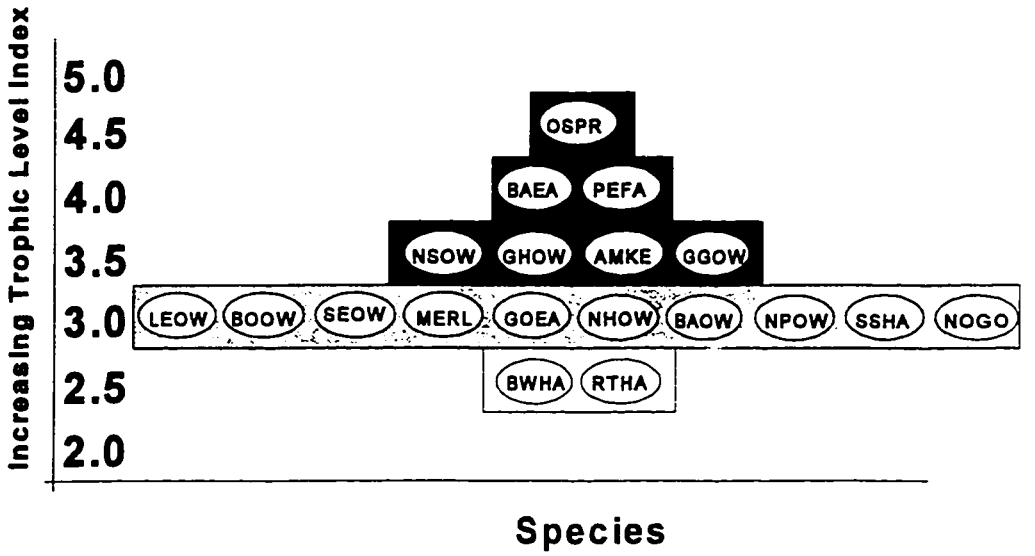


Figure 14. Trophic hierarchy of boreal raptors according to stable isotope ratio analysis.

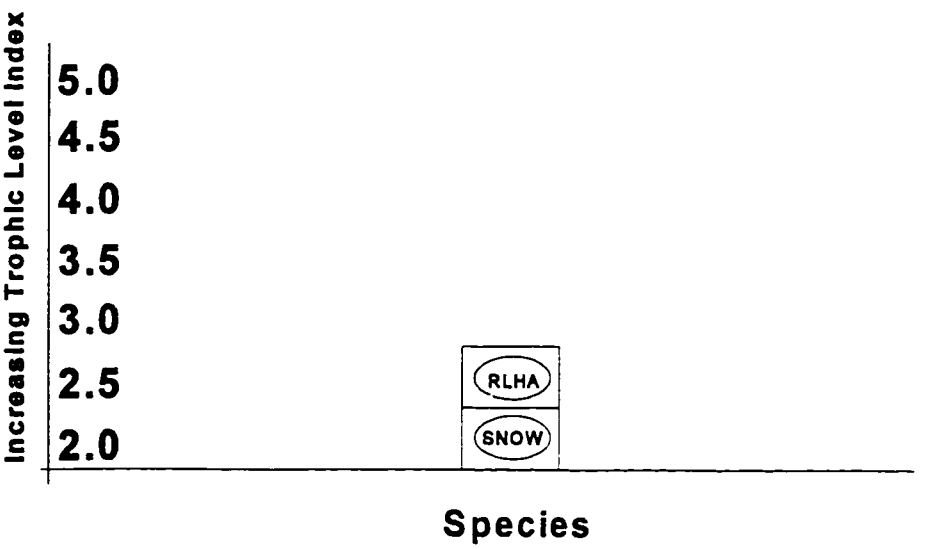


Figure 15. Trophic hierarchy of arctic raptors according to stable isotope ratio analysis.

enrichment in the prairie raptors, the effect is different on individual species (Tables 3-6, Figures 12-15). Swainson's Hawks and Short-eared Owls decrease from TL4 to TL3 from prairie to parkland ecoregions. Great Horned Owls decrease from TL 4 to TL 3.5 from prairie to parkland ecoregions. Red-tailed and Broad-winged Hawks decreased from TL3 to TL2.5 from parkland to boreal ecoregions. Most other species found in more than one ecoregion remained at the same trophic index level, and Merlins increased from TL3 to TL4 from the prairie to parkland ecoregions. Although rounding the TL numbers may make comparisons easier, the rounded numbers diminish the enrichment effect. Unrounded TL numbers of individual species show an increase in agricultural areas (parkland and prairie samples together) in 13 of 14 species having samples from more than one ecoregion (Table 2). The fact that Golden Eagles had lower TL values in the agricultural areas than in the boreal areas is lost when TL numbers are rounded to the nearest half.

Variability Of Diet Within A Species

Not all variation in individual $\delta^{15}N$ values within a species is derived from an enrichment factor. The distribution of data points within a species can be caused by variations between individual diet selections, the location of populations within an ecoregion, and the age of the individual raptors.

Individuals eating primarily high trophic level feeding prey will have a $\delta^{15}N$ value higher than the species' mean $\delta^{15}N$ value. Those raptors eating low trophic level feeding prey will have relatively lower isotope values.

Peregrine Falcon $\delta^{15}N$ values plotted by location of sample collection indicated a difference between $\delta^{15}N$ values from locations where large sample sizes were obtained from two major nesting areas within an ecoregion (Figure 16). Samples from an area where the falcons are nesting near the Peace River, Alberta were found to have a significantly different mean than those nesting near or along Lake Athabasca ($U_{(2),\,13,7}=85$, $Z_{0.05\,(2)} = 3.09$, $p<0.002$).

Different age classes of raptor species can also affect $\delta^{15}N$ values. A small sample of feathers from Bald Eagles where the age of the donating bird was known, indicate slight relative enrichment with increasing age class (slope = 0.13)(Figure 17). Ten of the 27 species of raptors had sufficient samples from both adults and juveniles to test whether or not there was a significant difference

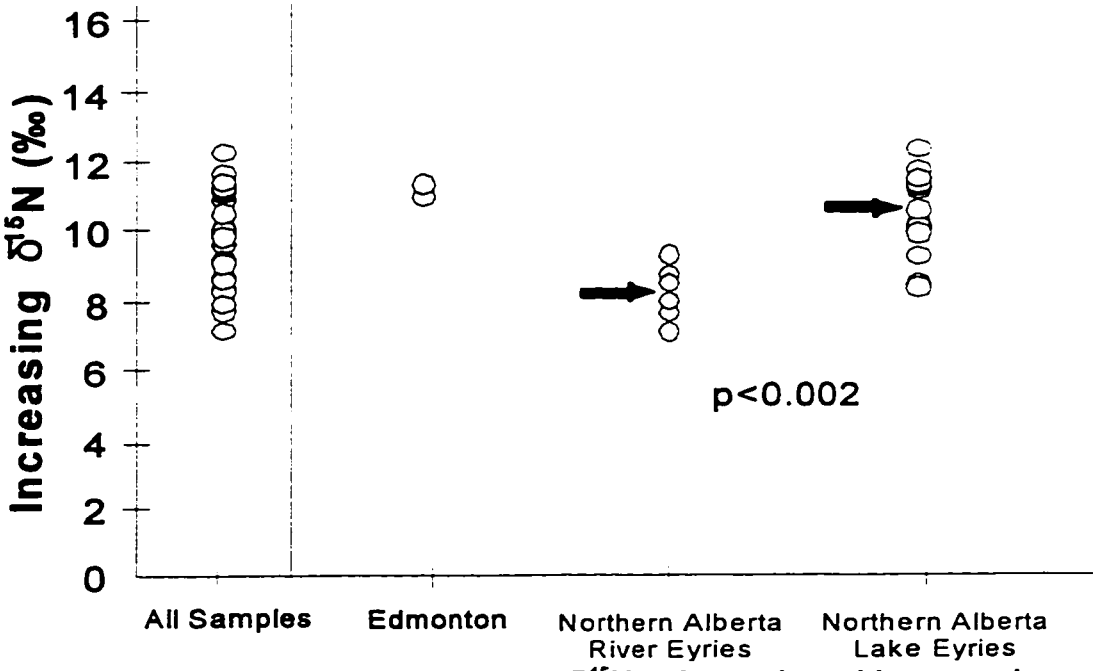


Figure 16. Individual Peregrine Falcon $\delta^{15}N$ values plotted by sample collection location. River and lake eyrie means are significantly different using a Mann-Whitney-U test.

Figure 17. Relationship between increasing $\delta^{15}N$ values and increasing age of Bald Eagles. Samples were only included if the age of the eagle was known. Slope of line indicates an insignificant trend.

between their $\delta^{15}N$ values (Table 7, Figure 18). Of the 10 species, only Peregrine Falcons had a significant difference between adult and juvenile $\delta^{15}N$ values ($U_{(2),\ 11,7} = 68$, $Z_{0.05\ (2)} = 2.63$, $p<0.009$). The juvenile Peregrines had a mean $\delta^{15}N$ value of 8.46‰(n=11) , while the adults had a mean value of 10.31‰(n=7)(Table 7, Figure 18).

Age Class Comparisons Across Landscape Types

To test whether age class differences vary with landscape types, age class sub-samples of Great Horned Owl and Red-tailed Hawk $\delta^{15}N$ values were compared within landscape types (Table 8, Figure 19). Differences in age class means for Red-tailed Hawks were partially dependant upon the landscape type. Comparisons of the means of the age classes within the Red-tail Hawk samples had showed a significant difference within the boreal region ($U_{(2),5,3} = 15$, $Z_{0.05\ (2)} = 2.09$, $p<0.04$)(Figure 19). Whereas, the difference was insignificant when the age class samples were analyzed without separating the samples into landscape types ($U_{(2),\ 28,16} = 300$, $Z_{0.05\ (2)} = 1.84$, $p=0.06$)(Table 7, Figure 18). The difference between the sub-sample $\delta^{15}N$ value means from the agricultural system was not significant ($U_{(2),\ 23,12} = 186$, $Z_{0.05\ (2)} = 0.71$, $p=0.42$).

To test whether landscape type differences vary by age classes, landscape type sub-samples of Great Horned Owl and Red-tailed Hawk $\delta^{15}N$ values were compared within age classes (Table 8, Figure 20). The only significant difference between sub-samples were between Red-tailed Hawk juvenile samples collected from boreal and agricultural areas($U_{(2),\ 24,5} = 117$, $Z_{0.05\ (2)} = 3.12$, $p<0.002$)(Table 8, Figure 20).

Within Nest Variation

There were 22 nests of 11 species which had samples from individual nestlings. Nestlings from most nests had very similar $\delta^{15}N$ values. However, $\delta^{15}N$ values of nestlings from three nests were significantly different (Table 9, Figure 21). The difference in the $\delta^{15}N$ values between siblings translate to a difference in trophic level index numbers from 1 in a Cooper's Hawk nest and an Osprey nest to 1.5 in Northern Goshawk nest (Table 9). For these samples, carbon ratios were also analyzed since base levels of both carbon and nitrogen would be the same for all nestlings. Since both carbon and nitrogen are being analyzed to compare differences within nests, the carbon isotope values can be plotted against the nitrogen isotope values in the same manner as figures 1 and 2 (Figure 21).

Table 7. Mean $\delta^{15}N$ values of adults and juveniles. Mann Whitney- U tests were used for statistical analysis.

Species	Age	n	Mean δ15N (‰)	U Value (2 Tailed)	Z Value (α=0.05, 2 Tailed)	Probability
Northen Goshawk	Adult	8	6.83	53	0.70	p=0.484
	Juv.	11	6.87			
Sharp-shinned Hawk	Adult	12	7.00	34	0.38	p=0.719
	Juv.	5	6.28			
Red-tailed Hawk	Adult	16	7.74	300	1.84	p=0.064
	Juv.	28	6.78			
Northern Hawk Owl	Adult	7	7.05	20	0.32	p=0.749
	Juv.	5	7.33			
Cooper's Hawk	Adult	6	8.49	56	1.83	p=0.069
	Juv.	12	7.14			
Long-eared Owl	Adult	8	7.87	27	0.32	p=0.749
	Juv.	6	7.99			
Swainson's Hawk	Adult	10	7.87	72	0.09	p=0.936
	Juv.	14	7.80			
Prairie Falcon	Adult	5	10.07	42	1.59	p=0.112
	Juv.	11	8.17			
Great Horned Owl	Adult	27	9.07	231	1.14	p=0.254
	Juv.	14	8.10			
Peregrine Falcon	Adult	7	10.31	68	2.63	p<0.009*
	Juv.	11	8.46			

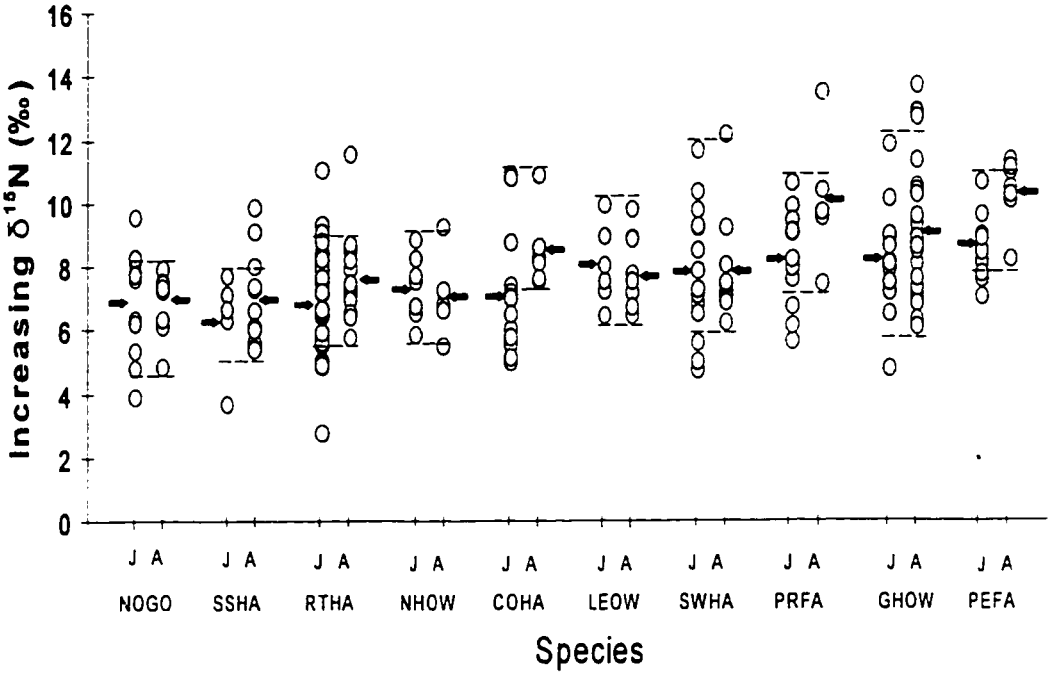


Figure 18. $\delta^{15}N$ values of adult (A) and juvenile (J) samples from 10 species of raptors where ages were known during sample collection. Arrows indicate means and dotted lines indicate areas where values overlap.

Table 8. Statistical comparison of $\delta^{15}N$ value means between landscape type and age classification sub-sets of Great Horned Owl and Red-tail Hawk samples. Mann Whitney-U tests were used for statistical analysis.

Species		n	Mean δ15N (‰)	U Value (2 Tailed)	Z Value (α=0.05, 2 Tailed)	Probability
GHOW	Boreal Adults	10	8.11	33	0.92	p=0.358
	vs. Boreal Juvs.	5	8.30			
	Agric. Adults	17	9.64	169	2.19	p=0.060
	vs. Agric. Juvs.	9	7.99			
	Boreal Adults	10	8.11	118	1.63	p=0.103
	vs. Agric. Adults	17	9.64			
	Boreal Juvs.	5	8.30	26	0.40	p=0.689
	vs. Agric. Juvs.	9	7.99			
RTHA	Boreal Adults	4	6.94	15	2.09	p<0.038*
	vs. Boreal Juvs.	6	4.41			
	Agric. Adults	12	8.01	186	0.71	p=0.482
	vs. Agric. Juvs.	23	7.19			
	Boreal Adults	3	6.94	26	0.808	p=0.418
	vs. Agric. Adults	13	8.01			
	Boreal Juvs.	5	4.41	117	3.12	p<0.002*
	vs. Agric. Juvs.	24	7.19			

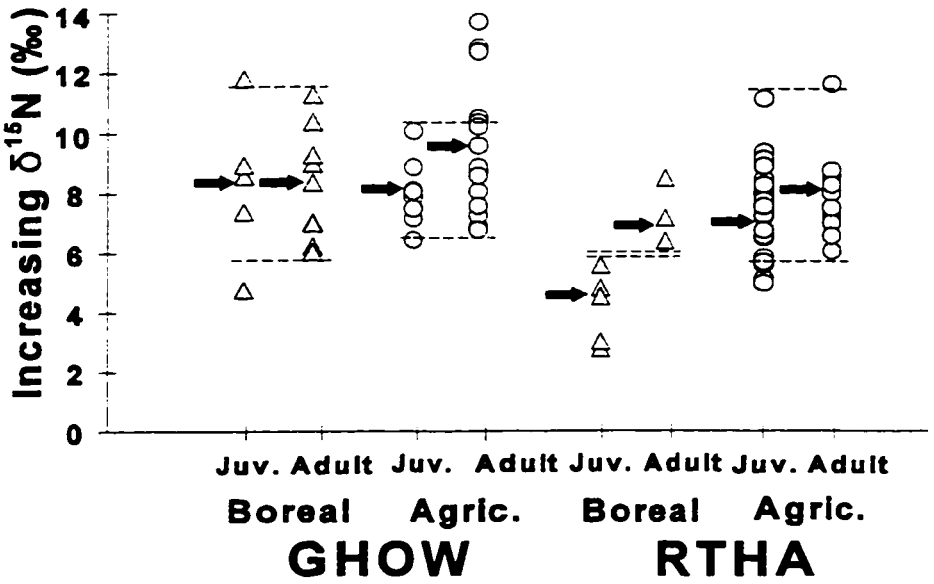


Figure 19. A comparison of different age group $\delta^{15}N$ values within landscape types for Great Horned Owls and Red-tailed Hawks. Arrows indicate means and dotted lines indicate area where values overlap.

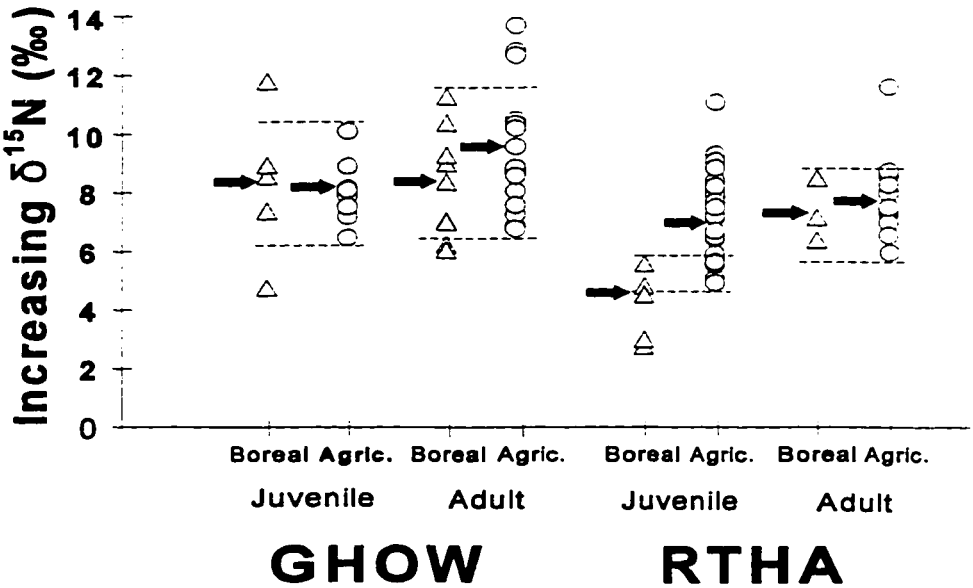


Figure 20. Comparison of different landscape type $\delta^{15}N$ values within age group classes for Great Horned Owls and Red-tailed Hawks.

Table 9. Differences in isotope ratios between siblings within single nests. Differences are given in $\delta^{15}N$ values and in TL index numbers.

Species	Largest Difference Between Sibling δ15N Values (‰)	Difference in Trophic Level Index Values*	Difference in TL Values to Nearest TL=0.5
Northern Goshawk	4.79	1.31	1.5
Cooper's Hawk	4.26	1.15	1.0
Osprey	3.61	0.94	1.0

*Using Formula 2

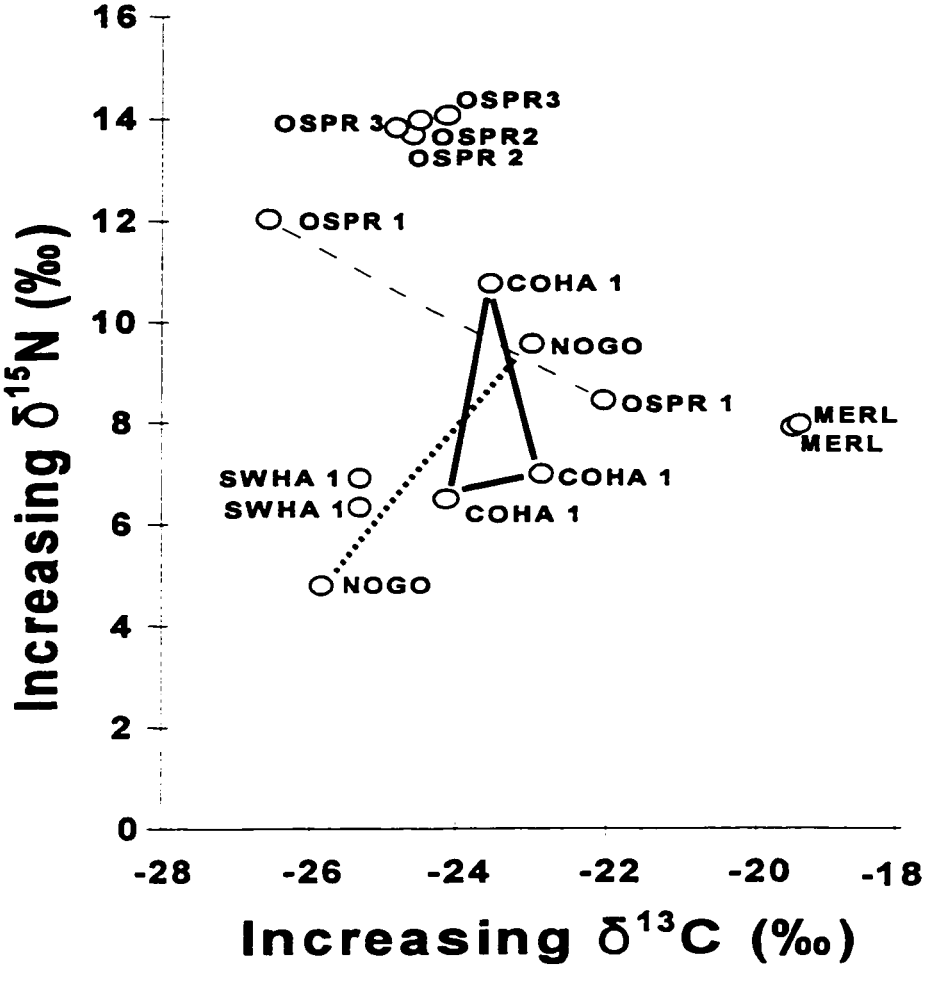


Figure 21. Relationship of $\delta^{15}N$ and $\delta^{13}C$ values for individual nestlings in selected nests. Numbers after name codes represent nest number. Merlin, Swainson's Hawk and Osprey nests 2 and 3 are included to demonstrate nests where nestling isotope values are similar. Osprey nest 1, Cooper's Hawk nest 1 and the Northern Goshawk nest all have one nestling with disimilar isotope values. Lines connect siblings.

Where there was a difference in nitrogen in the three species mentioned above, there was a positive difference in carbon values in the Northern Goshawk samples, no significant change in carbon values in the Cooper's Hawk samples, and a negative difference between carbon values of the Osprey samples.

3.4 Discussion

The increases in the $\delta^{15}N$ values between the captive grown quail and their feed and between the captive Peregrine Falcons and the quail, conforms with the concept of bioaccumulation of heavy nitrogen through a food chain. To understand why there was a very large increase between the quail and falcons, further captive studies focussing on the diet-related causes of fractionation in captive birds are required.

The concept of ^{13}C bioaccumulation through food chains was also supported by the results of analyzing the members of the captive falcon food chain. Therefore, plotting $\delta^{15}N$ and $\delta^{13}C$ values from a single system against each other can lead to conclusions of the relative trophic position of animals within single systems.

Finding clear trophic positions of multiple species of raptors from multiple systems by using both $\delta^{15}N$ and $\delta^{13}C$ data was found to be impossible. Increases in $\delta^{15}N$ did not correlate with increases in $\delta^{13}C$ (Figure 2). Analyzing both elements together in tissues collected from different locations and habitats across Alberta produced no discernible pattern. The main reason is that different systems are tapping into potentially different sources of carbon at the base of the food web systems. Carbon isotope ratios are highly dependent upon 1) the type of photosynthesis used in plants and 2) the source of the carbon being used for building plant tissue (DeNiro and Epstein 1978). Plants using C_3 vs. C_4 photosynthesis will fractionate carbon isotopes at different rates and therefore have different isotope ratios in their respective tissues. C_3 plants use the enzyme ribulose biphosphate carboxylase to fix atmospheric CO_2 and they have $\delta^{13}C$ values that range from -33 ‰ to -22‰ with an average of -27‰. C_4 plants use the enzyme phosphenol pyruvate carboxylase during fixation forming a 4-carbon intermediate compound. The difference in chemical pathways leads to differences in amounts of fractionation producing $\delta^{13}C$ values of -16‰ to -9‰

with an average of -12.5‰ (DeNiro and Epstein 1978). In Alberta there are very few C_4 plants other than the corn crops of the south. Therefore, only raptor feathers collected in regions where corn crops are grown could possibly be affected by differences in the type of photosynthesis at the base of food webs. However, there is the possibility of migrating individuals of some species which could have bred in a region dominated by C_4 plants the previous year, and then bred in an area dominated by C_3 plants the year the feathers were collected. Since the feathers represent the diet of the previous year, the data may not represent the diet in the year the samples were analyzed. Another probable cause for differences in carbon isotope ratios is the source of the carbon being incorporated into tissue by plants. Sources of carbon could be from organic sinks such as decomposing plant litter and animals or inorganic carbon such as dissolved inorganic carbon in water. Phytoplankton utilizing inorganic carbon could have much more negative values than phytoplankton utilizing organic carbon that fell or was leached into the water system (Fry and Sherr 1984). Also, food webs that begin with the consumption of phytoplankton with very negative $\delta^{13}C$ values will produce raptors at the top of the food web with lower values than those in food web systems where the base of the food web is terrestrial, particulate, organic carbon (Fry and Sherr 1984). With such possible heterogeneity at the base of food webs across Alberta, it was not surprising to have the carbon isotope ratios in the raptor tissue samples not correlating with the bioaccumulation of heavy nitrogen with increasing trophic level. Therefore, carbon isotope analysis was not used in most subsequent comparisons.

Stable Isotope Ratios and Trophic Relationships of Wild Raptors

According to Murie (1929), Sutton and Parmelee (1956) and Earhart and Johnson (1970), inland Snowy Owls subsist almost exclusively on rodents. Such a diet would lead to relatively low $\delta^{15}N$ values. At the opposite end of the scale are piscivorous raptors. Since the probability of there being more trophic levels within aquatic systems (Goering *et al.* 1990), raptors such as Bald Eagles and Ospreys which feed at the top of aquatic food webs will have relatively high $\delta^{15}N$ values. These predictions hold true in the stable isotope ratio analysis results since Snowy Owls had by far the least amount of heavy nitrogen, while Bald Eagles and Ospreys had the most in all ecoregions (Figures 3a and b).

Artificial Enrichment

The results plotted in figures 3a and b both agree and disagree with raptor diet studies conducted using traditional methods as discussed in the introduction. It may be true that individuals of a raptor species may have variable $\delta^{15}N$ values due to different prey availability among hunting habitats, but the idea of nitrogen sources differing between locations within an ecosystem cannot be dismissed.

It has recently been discovered that plants utilizing different sources of nitrogen in northern boreal forests can lead to plants within the same ecosystem having different nitrogen isotope ratios. Coexisting plant species under severe nutrient limitation may tap several different sources of nitrogen: NH_4^+ NO_3^- and organic N from the soil, atmospheric N_2 and N in precipitation (Michelsen *et al.* 1996). *Picea* sp. that utilize nutrients from leaf litter or inorganic nitrogen from ammonium in the soil were found to have $\delta^{15}N$ values of around -7.7‰. Shrubs using mycorrhizae produced $\delta^{15}N$ values around -4.3‰, while grass exploiting deeper soil horizons tapped into more positive nitrogen reserves resulting in $\delta^{15}N$ values around +0.9‰ (Schulze *et al.* 1994).

Three species of raptors, Ferruginous Hawks, Prairie Falcons and Burrowing Owls, have higher $\delta^{15}N$ values than what would be predicted form the literature. If Ferruginous Hawks are known to be small mammal specialists (Schmutz and Hungle 1989, Woffinden and Murphy 1989), why do they have similar values to that of Peregrine Falcons whose higher values are probably due to consuming insectivorous or piscivorous birds (Cade 1951, Hunter *et al.* 1988, Dekker 1988)? Like the possible heterogeneity in the boreal sources of nitrogen, the answer may lay in the soil. However, unlike the boreal soil differences, enrichment of heavy nitrogen in the prairie soils may be due to long term use of intense fertilizing regimes on the southern agricultural regions of Alberta (K. Hobson pers. comm.). Plants growing in soil with enriched ^{15}N levels would also be enriched, and would form the base for food webs with enriched $\delta^{15}N$ values in all organisms. Data from Red-tailed Hawks separated into agricultural and boreal sub-samples indicates that enriched isotope ratios are present in the agricultural systems (Figure 6). Relatively high amounts of heavy nitrogen in agricultural areas as compared to boreal regions is also supported by species having higher TL numbers in agricultural areas than in boreal regions (Table 2).

Without a correction formula to account for possible artificial enrichment or to make meaningful comparisons between species, the raptor samples should originate from birds within the same type of landscape (eg. boreal forest, parkland, prairie or arctic), or even better, from within the same ecosystem within an ecoregion. When the $\delta^{15}N$ values of individuals are organized into geographically separate sub-samples, more accurate trophic hierarchies are developed since any variation in $\delta^{15}N$ values due to differences in ecoregion sources of nitrogen are removed. Without Red-tailed Hawk samples from prairie and parkland areas, the hawks relative placement in a boreal trophic level hierarchy is lower (Figures 8a-10b and 12-14). Without seemingly artificially enriched prairie species samples mixed with the boreal samples, Great Horned Owl isotope values place the species at a relatively high trophic level, which agrees with results from traditional methods (Maser and Brodie 1966, Brodie and Maser 1967, Maser *et al.* 1970, Marti 1974, Bosakowski *et al.* 1989, Weir and Hanson 1989, Aigner *et al.* 1994). The main problem with sub-sets is that they include smaller sample sizes and the relative placement of species in hierarchical comparisons can be artificially changed. To study the hiearchical trophic relationships between different raptor species, it is suggested that large sample sizes are collected from all representative species within a region.

Within Species Variation Of Isotope Values

When samples are categorized by ecoregion and the variable amounts of artificial enrichment have been reduced, the bioaccumulation of heavy nitrogen by trophic level is the biological cause of variable $\delta^{15}N$ values. However, to assume that all variation between $\delta^{15}N$ values within a species is probably due to a raptor's preference of prey is unwise. The diet of a raptor is not a simple relationship between a predator and it's prey, but the interaction between a raptor and it's environment.

The simplest cause of variation of individual isotope values within a species is hunting habits of the individual raptors. An individual raptor may be a generalist, consuming most edible items it can hunt or find, or a specialist, catching only specific types of prey. Each prey item also finds itself in a complex relationship with it's own surroundings. There are many possible pathways for isotopes to travel even before being ingested by raptors. Multiple sources of isotopes at the bottom of food webs can exist and raptors can be feeding at the top of multiple food webs. The combinations of pathways are numerous.

When individuals are compared within a species, it is important to remember that there may be a locational effect on the $\delta^{15}N$ values within an ecoregion. When large samples of data points are organized by locations within an ecoregion, the values seem to be affected by the location from which the samples are taken. However, the different locations may not be affecting the values due to different sources of nitrogen, but by forcing the raptors into choosing different prey from different trophic levels. To some extent, prey selection is being made for the individuals due to differing prey availability in different locations. A spread of data points includes individuals which are feeding on a certain type of prey, but may feed on other prey if they were available. A good example of how location can affect isotope values is provided in figure 16. The spread of the original Peregrine Falcon data points suggest a range of potential prey items or many sources of nitrogen at the base of the Peregrine Falcons food webs. When the values are separated by location, the significant difference between values from falcons nesting on cliffs on Lake Athabasca, and those nesting on cliffs on the Peace River can be explained by the potential prey in the area. The lake nesting birds have access to more piscivorous terns and gulls, while the river nesting falcons have greater access to herbivorous duck species (G. Holroyd pers. comm.). Therefore, the prey availability in different locations can cause a spread in isotope data. Analysis of potential prey items within the nesting locations will help determine which prey items are more important to the Peregrine Falcons in those areas.

Another reason not to assume that all variation between $\delta^{15}N$ values within a species is probably caused primarily by a raptors preference of prey may be due to the age of the individuals. While adult birds have had time to develop their hunting skills, immature raptors may have a limited diet selection due to the lack of hunting skills. For example, immature eagles tend to eat relatively more carrion, while adult eagles eat relatively more captured fish (Gerrard and Bortolotti 1988). As the eagles get older and develop their hunting skills, the more they can supplement their diets with live fish. As discussed previously, fish would have relatively higher isotope values than dead mammals (Goering *et al.* 1990). Therefore, with the assumption that most of the carrion the immature eagles are consuming is not fish, it may be possible to use the range of the isotope data as a measure of the relative age of the eagles (Figure 17). If most of the carrion the immature eagles eat is dead fish, then any differences in isotope ratios between adults and immatures would be minimal. This study

would only be applicable to immatures over the age of one. If they are young of the year, their feathers would reflect the diet provided to them by their parents. Increased sample sizes are required to determine if the trend is significant. If a significant relationship is demonstrated, there is the possibility that the age of individual Bald Eagles could be detected with stable isotope ratio analysis.

Shifts in Diet Selection

As in the example with varying age groups in eagles, there is a possibility that a difference exists between the $\delta^{15}N$ values of juveniles and adult raptors. Stable isotope ratio analysis can determine if adult raptors change their prey selection after they are finished feeding their young. For Red-tailed Hawks in central Missouri, hunting efficiency during nesting period is maximized by taking larger prey, but after the nesting period, the average size of the prey was smaller by 50% (Toland 1990). Prey selection by adult Burrowing Owls can become less variable after young have fledged (Longhurst 1942). Prairie Falcon nestling diet in southern Alberta is 95% ground squirrel by biomass. However, after fledgling, many ground squirrels have started to hibernate and Prairie Falcons are often observed hunting shorebirds (G. Holroyd pers. comm.). Such a switch would result in higher $\delta^{15}N$ values in adult feathers. A shift in prey selection is also speculated to be performed by Peregrine Falcons (W. Nelson and G. Holroyd pers. comm.). If the different prey feed at different trophic levels, the shift will be detectable by comparing the $\delta^{15}N$ values in nestling feathers and adult feathers. The nestling feathers are a good representation of what the young were being fed at the nest, since all initial feathers are grown at the nest. If the samples were from adult raptors which grew their feathers soon after the post breeding moult, the isotope values will reflect their post breeding diet. The significant differences between juvenile and adult values for Peregrine Falcons, and the similar trend in Red-tailed Hawk, Cooper's Hawk and Prairie Falcons indicate a possible prey shift (Table 7, Figure 18). A switch from mammals to smaller birds, which can be eaten while flying or are not worth flying back to a centrally placed nest, would be reflected in an increase in mean $\delta^{15}N$ values.

It is possible that differences in metabolic rate between adult and juvenile birds could cause detectable differences between the $\delta^{15}N$ values of the two groups. Growing juvenile birds, especially in the first four weeks, have a higher basal metabolic rate than full grown adult birds (Freeman 1983, Whittow 1986). However, during the moulting period, domestic fowl (*Gallus domesticus*) were

found to have basal metabolic rate increases of 45% (Whittow 1986). In fact, an adult fowl's basal metabolic rate was at it's peak during the regrowth of primary flight feathers. If the same changes occur in the metabolic rates of raptors, the increase in the adult metabolic rates during feather growth could be similar to the high rates of juveniles. Therefore, the differences found between adult and juvenile $\delta^{15}N$ values are more likely to be due differences in diet than differences in metabolic rates. The question of how much different metabolic rates change isotope ratios will require more investigation beginning with the determination of metabolic rate differences between adults and juvenile raptors.

It is important to note that the results for this section are based on the assumption that the breeding adults have returned from the previous year to the same nest, and that they feed their young the same prey types year after year. The adult feathers represent the diet from the previous year when the feathers were grown after the breeding season. Although such a collection may be unrealistic, to determine if the trend detected in 4 of 11 species analyzed in this study is authentic, feathers should be collected from young one year and then from those young's parents the subsequent year.

Age Class Comparisons Across Landscape Types

In an attempt to determine whether age classes or landscape type are more responsible for causing variability in isotope data, few significant differences were detected. Location differences were significant only between juvenile Red-tailed Hawk isotope values. Differences attributed to age class were also significant in Red-tailed Hawks, but only in the boreal forest.

Even though stable isotope analysis indicates a trend where birds growing feathers in agricultural areas have relatively enriched isotope values, a statistically significant relationship has not been detected in any species other than Red-tailed Hawks. A simple solution may be larger sample sizes. Another problem may be the mobility of adult raptors. An attempt to discover stable isotope variation due to differences in landscape types may be futile. The location of where the feathers were grown the previous year may be different in the subsequent year. Feathers grown in the prairies one year but collected in the boreal forest the next would lead to misinterpretation of the isotope values.

Raptor Species And Their Diets
as Determined By Stable Isotope Ratio Analysis

Stable isotope $\delta^{15}N$ values should not be compared across ecoregion types. However, the interpretation of $\delta^{15}N$ values can be used to examine the diets of individual raptor species within ecoregions.

Owls

It is generally agreed that small mammals play an important role in the diet of many owl species (Earhart and Johnson 1970, Maser *et al.* 1970, Marti 1974, Roth and Powers 1979, Marks and Marks 1981, Hayward and Garton 1988). The similar means of the $\delta^{15}N$ values across most owl species indicates that from a trophic level point of view, the diets of most species of owls are similar and located in relatively low trophic levels (Figures 8a and 11b). However, every species of owl found in Alberta have been observed to occasionally prey upon birds, amphibians and/or invertebrates in studies conducted outside of Alberta (Cahn and Kemp 1930, Graber 1962, Earhart and Johnson 1970, Thomsen 1971, Glue 1972, Korpimäki 1972, Huges 1982, Hayward and Garton 1988). Data points above and below the means for each species would indicate that prey selection is not limited to a single trophic level. If all owls ate small herbivorous rodents, then the variability of values within a species would be limited and low. Figures 8b, 9b and 10b indicate that every species contain individuals with different feeding preferences.

Amongst owl species growing their feathers in the prairie ecoregion, Great Horned, Short-eared and Burrowing Owls all had higher than average trophic index numbers compared all other raptors sampled except Bald Eagles (Figure 12). Even though a comparison of TL numbers across ecosystems should not be considered, their relative trophic placement amongst the other raptor species within an ecoregion can be contrasted across ecoregions. The owl species in the boreal forest and parkland regions were interspersed with other raptors, but generally found lower than most other raptor species. Either prairie owls are feeding at trophic levels relatively higher than owls in other regions, or the other species of prairie raptors are feeding in relatively low trophic levels.

Great Horned Owls will prey upon a wide variety of prey. They tend to select prey such as rabbits, voles, mice, shrews, waterfowl, gallinaceous birds, shorebirds, passerines, amphibians, reptiles, fish, invertebrates and even other

raptors (Maser and Brodie 1966, Brodie and Maser 1967, Maser *et al.* 1970, Marti 1974, Bosakowski *et al.* 1989, Weir and Hanson 1989, Aigner *et al.* 1994). A large standard deviation in the $\delta^{15}N$ values of Great Horned Owls would indicate a specialization of certain diet items. Those Great Horned Owls which had values far below average could be concentrating on herbivorous mammals and birds, while those which had values far higher than the average would be selecting prey such as insectivorous birds, amphibians, reptiles, fish or some type of piscivorous prey. If all of the Great Horned Owls had highly variable diets, all of their $\delta^{15}N$ values would be similar due to the averaging effect of isotope assimilation. However, the samples from the parkland region had a standard deviation that was one half the standard deviation of the samples from the prairies. The small standard deviation of the Great Horned Owls of the parkland region may be due to the fact that the majority of the owls might have been eating prey items with variable isotope values. The other explanation is that the majority of the owls were concentrating on prey all having mid-ranged isotope values (Tables 3 and 4, Figures 8a and 9a). The geographical differences that influenced the isotope data would not have been apparent had the samples not been separated into ecoregions.

Burrowing Owls are known to eat birds, insects or other invertebrates, while other members of the species concentrate only on herbivorous mammals (Neft 1941, Glover 1953, Coulombe 1971, Thomsen 1971, Marti 1974, John and Romanow 1993). Although they have an average standard deviation amongst prairie raptors, Burrowing Owls had one of the largest range of $\delta^{15}N$ values, indicating a relatively mixed diet for most individuals while a few were concentrated on more specific prey (Table 3, Figure 8b). Some of the Burrowing Owls focussed on prey comparable to all other prairie raptors with low $\delta^{15}N$ values and were probably eating herbivores. Other Burrowing Owls consumed prey from higher trophic level such as birds and insects.

Although most Short-eared Owls feed primarily on small mammals (Earhart and Johnson 1970, Maser *et al.* 1971, Hughes 1982), they have been documented to consume high percentages of birds (Munro 1929, Fisler 1960, Glue 1972, Taylor 1984). As compared to other prairie raptors, the relatively enriched Short-eared Owl samples from the prairie region probably indicate they were feeding on birds (Table 3, Figure 8b). The $\delta^{15}N$ values of Short-eared Owls from boreal and

parkland areas were closer to the average of all other raptors from those regions (Tables 4 and 5, Figures 9b and 10b).

The relatively small variability in $\delta^{15}N$ values from Barred Owls and Northern Hawk-Owls, suggest their prey selections are relatively less variable (Table 5, Figures 10a and b), and they have had fewer individuals concentrating on prey from extreme trophic levels.

Snowy Owls are known lemming specialists. When lemmings are abundant, Snowy Owls will feed on little else (Murie 1929, Sutton and Parmelee 1956 and Earhart and Johnson 1970). The low $\delta^{15}N$ values of the Snowy Owl samples indicate that they were eating low trophic level feeding prey. However, they do have a standard deviation close to that of Peregrine Falcons and Merlins in the boreal forest. The consumption of high levels of bird prey by the Snowy Owl has been documented (Murie 1929, Gross 1944). In the absence of high numbers of lemmings, Snowy Owls are known to switch to a diet of seabirds (Williams and Frank 1979). This does not appear to be the case of the owls sampled for this study, as a seabird diet would lead to Snowy Owl feathers having relatively enriched $\delta^{15}N$ values as those of piscivorous raptors (Hobson 1992, 1993). The standard deviation of the Snowy Owl is the same as that of the Rough-legged Hawks, another arctic breeding raptor that also specializes on lemmings (Reid *et al.* 1997a and b)(Table 6, Figure 11a). These raptors may have similarly variable diets.

The relative placement of the Great Gray Owl's mean $\delta^{15}N$ value above Short-eared and Long-eared Owls, and the variability of the values around the mean (Figures 10a and b), indicate that the diet of this species may not be as simple as the literature would predict. Great Gray Owl diets have been shown to usually consist of little more than small mammals (Earhart and Johnson 1970, Bull *et al.* 1989, Bull and Duncan 1993). While most Short-eared and Long-eared Owls prey on small mammals (Earhart and Johnson 1970, Maser *et al.* 1971, Marks and Yensen 1980, Hughes 1982, Hooper and Nyhof 1986), they can both have a large bird component to their diets (Munro 1929, Fisler 1960, Glue 1972, Fitzner and Fitzner 1975, Taylor 1984, Sudmann 1994). However, half of the Great Gray Owl $\delta^{15}N$ values are higher than those of Short-eared and Long-eared Owls sampled from boreal regions (Figure 10b). Great Gray Owls do eat shrews (Earhart and Johnson 1970, Bull and Duncan 1993). One explanation for the

very high isotope values for some of the owls could be that they are shrew specialists, since the insectivorous shrews would have high $\delta^{15}N$ values. Northern Saw-whet Owl diets are known to have relatively high component of shrews in early succession forests (Dinsmore and Clark 1991) and since a great many of their $\delta^{15}N$ values are similar to those of Great Gray Owls, it may be possible to predict which owls are feeding in either early or late successional forests. Before such conclusions can be made, many more shrew abundance studies would have to be conducted to ensure that the isotope value interpretations are valid. If the relatively high values for the Great Gray Owls in Alberta are due to trophic level effects, a more careful study utilizing more traditional methods may be required.

The $\delta^{15}N$ value distribution for the Barred Owl presents an example of how more customary methods of studying raptor diet selection can work in conjunction with stable isotope ratio analysis. Traditional methods document some Barred Owls preying upon amphibians (Cahn and Kemp 1930, Earhart and Johnson 1970). In fact, one of the two individuals having the highest $\delta^{15}N$ values was known to consume frogs early in the breeding season (Takats 1998). The high owl $\delta^{15}N$ values are probably due to the frogs which would have had high values themselves because they are known insectivores and feed in aquatic food chains. Even though frog remains were not found later in the season near this owl nest, the high isotope ratio suggests that amphibians could have been an important part of the diet during the period of moult as well. The sample for the second Barred Owl with the high $\delta^{15}N$ values in figure 10b, came from a museum specimen which had been dead for over 60 years. To study the dietary habits of this owl using traditional methods is obviously impossible now, but using stable isotope ratio analysis it is possible to state that the second owl was eating at a similarly high trophic level.

Buteo Hawks

Traditional diet study methods indicate that Red-tailed Hawks can have almost as varied a diet as Great Horned Owls. Though a majority of prey is made up of small mammals, Red-tailed Hawks have been known to catch gallinaceous birds, ducks, egrets, passerines, reptiles and also other raptors (Peyton 1945, Seidensticker 1970, Courser and Dinsmore 1971, Dunn and Tessaglia 1994). Even though it was documented in the winter (Stalmaster 1980), the fact that they have been observed feeding on dead fish could mean it was capitalizing on

them during other seasons. The variability in $\delta^{15}N$ values indicates that there are some Red-tailed Hawks specializing on low trophic level feeding prey, and others that are eating almost exclusively heavy nitrogen enriched prey. The Red-tailed Hawks of the boreal forest were feeding at the lowest trophic level relative to the other boreal raptors. This placement indicates a diet made up of mostly herbivorous prey. Red-tailed Hawks of the prairie and parkland seem to include more prey from higher trophic levels, relative to the other raptor species in those regions.

Swainson's Hawks chose from a continuum of dietary items ranging from small mammals to birds to insects (Munro 1929, Schmutz and Hungle 1989). Many Swainson's Hawks are specialists at either end of the continuum as indicated by the isotope data with many $\delta^{15}N$ signatures with both relatively high and low values. The high placement of the Swainson's Hawk's in the prairie ecoregion above many other species seems high for a bird feeding on only herbivorous prey (Figure12). This would indicate that the hawks are including more higher trophic level feeding prey than the Ferruginous, Red-tailed and Broad-winged Hawks (Figure 8a and b).

Mendall (1944), Rusch and Doerr (1972), Rosenfield and Gratson (1981) and Dunn and Tessaglia (1994) indicate that the diet of the Broad-winged Hawk has the potential to be more variable than the Red-tailed and Swainson's Hawks. Broad-winged Hawks are known to eat large numbers of birds, amphibians and invertebrates, as well as, small mammals. The unpredicted low isotope ratios suggests that most of the Broad-winged Hawks sampled for this study concentrated on eating prey from relatively low trophic levels, as the Broad-winged Hawks had the lowest mean of all parkland raptors and the second lowest mean of all boreal raptors (Tables 4 and 5, Figures 9a-10b). The most positive data point for both species in the parkland region indicate individuals which are focussing on prey from higher trophic levels which could be insectivorous birds, amphibians or invertebrates (Figure 10b).

Most of the relatively low values for the Rough-legged Hawks are probably due to the hawks concentrating on lemmings (Reid *et al.* 1997a and b)(Figure 11b). However, if both Rough-legged Hawks and Snowy Owls are lemming specialists, what explains the relatively high variability in their Rough-legged Hawk values? It may be possible that the isotope analysis has detected a more variable diet

than just lemmings. The variability within this species could be due to the inclusion of high number of shrews (Munro 1929). Rough-legged Hawks, like the other buteos would be capable of catching some birds to supplement their diets. Little work has documented the summer diet of this species, and continued research using traditional methods may detect a more varied diet than currently known.

The rise and fall of Ferruginous Hawk populations with the rise and fall of prairie dog, ground squirrel and rabbit populations indicates that this hawk has a narrow dietary selection (Schmutz and Hungle 1989, Woffinden and Murphy 1989). The placement of this species indicates that the hawks sampled for isotope analysis ate comparatively similar diets, probably herbivorous mammals, as the Prairie Falcons and Swainson's Hawks (Figure12). The $\delta^{15}N$ values of the Ferruginous Hawk that were higher than its mean may indicate individuals which capture relatively more passerines, shorebirds and snakes as these prey items have been documented at some nests (Fitzner *et al.* 1977)(Figure 8b).

Falcons

As a family group, the falcons had the most variable $\delta^{15}N$ values (Figures 8a-10b). Surprisingly, the Peregrine Falcons' values were the least variable of the four falcon species. Most peregrines across North America prey on a wide variety of birds from waterfowl, gulls, shorebirds, woodpeckers and passerines (Cade 1951, Hunter *et al.* 1988, Dekker 1988). While birds are the most important prey, Peregrine Falcons have been known to take rodents (Court *et al.* 1988, Bradley and Oliphant 1989), lagomorphs (Henny and Nelson 1981, Mindell 1983), muskrats *(Ondatra zibethicus)* (Johnson-Beaver 1979), ground squirrels (Court *et al.* 1988), bats (US Fish and Wildlife Service 1987), dragonflies (Dekker 1980, J.M.D. pers. obs) and even fish (Ratcliff 1980). Therefore, if the potentially highly variable diets of Peregrine Falcons produce the least variable isotope values, then individual Peregrine Falcons are probably eating varied diets resulting in similar $\delta^{15}N$ values between individuals (Figures 10a and b).

In the literature where traditional methods have been used, there are few mentions of Merlins eating mammalian prey. The results of customary diet study methods indicate that Merlins are bird hunting specialists (Beebe 1974, Hodson 1978, Sohdi 1992). If this is the case, the highly variable isotope values of prairie and parkland Merlins must come from bird prey from different trophic

levels (Figures 8a and 9a). Granivorous birds would provide low basal ratio values while insectivorous birds would provide high basal ratios.

While the smallest falcon in Alberta, the American Kestrel, eats prey ranging from insects, reptiles, birds and small mammals (Mendall 1944, Collopy 1977, Craig and Trost 1979, Elliot and Cowan 1983), the relatively high values within both the prairie and parkland ecoregions could be caused by a strict diet of predatory dragonflies (Figures 9b and 10b). If the dragonflies are feeding on insects that are in turn feeding on other animals, the bioaccumulation through the insect food chain would enrich the kestrel isotope values. The lowest kestrel isotope values could be caused by diets subsisting wholly on herbivorous grasshoppers. However, many of the relatively high isotope values within ecoregions could be due to the consumption of insectivorous birds, while the low kestrel isotope values could be due to herbivorous mammals.

Ground squirrels can almost make up the entire diet of Prairie Falcons (Holthuijzen 1990, Hunt 1993). Although, like other raptors, the falcons will take advantage of abundant bird prey if the numbers of their regular prey items are reduced (Steenhof and Kochert 1988). It is possible that the wide range of $\delta^{15}N$ values comes from some falcons that had started to hunt shorebirds because ground squirrels had begun to hibernate (G.Holroyd pers. comm.)(Figure 8b). If the falcons in southern Alberta were only taking ground squirrels, the range of isotope values would be very small and the overall mean would be relatively low as compared to the other falcons. The wide range of isotope values found in the Prairie Falcon samples indicates that many falcons were consuming prey other than ground squirrels. The placement of Prairie Falcons above Merlins and Sharp-shinned Hawks, birds known to prey on birds, is another indication that the Prairie Falcons were eating prey eating at a trophic level which would include birds. (Figure 12)

Accipiters

Of the forest hawks, the Northern Goshawk's size allows it to capture medium sized mammals such as hares, and birds such as and grouse (Mannan and Boal 1990, Bosakowski *et al.* 1992). These prey items have the potential to make up the majority of the prey biomass assimilated into the hawks' tissues, leading to relatively low $\delta^{15}N$ values. The Northern Goshawk is also capable of taking many other species of birds, such as insectivorous woodpeckers (Schnell 1958,

Kennedy 1991, Reynolds *et al.* 1992), which would produce relatively high $\delta^{15}N$ values. Thus the potential range of values for Northern Goshawks would be predicted to be wide. The standard deviation of isotope values of the Goshawks sampled indicate that many have a balanced diet of high and low trophic level feeding prey (Table 5, Figure 10a). However, the distribution of a few data points, indicates that a few individuals specialize on high trophic level feeding prey such as woodpeckers and some focus on low trophic level feeding prey such as hares or grouse (Figures 10b).

Most diet studies using traditional methods have concluded that both Sharp-shinned and Cooper's Hawks are bird specialists (Mendall 1944, Reynolds and Meslow 1984, Bosakowski *et al.* 1992). However, recent studies and the isotope values resulting from the analysis in this study indicate otherwise. Quinn (1991) and Bielefeldt *et al.* (1992) both discuss how direct observations of both species can lead to new conclusions about the relative importance of mammalian prey to their diets. Most previous studies were conducted using prey and/or pellet analysis alone leading to results biased towards avian prey. While some direct observation of prey deliveries still document deliveries of mostly avian prey (Kennedy and Wilson 1986), other researchers have found mammalian prey making up 58% of the prey delivered (Quinn 1991, Bielefeldt 1992). Sharp-shinned Hawks have one of the lowest $\delta^{15}N$ value means in the prairie, parkland and boreal samples (Tables 3-5, Figures 8a-10b, and 12-14). The Cooper's Hawk mean is also lower than 10 other raptor species in the parkland region (Table 4, Figures 9a and b). The Cooper's Hawk $\delta^{15}N$ value mean placed it in the same TL index as Long-eared and Short-eared Owls in the parkland ecoregion. The relatively low $\delta^{15}N$ values of the two smaller accipiters indicate the possible great importance of low trophic level feeding prey such as small mammals. The higher than average values are probably due to individuals specializing on avian prey, while those having values near the respective means could be preying on a mixture of mammals and birds, or a diet concentrating on prey with mid-ranged isotope values.

Eagles, Ospreys and Northern Harriers

Similar to falcons, the Northern Harrier can have a highly variable diet, preying upon birds, reptiles, amphibians, mammals and invertebrates (Mendall 1944, Phelan and Robertson 1978, Dunn and Tessaglia 1994). One would predict that those values above the mean $\delta^{15}N$ value would be caused by such prey as

shorebirds or amphibians, and those below average would be due to the consumption of small mammals. The relatively large standard deviation of the Northern Harrier samples indicates that there are many individuals that specialize on certain prey types (Figure 9a). If most of the individuals were generalists, the standard deviation would be smaller since most of the harriers would have similar $\delta^{15}N$ values due to the averaging effects associated with assimilation of the isotopes from prey.

Large herbivorous mammalian prey would be the main reason for the relatively low values for Golden Eagles. Whether the eagles are killing rabbits, marmots and/or ground squirrels, or feeding on deer (Knight and Erickson 1978, Collopy 1983, Marr and Knight 1983, Steenhof and Kochert 1988), the resulting values will be relatively lower than if they were feeding on birds or fish. The mean of the prairie Golden Eagles indicates they are feeding at a low trophic level, but the $\delta^{15}N$ values of boreal Golden Eagles indicate that they must be taking some prey from higher trophic levels (Figure 10b). There are reports where Golden Eagles have attacked other birds such as ducks, Black-billed Magpies (*Pica pica*), Northern Flickers (*Colaptes auratus*) Great Blue Herons (*Ardea herodias*), Short-eared Owls, American Kestrels, and Peregrine Falcons (Kelleher and O'Malia 1971, Marr and Knight 1983, Mayers and Tomlinson 1988). The observation of a Golden Eagle attacking a Whooping Crane (*Grus americana*), may indicate a tendency to attack the more common Sandhill Crane *(Grus canadensis*) (Windingstad *et al.* 1981). The relatively low mean isotope value for the Golden Eagle as compared to that of the Bald Eagle, demonstrate the difference between diets from terrestrial food webs, as opposed to an aquatic food web.

Aquatic food webs are far more diverse than terrestrial systems in the number of trophic interactions (Goering 1990). The higher the number of trophic levels, the higher degree of bioaccumulation of heavy nitrogen. Thus, piscivorous raptors have the highest $\delta^{15}N$ values (Tables 3-5, Figures 8b, 9b and 10b). No other species in this study had values over 11‰. Customary methods of studying diet have led to the conclusion that Osprey subsist almost entirely on fish (Ogden 1977, Gerrard and Bortolotti 1988). On rare occasions they will substitute fish in their diets with rodents, birds, small invertebrates and crustaceans, especially if the fish populations are low (Ogden 1977, Mills 1977). Ospreys had the highest isotope values of all raptors, which reflects an aquatic diet. The individual Bald Eagles with $\delta^{15}N$ values higher than any of the individual Ospreys, may be due to

the larger size of Bald Eagles which allows them to catch larger fish than Ospreys (Fielder 1982, Peterson 1986, Gerrard and Bortolotti 1988). The larger the fish, the higher the trophic level that particular fish can feed at. The higher the trophic level, the more bioaccumulation of heavy nitrogen which leads to relatively higher values in the Bald Eagles. Higher values in the Bald Eagle may also be derived from eating other piscivorous birds such as loons, grebes, herons, cormorants and piscivorous ducks (Brooks 1922, Hobson *et al.* 1989, Norman *et al.* 1989). However, the $\delta^{15}N$ values from Bald Eagles that are higher than the Osprey values are from samples collected in the prairie region. Therefore, there may be some artificial enrichment of $\delta^{15}N$ values from the prairie ecoregion.

The probable cause for the mean for Bald Eagles being lower than the Ospreys', is that carrion, herbivorous birds such as waterfowl and gallinaceous birds, and small and medium sized mammals also play an important role in the diet of Bald Eagles (Fielder 1982, Marr *et al.* 1995). Since immature eagles tend to eat relatively more carrion and adult eagles eat relatively more captured fish (Gerrard and Bortolotti 1988), it may be possible to use the range of the isotope data as a measure of the relative age of the eagles (Figure 17). Other raptors had values that were the same as some of the Osprey and Bald Eagle, but this does not mean that they catch fish, although it is possible that the other raptors may be eating dead fish or prey which are piscivorous themselves. Some fish may also be at the top of relatively short food chains, thus giving Bald Eagles and Osprey similar values as those raptors consuming terrestrial prey.

Within Nest Variations

Samples from more than one nestling within nests allowed for the comparison of sibling $\delta^{15}N$ values. One would assume that all nestlings in a nest would be fed the same prey items. If this was the case, there should have been no significant differences between sibling values (Table 9, Figure 21). Two possible explanations for nestlings having different isotope values are 1) they were fed different prey items and 2) those nestlings with higher values were unhealthy.

It is possible that the parent birds could deliver prey which some members of the family group dislike to the point of not eating those items. Although, it is hard to imagine a group of nestlings with finicky diet preferences. The main objective for a nestling is to survive, and it's instincts would have it eat anything edible that

the parent birds bring back to the nest. If however, there is a wide choice of prey items brought to the nest, many prey items may be plentiful for all of the siblings but the more dominant sibling(s) may be able to hoard some isotopically different prey items or vice versa. The unique food being eaten by only one or two of the nestlings could change those nestlings' averaged isotope values.

Another explanation for different isotope values among siblings could be that one or more of the siblings are starving. Healthy, well fed nestlings would be deriving their isotopes from the food they are ingesting. While underfed nestlings would have some of their tissues isotope values derived from their food, they could also be "eating themselves". If a starving nestling is relying heavily on reserves and starts to break down it's own tissues to fuel metabolism, from a bioaccumulation point of view, this is no different than eating food. The final isotope values for starving nestlings could be higher than their siblings because they may have bioaccumulated more heavy nitrogen on top of the amounts derived from the food supplied to all of the nestlings. Differing metabolic rates due to differing growth rates between dominant siblings and the starving siblings may also be a cause of different isotope ratios values.

The analysis of both nitrogen and carbon to answer within-nest questions is acceptable since base levels of both carbon and nitrogen would be the same for all nestlings. The relationship between increases in heavy carbon and increases in heavy nitrogen offers a way to determine if the differences between siblings is probably due to starvation or the consumption of different prey items (Figure 21). As discussed previously, bioaccumulation of heavy nitrogen can be around 3-5‰ per trophic level and around 1-2‰ per trophic level for heavy carbon. An increase in both $\delta^{15}N$ and $\delta^{13}C$ values is shown by a shift up and to the right when they are plotted against each other. Such a shift means that bioaccumulation is occurring in both elements, such as in the case of the Northern Goshawks, and may indicate a sibling that is not getting it's share of the food being delivered to the nest.

Two of the Cooper's Hawk nestlings had similar nitrogen and carbon isotope values, while one other sibling had an increased nitrogen value but a carbon value close to the value of the other siblings. The carbon ratios should be relatively consistent in all samples since they came from food webs in central Alberta where all of the native plants in this area of the province are C_3 plants.

The large difference in the nitrogen values and no significant difference in the carbon values, indicate a possible difference in prey types. One dominant sibling may be hoarding a specific type of prey that originates from a higher trophic level than the prey that is available for the smaller siblings.

The relationship between Osprey nitrogen and carbon isotope values showed that one individual had an increase in nitrogen but a decrease in carbon. It is probable that such a large decrease in carbon is an error due to the same reasons regarding C_3 plants in central Alberta stated above. Therefore, no conclusion of whether or not the sibling is starving or consuming different prey can be made.

Within nest analysis of stable isotope could potentially be used to determine if nestlings are undernourished. By sampling the feathers from all nestlings within a nest, the general health of the chicks might be determined without using direct observations.

3.5 Conclusion

As with the more traditional methods, there are limitations with the technique of stable isotope analysis. Unlike the more customary diet study methods, isotopes can only indicate the trophic level at which prey are feeding, and not the species. Also, this technique requires expensive machinery which exist in low numbers at present.

The objective of this study was to demonstrate how stable isotope ratio analysis, used in conjunction with more traditional diet study techniques can produce conclusions which are potentially more accurate due to the reduction of biases associated with the customary methods. This relatively new tool will never replace pellet and/or prey remains analysis, or direct observations as they will always be techniques required to help interpret or confirm isotope results. While many traditional dietary studies have been conducted on some raptor species, many species lack dietary information due to remoteness of study areas, small sample sizes or rarity of the species. The usefulness of stable isotope analysis, is that it can detect interesting aspects of raptor diets which were either undetectable with traditional methods, or where those aspects are over looked

due to limited time or money. Therefore, if stable isotope analysis leads to conclusions that seem unexpected in understudied ecological aspects in Alberta, more work using traditional methods may be required to prove or disprove the conclusions made from the isotope analysis.

The isotope values for Broad-winged Hawks from Alberta indicate that this species is consistently consuming prey at a low trophic level. Now that isotope analysis may have produced results that are unexpected, there is a need to conduct field work to determine why the Broad-winged Hawk values are so low. Similarly, traditional methods should now be conducted to determine why Great Gray Owl isotope values from the boreal forest of Alberta were relatively higher than what the literature predicts.

The ranges and standard deviations of stable isotope values vary with each species. A large range of $\delta^{15}N$ values is an indication that some individuals are specialists on prey from either high or low trophic levels. The larger the standard deviation for a species the more individual specialists there are in a given species. To determine whether individual raptors of a species are specialists or generalists using traditional methods would take multiple years and a large budget. Analyzing feathers collected during one year would provide an indication of relative frequency of specialized prey selections.

As with the separation of the Peregrine Falcon samples into different locations within an ecoregion, the analysis of samples organized into populations can be the first step in the determination of the prey selection in different locations. After detecting differences in prey use, traditional methods can be used to determine if there are differences in the prey availability between locations. Analysis can then determine whether the raptors are specializing on limited prey items or if they are opportunists, taking advantage of abundant prey items in their area.

Stable isotope ratio analysis could play an important role in the determination of whether or not prey selection shifts occur after the rearing of the young is completed. While stable isotope analysis can indicate a possible shift, traditional diet study methods would be required to determine the possible prey items that could be consumed before and after a diet switch. Such studies using traditional

methods alone would take relatively more years of pellet and/or prey analysis or direct observations.

Sample sizes should be increased to confirm the possibility of an age dependent trend in isotope enrichment as in the example of the Bald Eagle age classes. If a significant trend can be established with larger sample sizes, stable isotopes can be used as a forensic tool. There is potential for stable isotope ratio analysis to be used to gauge the ages of eagle remains which have no reliable field marks to assist in aging the eagles.

The initial results of studying multiple raptor species from multiple geographical regions seem to generate more questions than answer ones already posed. In fact, the only time gross sampling, such as in this study, may be useful is when it is used to answer ecological questions at the landscape scale. This technique, used to study raptors from multiple ecosystems, can determine whether or not raptors are part of food webs that are based in marine, fresh water or terrestrial systems. To conclusively answer raptor diet questions, the questions must be narrowed and studies should analyze predators *and* their prey within a single landscape and preferably within a single ecosystem. A drawback of this technique is sample sizes being limited by the cost of analysis and obtaining enough feathers from rarer species. Trying to answer more specific questions using the analysis of isotopes will require sample collection efforts to be predetermined based on the number of species in a system and the size of sample analysis budgets.

3.6 Literature Cited

Aigner, P.A., M.L. Morrison, L.S. Hall and W.M. Block. 1994. Great horned owl food habits at Mono Lake, California. Southwest Naturalist 39:286-288.

Alisauskas, R.T. and K.A. Hobson. 1993. Determination of lesser snow goose diets and winter distribution using stable isotope analysis. Journal of Wildlife Management 57:49-54.

Balgooyen, T.G. 1971. Pellet regurgitation by captive sparrow hawks (Falco sparvarius). Condor 73: 382-385.

Beebe. F.L. 1974. Field studies of the Falconiformes of British Columbia. Occasional Papers of the British Columbia Provincial Museum, No. 17.

Bielefeldt, J., R.N. Rosenfield and J.H. Papp. 1992. Unfounded assumptions about diet of the Cooper's Hawk. Condor 94:427-436.

Bombin, M. and Muehlenbachs, K. 1985. $^{13}C/^{12}C$ ratios of Pleistocene mummified remains from Beringia. Quaternary Research 23: 123-129.

Bond, R.M. 1936. Eating habits of falcons with special reference to pellet analysis. Condor 38:72-76.

Bosakowski, T., D.G. Smith and R. Speiser. 1992. Niche overlap of two sympatric-nesting hawks Accipiter spp. In the New Jersey - New York highlands. Ecography 15:358-372.

Bosakowski, T., R. Speiser and D.G. Smith. 1989. Nesting ecology of forest-dwelling great horned owls, Bubo virginianus, in the eastern deciduous forest biome. Canadian Field-Naturalist 103:65-69.

Bradley, M. and L.W. Oliphant. 1991. The diet of peregrine falcons in Rankin Inlet, Northwest Territories: an unusally high proportion of mammalian prey. Condor 93:193-197.

Bradstreet, M.S.W. 1980. Thick-billed Murres and Black Guillemots in the Barrow Straight area, N.W.T. during spring: diets and food availability along ice edges. Canadian Journal of Zoology 58:2130-2140.

Brodie, E.D. Jr. and C. Maser. 1967. Analysis of great horned owl pellets from Deschutes County, Oregon. Murrelet 48:11-12.

Brooks, A. 1929a. Pellets of hawks and owls are misleading. Canadian Field Naturalist 43:160-161.

Brooks, A. 1929b. On pellets of hawks and owls. Condor 31:222-223.

Brooks, A. 1922. Notes on the abundance and habits of the Bald Eagle in British Columbia. Auk 39:556-559.

Brown, K.M. and P.J. Ewins. 1996. Technique-dependent biases in determination of diet composition: an example with Ring-billed Gulls. Condor 98:34-41.

Bull, E.L. and J.R. Duncan. 1993. Great gray owl (Strix nebulosa) *in* Birds of North America, No. 42, *Edited by* A. Poole and F.Gill. Philadelphia: The Academy of Natural Sciences, Washington D.C.The American Ornithologists' Union.

Bull, E.L., M.G. Henjum and R.S. Rohweder. 1989. Diet and optimal foraging of Great Gray Owls. Journal of Wildlife Management 53:47-50.

Cade, T.J. 1951. Food of the peregrine falcon, *Falco peregrinus*, in interior Alaska. Auk 68: 373.

Cahn, A.R. and J.T. Kemp. 1930. On the food of certain owls in east-central Illinois. Auk 47: 323-328.

Collopy, M.W. 1983. A comparison of direct observation and collections of prey remains in determining the diet of golden eagles. Journal of Wildlife Management 47:360-368.

Collopy, M.W. 1977. Food caching by female American Kestrels in winter. Condor 79:63-68.

Coulombe, H.N. 1971. Behavior and population ecology of the Burrowing Owls (Speotyto cunicularia) in the Imperial Valley of California. Condor 73:162-176.

Courser, W.D. and J.J. Dinsmore. 1971. Red-tailed Hawk preys on Cattle Egret. Auk 88:669-670.

Court, G.S., G. Cormack and D.A. Boag. 1988. Natural history of the Peregrine Falcon in the Keewatin District of the Northwest Territories. Arctic 41:17-30.

Craig, T.H. and C.H. Trost. 1979. The biology and nesting density of breeding American Kestrels and Long-eared Owls on the Big Lost River, Southeastern Idaho. Wilson Bulletin 91:50-61.

Craighead, J.J. and F.C. Craighead, Jr. 1956. Hawks, Owls and Wildlife. Stackpole Co., Harrisburg, Pennsylvania.

Dekker, D. 1980. Hunting success rates, foraging habits, and prey selection of peregrine falcons migrating through central Alberta. Canadian Field-Naturalist 94:371-382.

Dekker, D. 1988. Peregrine falcon and merlin predation on small shorebirds and passerines in Alberta. Canadian Journal of Zoology 66: 925-928.

DeNiro, M.J. 1987. Stable Isotopy and Archaeology. American Scientist 75:182-191.

DeNiro, M.J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica Cosmochimica Acta 42:495-506.

Dinsmore, S.J. and W.R. Clark. 1991. Food habits of the Northern Saw-whet Owl in central Iowa: effects of roost location. Journal of the Iowa Academy of Science 98:167-169.

Duncan, S. 1966. An analysis of the stomach contents of some Cooper's hawks (Accipiter cooperii). Auk 83:308.

Dunn, E.H. and D.L. Tessaglia. 1994. Predation of birds at feeders in the winter. Journal of Field Ornithology 65:8-16.

Earhart, C.M. and N.K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72:251-264.

Ehleringer, J.R. and P.W. Rundel. 1989. Stable isotopes: history, units, and instrumentation. Pages 1-15 *In* Stable Isotopes in Ecological Research. *Edited by* P.W. Rundel, J.R. Ehleringer and K.A. Nagy. Ecological Studies V. 68. Springer-Verlag New York Inc., New York.

Elliot, C.L. and C.A. Cowan. 1983. The food habits of an American kestrel (Falco sparverius) in interior Alaska. Murrelet 64: 63-64.

Errington, P.L. 1932. Technique of raptor food habits study. Condor 34:75-86.

Errington, P.L. 1933. Food habits of southern Wisconsin raptors. Part II. Hawks. Condor 35:19-29.

Fielder, P.C. 1982. Food habits of bald eagles along the mid-Columbia River, Washington. Murrelet 63:46-50.

Fisler, G.F. 1960. Changes in food habits of Short-eared Owls' feeding in a salt marsh. Condor 62:486-487.

Fitch, H.S., F. Swenson and D.F. Tillotson. 1946. Behavior and food habits of the Red-tailed Hawk. Condor 48:205-237.

Fitzner, R.E., D. Berry, L.L. Boyd and C.A. Rieck. 1977. Nesting of Ferruginous Hawks (*Buteo regalis*) in Washington. Condor 79:245-249.

Fitzner, R.E. and J.N. Fitzner. 1975. Winter food habits of short-eared owls in the Palouse prairie. Murrelet 56:2-4.

Freeman, B.M. 1983. Energy metabolism. Pages 137-146 *in* Physiology and Biochemistry of the Domestic Fowl, Vol. 4. *Edited by* B.M. Freeman, Academic Press, Toronto.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic composition. Limnology and Oceanography 33: 1182-1190.

Fry, B. and E. Sherr. 1984. 13C as indicators of carbon flow (a review). Contributions To Marine Science 27: 13.

Fry, B., A. Joern and P.L. Parker. 1978. Grasshopper food web analysis: Use of carbon isotope ratios to examine feeding relationships among terrestrial herbivores. Ecology 59:498-506.

Gerrard, M. And G.R. Bortolotti. 1988. The Bald Eagle: haunts and habits of a wilderness monarch. Western Prairie Books, Saskatoon, Saskatchewan.

Gill, F.B. 1989. Feeding adaptations. Pages 129-150 *In* Ornithology. W. H. Freeman and Company, New York.

Glover, F.A. 1953. Summer foods of the Burrowing Owl. Condor 55:275.

Glue, D.E. 1972. Bird prey taken by British owls. Bird Study 19:91-95.

Goering, J, V. Alexander and N. Haubenstock. 1990. Seasonal variability of stable carbon and nitrogen isotope ratios of organisms in a north Pacific bay. Estuarine, Coastal and Shelf Science 30:239-260.

Graber, R.R. 1962. Food and oxygen consumption in three species of owls (Strigidae). Condor 64:473-487.

Gross, A.O. 1944. Food of the snowy owl. Auk 61:1-18.

Hayward G.D. and E.O. Garton. 1988. Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. Oecologia 75:253-265.

Henry, C.J. and M.W. Nelson. 1981. Decline and present status of breeding peregrine falcons in Oregon. The Murrelet 62:43-53.

Hobson, K.A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. Condor 97:752-762.

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series 95: 7-18.

Hobson, K.A. 1992. Determination of trophic relationships within a high Arctic marine food web using 13C and 15N analysis. Marine Ecology Progress Series 84: 9-18.

Hobson, K.A. and Clark, R.G. 1992. Assessing avian diets using stable isotopes I: Turnover of ^{13}C in tissues. Condor 94:181-188.

Hobson, K.A. and H.E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series 84:9-18.

Hobson, K.A. and S. G. Sealy. 1991. Marine protein contributions to the diet of northern saw-whet owls on the Queen Charlotte Islands: a stable-isotope approach. Auk 108: 437-440.

Hobson, K.A., R.W. Knapton and W. Lysack. 1989. Population, diet and reproductive success of double-crested cormorants breeding on Lake Winnipegosis. Colonial Water Birds 12:

Hodson, K. 1978. Prey utilized by Merlins nesting in shortgrass prairie of southern Alberta. Canadian Field Naturalist 92:76-77.

Holthuijzen, A.M.A. 1990. Prey delivery, caching and retrieval rates in nesting Prairie Falcons. Condor 92:475-484.

Hooper, T.D. and M. Nyhof. 1986. Food habits of the long-eared owl in south-central British Columbia. Murrelet 67:28-30.

Huges, J.H. 1982. Prey of short-eared owls in southeastern Alaska. Murrelet 63:22-24.

Hunt, L.E. 1993. Diet and habitat use of nesting prairie falcons (*falco mexicanus*) in an agricultural landscape in southern Alberta. M.Sc. Thesis, University of Alberta. 60pp.

Hunter, R.E., J.A. Crawford, R.E. Ambrose. 1988. Prey selection by peregrine falcons during the nestling stage. Journal of Wildlife Management 52: 730-736.

Johnson-Beaver, L. 1979. Biology and management of peregrine falcons (*Falco peregrinus anatum*) in northwestern Alberta. Alberta Oil Sands Environmental Research Program, Project LS 22.3.1.

Kelleher, J. V. and W.F. O'Malia. 1971. Golden Eagle attacks a Mallard. Auk 88:186.

Kemp, D.J. and G.E. Rogers. 1972. Characterization of feather and scale proteins. Biochemistry 11:969-975.

Kennedy P.L. 1991. Reproductive strategies of northern goshawks and Cooper's hawks in north central New Mexico. PhD Dissertation, Logan, Utah: Utah State University, 222pp.

Kennedy, P.L. and D.R. Wilson. 1986. Prey size selection in nesting male and female Cooper's Hawks. Wilson Bulletin 98:110-115.

Knight, R.L. and A.W. Erickson. 1978. Marmots as a food source of golden eagles along the Columbia River. Murrelet 59:28-30.

Korpimäki, E. 1972. Food of the Pygmy Owl *Glaucidium passerinum* in the breeding season. Ornis Fennica 54: 1-29.

John, R.D. and J. Romanow. 1993. Feeding behavior of a Burrowing Owl Athene cunicularia in Ontario. Canadian Field Naturalist. 107:231-232.

Longhurst, W.M. 1942. The summer food of Burrowing Owls in Costilla County, Colorado. Condor 44:281-282.

Mannan, R.W. and C.W. Boal. 1990. Goshawk diets in logged and unlogged ponderosa pine forests in N. Arizona. Progress report, challenge, cost-share agreement, University of Arizona and Kaibab national forest. 10pp.

Marks, J.S. and V.A. Marks. 1981. Comparative food habits of the screech owl and long-eared owl in south-western Idaho. Murrelet 62:80-82.

Marks, J.S. and E. Yensen. 1980. Nest sites and food habits of long-eared owls in southwestern Idaho. Murrelet 61: 86-91.

Marr, N.V., W.D. Edge, R.G.Anthony and R. Valburg. 1995. Sheep carcass availability and use by Bald Eagles. Wilson Bulletin 107:251-257.

Marr, N.V. and R.L. Knight. 1983. Food habits of golden eagles in eastern Washington. Murrelet 64:73-77.

Marti, C.D. 1987. Raptor food habits studies. Pages 67-77 in Raptor Management Techniques Manual. Edited by B.A. Giron Pendleton, B.A. Millsap, K.W. Cline and D.M. Bird. National Wildlife Federation, Washington, D.C.

Marti, C.D. 1974. Feeding ecology of four sympatric owls. Condor 76:45-61.

Maser, C., E.W. Hammer and S.H. Anderson. 1970. Comparative food habits of three owl species in central Oregon. Murrelet 51: 29-33.

Maser, C. and E.D. Brodie, Jr. 1966. A study of owl pellet contents from Linn, Benton and Polk counties, Oregon. Murrelet 47:9-14.

Mayers, A. and F. Tomlinson. 1988. Adobe Creek Colorado, Release Site Report. The Peregrine Fund, Inc., Operation Report 1988, Boise, Idaho.

Mendall, H.L. 1944. Food of hawks and owls in Maine. Journal of Wildlife Management 8:198-208.

Meng, H.K. 1959. Food habits of nesting Cooper's hawks and goshawks in New York and Pennsylvania. Wilson Bulletin 71:169-174.

Mermann, T.J., D.A. Buehler, J.D. Fraser and J.K.D. Seegar. 1992. Assessing bias in studies of bald eagle food habits. Journal of Wildlife Management 56:73-78.

Michelsen, A., I.K. Schmidt, S. Jonasson, C. Quarmby and D. Sleep. 1996. Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of soil nitrogen.

Mills, H. 1977. Osprey feeding problems on New Jersey coast. Pages 105-108 *in* Transactions of the North American Osprey Research Conference. *Edited by* J.C. Ogden. US Department of the Interior, National Parks Service.

Minagawa, M. and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. Geochimica Cosmochimica Acta 48:1135-1140.

Mindell, D.P. 1983. Nesting raptors in southwestern Alaska: status, distribution, and aspects of biology. U.S. Department of the Interior, Bureau of Land Management, Alaska. BLM-Alaska Technical Report 8.

Mizutani, H., Y. Kabaya and E. Wada. 1991. Nitrogen and carbon isotope compositions relate linearly in cormorant tissues and its diet. Isotopenpraxis 4: 166-168.

Mizutani, H. and E. Wada. 1988. Isotope ratios in seabird rookeries and their ecological implications. Ecology 69:340-349.

Mizutani, H., H. Hasegawa and Wada, E. 1986. Biogeochemistry 2:221-247.

Munro, J.A. 1929. Notes on the food habits of certain raptors in British Columbia and Alberta. Condor 31:112-116.

Murie, O.J. 1929. Nesting of the Snowy Owl. Condor 31:3-12.

Neft, J.A. 1941. A note on the food of Burrowing Owls. Condor 43: 197-198.

Newton, I. 1979. Population Ecology of Raptors. Buteo Books, Vermillion, South Dakota, 399pp.

Norman, D.M., A.M. Breault and I.E. Moul. 1989. Bald eagle incursions and predation of great blue heron colonies. Colonial Water Birds 12: 215-217.

Ogden, J.C. 1977. Preliminary reports on a study of Florida Bay ospreys. Pages 144-151 *in Transactions of the North American Osprey Research Conference. Edited by* J.C. Ogden. US Department of the Interior, National Parks Service.

Owens, N.J.P. 1987. Natural variations in the ^{15}N in the marine environment. Advances in Marine Biology 24:389-451.

Peterson, A. 1986. Habitat Suitability Index Models: bald eagle breeding season. US Fish and Wildlife Service, Biological Report 82(10.126).

Peterson, B.J. and B. Fry. 1987. Stable isotopes in ecosystem studies. Ann. Rev. Ecol. Syst. 18:293-320.

Peterson, B.J., R.W. Howarth and R.H. Garrit. 1985. Multiple stable isotope used to trace the flow of organic matter in estuarine food webs. Science 227:1361-1363.

Peyton, S.B. 1945. Western Red-tailed Hawk catches Cooper's Hawk. Condor 47:167.

Phelan, F.J.S. and R.J. Robertson. 1978. Predatory responses of a raptor guild to changes in prey density. Canadian Journal of Zoology 56:2565-2572.

Quinn, M.S. 1991. Nest site and prey of a pair of sharp-shinned hawks in Alberta. Journal of Raptor Research 25:18-19.

Ratcliff, D. 1980. The Peregrine Falcon. Vermillion, South Dakota, Buteo Books.

Rau, G.H., A.J. Mearns, D.R. Young, R.J. Olsen, H.A. Schafer and J.R. Kaplan. 1983. Animal $^{13}C/^{12}C$ correlates with trophic level in palagic food webs. Ecology 64:1314-1318.

Reed, H.A. and E.F. Woods. 1964. Heterogeneity of feather proteins. Biochemical Journal 92:12-18.

Reid, D.G., C.J. Krebs and A.J. Kennedy. 1997a. Patternes of predation on non-cyclic lemmings. Ecological Monographs 67:89-108.

Reid, D.G., C.J. Krebs and A.J. Kennedy. 1997b. Limitation of collared lemming population growth at low densities by predation mortality. Oikos 73:387-398.

Reynolds, R.T., R.T. Graham, M.H. Reiser, R.L. Bassett, P.L. Kennedy, D.A. Boyce, Jr., G. Goodwin, R. Smith, and E.L. Fisher. 1992. Management Recommendations for the northern goshawk in the southwestern United States. USDA Forest Service General Technical Report, RM-217, 90pp.

Reynolds, R.T. and E.C. Meslow. 1984. Partitioning of food and niche characteristics of coexisting *Accipiter* during breeding. Auk 101: 761-779.

Rosenfield, R.N. and M.W. Gratson. 1981. Food brought by Broad-winged Hawks to Wisconsin nest. Journal Field Ornithology 55:246.

Roth, D. and L.R. Powers. 1979. Comparative feeding and roosting habits of three sympatric owls in southwestern Idaho. Murrelet 60: 12-15.

Rusch D.H. and P.D. Doerr. 1972. Broad-winged hawk nesting and food habits. Auk 89:139-145.

Schoeninger, M.J. and M.J. DeNiro. 1984. Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. Geochimica Cosmochimica Acta 48:625-639.

Schmutz, J.K. and D.J. Hungle. 1989. Populations of Ferruginous Hawks and Swainson's Hawks increase in synchrony with ground squirrels. Canadian Journal of Zoology 67:2596-2601.

Schnell, J.H 1958. Nest behavior and food habits of Goshawks in the Sierra Nevada of California. Condor 60: 377-403.

Schulze, E.D., F.S. Chapin, III and G.Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100:406-412.

Schulze, E.D., F.S. Chapin, III and G.Gebauer. 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100:406-412.

Seidensticker, J.C., IV. 1970. Food of nesting red-tailed hawks in south-central Montana. Murrelet 51: 38-39.

Sherrod, S.K. 1978. Diets of North American Falconiformes. Journal of Raptor Research 12:49-121.

Sohdi, N.S. 1992. Central place foraging and prey preparation by specialist predator the Merlin. Journal of Field Ornithology 63:71-76.

Southern, H.N. 1969. Prey taken by Tawny Owls during the breeding season. Ibis 111:293-299.

Stalmaster, M.V. 1980. Salmon carrion as a winter food source for red-tailed hawks. Murrelet 61:43-44.

Steenhof, K. and M.N. Kochert. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. Journal of Animal Ecology 57:37-48.

Sudmann, S., P.H. Becker and H. Wendeln. 1994. Short-eared owl (Asio flammeus) and long-eared owl (Asio otus) as predators in common tern (Sterna hirundo) colonies. Vogelwelt 115:121-126.

Sutton, G.M. and D.F. Parmelee. 1956. Breeding of the Snowy Owl in southeastern Baffin Island. Condor 58:273.

Sydeman, W.J., K.A. Hobson, P. Pyle and E.B. McLaren. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. Condor 99:327-336.

Takats, D.L. 1998. Barred owl habitat use and distribution in the Foothills Model Forest. Master of Science Thesis, University of Alberta. 139pp.

Taylor, D. 1984. Winter food habits of two sympatric owl species. Murrelet 65: 48-49.

Thomsen, L. 1971. Behavior and ecology of burrowing owls on the Oakland Municipal Airport. Condor 73:177-192.

Tieszen, L.L., T.W. Boutton, K.G. Tesdahl, and N.A. Slade. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for ^{13}C analysis of diet. Oecologia 57:32-37.

Toland, B.R. 1990. Nesting ecology of red-tailed hawks in central Missouri, USA. Transactions of the Missouri Academy of Science 24: 1-16.

Tyler, J.G. 1923. Observations of the habits of the Prairie Falcon. Condor 25:90-97.

US Fish and Wildlife Service. 1987. Revised Peregrine Falcon, Eastern Population Recovery Plan. US Fish and Wildlife Service, Newton Corner, MA.

Wada, E., M. Terazaki, Y. Kabaya and T. Nemoto. 1987. ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeographical structure of the food web. Deep-Sea Research 34:829-841.

Weir, D. and A. Hanson. 1989. Food habits of great horned owls, Bubo virginianus, in the northern tiaga of the Yukon Territory and Alaska. Canadian Field-Naturalist 103:12-17.

Whittow, G.C. 1986. Energy metabolism. Pages 253-268 *in* Avian Phyisology, 4th Edition. *Edited by* P.D. Sturkie, Springer-Verlag, New York.

Williams, P.L. and L.G. Frank. 1979. Diet of the Snowy Owl in the absence of small mammals. Condor 81:213-214.

Windingstad, R.M., H.E. Stiles and R.C. Drewien. 1981. Whooping Crane preyed upon by Golden Eagle. Auk 98:392-394.

Woffinden, D.N. and J.R. Murphy. 1989. Decline of a Ferruginous Hawk population: a 20 year summary. Journal of Wildlife Management 53:1127-1134.

Zar, J.H. 1984. Biostatistical Analysis, 2nd edition. Prentice Hall, Englewood Cliffs, New Jersey.

4.0 Summary

Thanks to the pioneering work by geologists and geochemists who realized that stable isotope ratios change in biological systems and began to determine how and why the ratios changed (Craig 1953, Park and Epstein 1960, Wickman 1952), ecologists now have a new tool to conduct diet study research on birds and animals. The rarity of relatively heavier isotopes makes them ideal for tracing them through natural systems where atoms exist mostly in the relatively light forms of isotopes. Stable isotope ratio analysis for the purpose of studying the diet habits of raptors takes advantage of the bioaccumulation properties of heavy nitrogen (^{15}N)(Mizutani *et al.* 1986, Mizutani and Wada 1988, Mizutani *et al.* 1990, Hobson and Sealy 1991, Hobson 1993, Hobson *et al.* 1994, Thompson and Furness 1995). With increasing trophic levels, the relative amount of the heavy nitrogen isotope increases. Therefore, those animals feeding at the top of a food web system such as birds of prey will have much higher ratio values than their prey animals. The higher the isotope values in a raptor's tissues, the more trophic levels are below it in a food web. To analyze stable isotope ratio values, feathers were chosen as relatively easy tissue to obtain, they do not require the destruction of the raptors, and the ratio values of feathers are close to the mean of the ratios of all organ tissues considered together (Mizutani *et al.* 1986).

4.1 Summary of Results

Stable isotope ratio analysis of large raptor feathers requires a sampling protocol. During the time that large feathers grow, it is possible for metabolic rates or variable diets to cause changes in the isotope values along a single feather. Samples from three primary feathers from Golden Eagles, Great Gray Owls, Peregrine Falcons and captive Peregrine Falcons were analyzed by stable isotope ratio analysis and the results were tested using analysis of variance. Any differences in stable isotope ratio values between locations within a feather were insignificant.

As an exploration of the possible applications of stable isotope ratio analysis to birds of prey, feathers from 27 species of raptors commonly found in Alberta were analyzed to determine the relative trophic hierarchy of the raptors. The results of the 27 species indicated that the raptor samples originating in the

prairie ecoregion of Alberta had relatively higher $\delta^{15}N$ values than samples obtained in the parkland or boreal regions. A significant difference between boreal and agricultural area isotope values was detected in the Red-tailed Hawk feathers ($p<0.005$). Even though analysis of samples from Great Horned Owls from agricultural and boreal regions indicated a slight enrichment in the agricultural Great Horned Owls, the effect was not significant. All isotope ratios were converted into trophic level index numbers. When plotted by increasing trophic level, the index numbers make relative trophic level placement of raptors within ecoregions more apparent. The index numbers indicated that the prairies had relatively more raptors with enriched levels of heavy nitrogen than did the parkland and boreal ecoregions. The artificial enrichment of raptor tissues on the prairies is probably caused by long term fertilizer use in agricultural practices. Until the degree of how all species are affected by the enrichment factor has been determined, it is recommended that raptor isotope values not be compared between ecoregions.

In all applicable ecoregions, piscivorous raptors always had the highest mean $\delta^{15}N$ values. The relative trophic placement of other species changed depending on where the ecoregion the samples were obtained.

Some variability of isotope values within species was caused by sample locations within ecoregions and by differences in age classes. Peregrine Falcons had a significant difference between adult and juvenile isotope ratio values. The differences between isotope values of the age classes suggests a possible difference between what adults feed nestlings and what adults prey upon after their nestlings have left the nest. There were 3 species which each had a nest where there were marked differences in the $\delta^{15}N$ values of the nestlings.

4.2 Implications

The lack of variation of $\delta^{15}N$ values within the large primary feathers of raptors means that when samples are being collected by volunteer banders, they need not worry where they remove the 250 µg of tissue sample. Each bander may have their own opinion on where sample removal is appropriate. The location of where samples can be removed from museum specimens may differ between

museums. Having a choice of where to remove sample tissue will assist in obtaining support from volunteers and museums, who play vital roles in the ability to obtain sufficient sample sizes from large geographical regions.

While traditional dietary studies have been conducted on many raptor species, there are some species which lack dietary information due to remoteness of study areas, small sample sizes or rarity of the species. The averaging effect of stable isotope ratio analysis can be useful when used in conjunction with traditional methods since it represents the prey tissue assimilated into the predator, not just the prey consumed. This study has demonstrated that stable isotope ratio analysis can detect interesting aspects of raptor diets. For example, the low values of Cooper's and Sharp-shinned Hawks support relatively new ideas on the inclusion of large percentages of small mammals in their diets (Quinn 1991, and Bielefeldt *et al.* 1992). A better way to utilize stable isotope analysis is by having the isotope values indicate what trophic level the raptors are feeding at, and then using traditional methods to determine the prey species that the raptors are selecting to consume. For example, in this study Broad-winged Hawk samples from Alberta resulted in unexpectedly low isotope ratio values, and Great Gray Owl samples resulted in unexpectedly high isotope ratio values. Now traditional methods should be used to examine why the isotope values are indicating that Alberta Broad-winged Hawks and Great Gray Owls are eating at different trophic levels than what the literature suggests (Mendall 1944, Earhart and Johnson 1970, Rusch and Doerr 1972, Rosenfield and Gratson 1981, Bull *et al.* 1989, Bull and Duncan 1993, Dunn and Tessaglia 1994). However, the results of trophic level study demonstrate the need for caution when analyzing and comparing isotope values from large samples collected across multiple landscape types. The agricultural enrichment factor, diet selections between age classes and locations within ecoregions and original sources of nitrogen isotopes should all be considered when comparing the variability of $\delta^{15}N$ values between species and within species. Taking into account the causes of variability, biological aspects of raptor diets can be studied at the individual, species, and ecoregion guild levels using a combination of stable isotope ratio analysis and more traditional methods. A holistic approach using as many methods as possible will result in the most accurate conclusions about raptor diets.

4.3 Recommendations For Future Research

Stable isotope ratio analysis as a technique for studying raptor diets is still in its infancy. There are many factors which could be causing fractionation of isotopes that need to be explored before there results can be properly interpreted. Even though stable isotopes ratios did not differ significantly within a single feather, how does the analysis of feathers from different parts of the bird's body effect the ratios? The exact timing of the development of each feather tract of any species being studied should be known in order to be sure when and where the feather was grown. The time of the year and location of where a feather was grown must be known so that the results of traditional methods can be used to help interpret the isotope results. Species which consistently have arrested moults or that do not moult every feather every year should have their moulting patterns well documented before it can be decided which type of feather is the best to sample.

Physiological questions remain about the growth rates of feather proteins and how they affect isotope fractionation. Potential differences between the metabolic rates of age classes and between species may alter bioaccumulation and fractionation rates in feathers during their growth. Also, how long it takes for isotopes to reach growing feather tissue from external sources is not known and needs research. If the isotopes from food sources are assimilated into feather tissue as soon as the food's isotopes enter the blood stream would mean that the isotopes in the feathers represent the diet of the raptor only during the growth of the feather. However, if the feathers receive nutrients from pooled resources in the body's tissue during growth, the isotopes in the feathers may represent a time period as long as the time it took for those resources to be pooled into the body. Using isotopically labelled food and water, the amount of time it takes for nutrients to reach feather tissue could be determined using captive birds.

There is also a problem with obtaining sufficient samples sizes for many species. Thus, the smallest sample size that is sufficient to produce reliable isotope ratio results needs to be agreed upon by those who want to use the technique and so results are standardized among different studies. In ecology, it is not unusual to be required to obtain hundreds of samples to ensure significant results.

However, the cost and the ability to obtain and analyze hundreds of feather samples may not be possible for stable isotope analysis. At least ten samples per species within an ecoregion should be considered the minimum, although if more can be obtained, the conclusions based on the interpretation of isotope values will be more precise.

As of now, stable isotope analysis is limited to determining the relative trophic level of the prey that a raptor may be consuming. If the effect of the different metabolic rates of different taxa of prey affect the rates of bioaccumulation and fractionation can be determined, then stable isotope analysis may be useful to determine the main type of prey a raptor is consuming. Analyzing specific amino-acids of the prey and tracing them into the tissues of the consumer may be another way to possibly determine the prey species being eaten by raptors. In the future, it may be possible to conclude that an American Kestrel is eating mostly small rodents, insects or birds, as opposed to only determining at what trophic level the kestrel's prey is eating.

This study has indicated that cross-ecoregion comparisons are inadvisable at this time. It recommended that this technique be used to answer more focussed questions. Investigations of raptor diets within an ecoregion, ecosystem or species will produce more accurate conclusions. By determining the basal isotope ratios within each ecosystem, Trophic Level Index numbers may become useful in comparing raptor species across ecoregions. However, stable isotope analysis is better suited to study the relationships between organisms within smaller systems. Unfocussed questions lead to very general results which have little value to the study of raptors.

By addressing the above limitations of stable isotope ratio analysis, there is potential for this technique to become an important tool for studying the diets of raptors in the near future.

4.4 Literature Cited

Bielefeldt, J., R.N. Rosenfield and J.H. Papp. 1992. Unfounded assumptions about diet of the Cooper's Hawk. Condor 94:427-436.

Bull, E.L. and J.R. Duncan. 1993. Great gray owl (Strix nebulosa) *in* Birds of North America, No. 42, *Edited by* A. Poole and F.Gill. Philadelphia: The Academy of Natural Sciences, Washington D.C.The American Ornithologists' Union.

Bull, E.L., M.G. Henjum and R.S. Rohweder. 1989. Diet and optimal foraging of Great Gray Owls. Journal of Wildlife Management 53:47-50.

Craig, H. 1953. The geochemistry of stable carbon isotopes. Geochimica Cosmochimica Acta 3: 53-92.

Dunn, E.H. and D.L. Tessaglia. 1994. Predation of birds at feeders in the winter. Journal of Field Ornithology 65:8-16.

Earhart, C.M. and N.K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72:251-264.

Hobson, K.A. 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series 95: 7-18.

Hobson, K.A., J.F. Piatt and J. Pitocchelli. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63:786-798.

Hobson, K.A. and S. G. Sealy. 1991. Marine protein contributions to the diet of northern saw-whet owls on the Queen Charlotte Islands: a stable-isotope approach. Auk 108: 437-440.

Mendall, H.L. 1944. Food of hawks and owls in Maine. Journal of Wildlife Management 8:198-208.

Mizutani, H., M. Fukuda, Y. Kabaya and E. Wada. 1990. Carbon isotope ratio of feathers reveals feeding behaviour of cormorants. Auk 107:400-403.

Mizutani, H. and E. Wada. 1988. Isotope ratios in seabird rookeries and the ecological implications. Ecology 69: 340-349.

Mizutani, H., H. Hasegawa and Wada, E. 1986.Biogeochemistry 2:221-247.

Park, R. and S. Epstein. 1960. Carbon isotope fractionation in plants. Geochimica Cosmochimica Acta 21:110-126.

Quinn, M.S. 1991. Nest site and prey of a pair of sharp-shinned hawks in Alberta. Journal of Raptor Research 25:18-19.

Rosenfield, R.N. and M.W. Gratson. 1981. Food brought by Broad-winged Hawks to Wisconsin nest. Journal Field Ornithology 55:246.

Rusch D.H. and P.D. Doerr. 1972. Broad-winged hawk nesting and food habits. Auk 89:139-145.

Thompson, D.R. and R.W. Furness. 1995. Stable-isotope ratios of carbon and nitrogen in feathers indicate seasonal dietary shifts in northern fulmars. Auk 112:493-498.

Wickman, F.E. 1952. Variations in the relative abundance of the carbon isotopes in plants. Geochimica Cosmochimica Acta 2: 636-639.

Appendix 1 - Mass Spectrometer Specifications

Combustion system - Fisons NA1500 NC

Mass Spectrometer - Finnigan Mat 252 with carbon and nitrogen analyzers

Combustion temperature - 1021°C

Copper tube temperature - 650°C

GC oven temperature - 50°C

Carrier gas - helium, Matheson UHP grade (head pressure 13 psi)

Combustion gas - oxygen, Matheson Purity grade (head pressure 40 psi)

Reference gases - carbon dioxide, Matheson Coleman instrument grade
δ = -42.00‰ (head pressure 35 psi)
nitrogen, Matheson Coleman instrument grade
δ = -1.79‰

Calibration gases = carbon dioxide, Oztech	$\delta^{13}C$ (PDB) = -36.49‰
	$\delta^{18}O$ (PDB) = -25.56‰
	$\delta^{18}O$ (SMOW) = +15.06‰
nitrogen, Oztech	$\delta^{15}N$ (Air) = -1.89‰

Appendix 2 - Raw Data and Analysis of Variance For Feather Samples

δ^{15}Nitrogen Analysis

Analysis Number	Species	Feather	Location	Replicates	Isotope Ratio
1	GOEA	1	Tip	1	5.48
2	GOEA	1	Tip	2	5.65
3	GOEA	1	Tip	3	5.45
4	GOEA	1	Mid	1	5.18
5	GOEA	1	Mid	2	5.12
6	GOEA	1	Mid	3	5.18
7	GOEA	1	Cal	1	5.48
8	GOEA	1	Cal	2	5.11
9	GOEA	1	Cal	3	5.12
10	GOEA	2	Tip	1	5.80
11	GOEA	2	Tip	2	5.94
12	GOEA	2	Tip	3	5.59
13	GOEA	2	Mid	1	6.40
14	GOEA	2	Mid	2	6.59
15	GOEA	2	Mid	3	6.49
16	GOEA	2	Cal	1	5.54
17	GOEA	2	Cal	2	5.46
18	GOEA	2	Cal	3	5.63
19	GOEA	3	Tip	1	6.80
20	GOEA	3	Tip	2	6.76
21	GOEA	3	Tip	3	6.69
22	GOEA	3	Mid	1	6.20
23	GOEA	3	Mid	2	6.27
24	GOEA	3	Mid	3	6.14
25	GOEA	3	Cal	1	6.55
26	GOEA	3	Cal	2	6.71
27	GOEA	3	Cal	3	6.75
28	GGOW	1	Tip	1	7.96
29	GGOW	1	Tip	2	7.89
30	GGOW	1	Tip	3	7.83

31	GGOW	1	Mid	1	7.77
32	GGOW	1	Mid	2	7.76
33	GGOW	1	Mid	3	7.37
34	GGOW	1	Cal	1	9.36
35	GGOW	1	Cal	2	9.11
36	GGOW	1	Cal	3	9.41
37	GGOW	2	Tip	1	6.55
38	GGOW	2	Tip	2	6.58
39	GGOW	2	Tip	3	6.57
40	GGOW	2	Mid	1	6.20
41	GGOW	2	Mid	2	6.25
42	GGOW	2	Mid	3	6.25
43	GGOW	2	Cal	1	7.93
44	GGOW	2	Cal	2	7.62
45	GGOW	2	Cal	3	7.95
46	GGOW	3	Tip	1	7.09
47	GGOW	3	Tip	2	7.11
48	GGOW	3	Tip	3	7.17
49	GGOW	3	Mid	1	8.22
50	GGOW	3	Mid	2	8.10
51	GGOW	3	Mid	3	7.99
52	GGOW	3	Cal	1	8.26
53	GGOW	3	Cal	2	8.39
54	GGOW	3	Cal	3	8.18
55	PEFA	1	Tip	1	11.44
56	PEFA	1	Tip	2	11.24
57	PEFA	1	Tip	3	11.15
58	PEFA	1	Mid	1	11.81
59	PEFA	1	Mid	2	11.49
60	PEFA	1	Mid	3	11.70
61	PEFA	1	Cal	1	10.33
62	PEFA	1	Cal	2	10.40
63	PEFA	1	Cal	3	10.37
64	PEFA	2	Tip	1	10.35
65	PEFA	2	Tip	2	10.27
66	PEFA	2	Tip	3	10.09
67	PEFA	2	Mid	1	10.18

68	PEFA	2	Mid	2	10.31
69	PEFA	2	Mid	3	10.13
70	PEFA	2	Cal	1	10.61
71	PEFA	2	Cal	2	10.81
72	PEFA	2	Cal	3	10.82
73	PEFA	3	Tip	1	11.28
74	PEFA	3	Tip	2	11.28
75	PEFA	3	Tip	3	11.12
76	PEFA	3	Mid	1	10.80
77	PEFA	3	Mid	2	10.95
78	PEFA	3	Mid	3	9.86
79	PEFA	3	Cal	1	10.39
80	PEFA	3	Cal	2	10.99
81	PEFA	3	Cal	3	10.73
82	WAIN	1	Tip	1	7.71
83	WAIN	1	Tip	2	8.78
84	WAIN	1	Tip	3	8.14
85	WAIN	1	Mid	1	7.87
86	WAIN	1	Mid	2	8.19
87	WAIN	1	Mid	3	7.83
88	WAIN	1	Cal	1	7.86
89	WAIN	1	Cal	2	7.69
90	WAIN	1	Cal	3	7.76
91	WAIN	2	Tip	1	8.41
92	WAIN	2	Tip	2	8.24
93	WAIN	2	Tip	3	8.92
94	WAIN	2	Mid	1	9.33
95	WAIN	2	Mid	2	9.09
96	WAIN	2	Mid	3	8.94
97	WAIN	2	Cal	1	8.22
98	WAIN	2	Cal	2	8.24
99	WAIN	2	Cal	3	8.75
100	WAIN	3	Tip	1	8.62
101	WAIN	3	Tip	2	8.92
102	WAIN	3	Tip	3	9.49
103	WAIN	3	Mid	1	8.41
104	WAIN	3	Mid	2	8.38

105	WAIN	3	Mid	3	8.59
106	WAIN	3	Cal	1	8.17
107	WAIN	3	Cal	2	7.78
108	WAIN	3	Cal	3	8.18

GOEA = Golden Eagle
GGOW = Great Gray Owl
PEFA = Peregrine Falcon
WAIN = Captive Peregrine Falcon

Tip = Tip of feather
Mid = Middle of feather
Cal = Calamus of feather

The SAS System
General Linear Models Procedure
Class Level Information

Class	Levels	Values
SPECIES	4	1 2 3 4 (GOEA, GGOW, PEFA, WAIN)
FEATHER	3	1 2 3 (Individual #1, #2, #3)
LOCATION	3	1 2 3 (Tip, Mid, Cal)

Number of observations in data set = 108

General Linear Models Procedure
Dependent Variable: RATIO

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	35	367.8011	10.5086	228.53	0.0001
Error	72	3.3109	0.0460		
Corrected Total	107	371.1120			

R-Square	C.V.	Root MSE	RATIO Mean
0.9911	2.6188	0.2144	8.1885

Source	Degrees of Freedom	Sum of Squares	Mean Square	F Value	Pr > F
Species	3	326.9349	108.9783	2369.90	0.0001
Feather(Species)	8	20.6819	2.5852	56.22	0.0001
Location	2	0.1607	0.0803	1.75	0.1816
Location*Species	6	10.6867	1.7811	38.73	0.0001
Location*Feather(Species)	16	9.3370	0.5836	12.69	0.0001

Tests of Hypotheses using the Mean Square for Feather(Species) as an error term:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F Value	Pr > F
SPECIES	3	326.9349	108.9783	42.15	0.0001

Tests of Hypotheses using the Mean Square for Location*Feather(Species) as an error term

Source	Degrees of Freedom	Sum of Squares	Mean Square	F Value	Pr > F
Location	2	0.1607	0.0803	0.14	0.8724
Location*Species	6	10.6867	1.7811	3.05	0.0347

δ^{13}Carbon Analysis

Analysis Number	Species	Feather	Location	Replicates	Isotope Ratio
1	GOEA	1	Tip	1	-21.12
2	GOEA	1	Tip	2	-25.47
3	GOEA	1	Tip	3	-20.54
4	GOEA	1	Mid	1	-20.36
5	GOEA	1	Mid	2	-21.92
6	GOEA	1	Mid	3	-21.92
7	GOEA	1	Cal	1	-18.50
8	GOEA	1	Cal	2	-20.95
9	GOEA	1	Cal	3	-20.97
10	GOEA	2	Tip	1	-22.14
11	GOEA	2	Tip	2	-22.11
12	GOEA	2	Tip	3	-22.44
13	GOEA	2	Mid	1	-21.66
14	GOEA	2	Mid	2	-21.78
15	GOEA	2	Mid	3	-21.49
16	GOEA	2	Cal	1	-21.68
17	GOEA	2	Cal	2	-21.65
18	GOEA	2	Cal	3	-21.65
19	GOEA	3	Tip	1	-22.10
20	GOEA	3	Tip	2	-22.27
21	GOEA	3	Tip	3	-22.12
22	GOEA	3	Mid	1	-22.23
23	GOEA	3	Mid	2	-22.32
24	GOEA	3	Mid	3	-22.40
25	GOEA	3	Cal	1	-22.49
26	GOEA	3	Cal	2	-22.54
27	GOEA	3	Cal	3	-22.51
28	GGOW	1	Tip	1	-23.87
29	GGOW	1	Tip	2	-23.61
30	GGOW	1	Tip	3	-23.90
31	GGOW	1	Mid	1	-23.78
32	GGOW	1	Mid	2	-24.02
33	GGOW	1	Mid	3	-24.15

34	GGOW	1	Cal	1	-23.12
35	GGOW	1	Cal	2	-23.74
36	GGOW	1	Cal	3	-23.27
37	GGOW	2	Tip	1	-23.68
38	GGOW	2	Tip	2	-23.68
39	GGOW	2	Tip	3	-23.74
40	GGOW	2	Mid	1	-23.62
41	GGOW	2	Mid	2	-23.68
42	GGOW	2	Mid	3	-23.64
43	GGOW	2	Cal	1	-23.55
44	GGOW	2	Cal	2	-23.62
45	GGOW	2	Cal	3	-23.55
46	GGOW	3	Tip	1	-23.36
47	GGOW	3	Tip	2	-23.50
48	GGOW	3	Tip	3	-23.57
49	GGOW	3	Mid	1	-22.80
50	GGOW	3	Mid	2	-22.82
51	GGOW	3	Mid	3	-22.73
52	GGOW	3	Cal	1	-22.90
53	GGOW	3	Cal	2	-18.43
54	GGOW	3	Cal	3	-22.99
55	PEFA	1	Tip	1	-22.65
56	PEFA	1	Tip	2	-22.25
57	PEFA	1	Tip	3	-22.05
58	PEFA	1	Mid	1	-22.71
59	PEFA	1	Mid	2	-22.76
60	PEFA	1	Mid	3	-22.79
61	PEFA	1	Cal	1	-24.48
62	PEFA	1	Cal	2	-24.60
63	PEFA	1	Cal	3	-24.72
64	PEFA	2	Tip	1	-23.35
65	PEFA	2	Tip	2	-23.65
66	PEFA	2	Tip	3	-23.83
67	PEFA	2	Mid	1	-23.14
68	PEFA	2	Mid	2	-22.31
69	PEFA	2	Mid	3	-23.29
70	PEFA	2	Cal	1	-24.06

71	PEFA	2	Cal	2	-24.02
72	PEFA	2	Cal	3	-24.02
73	PEFA	3	Tip	1	-22.83
74	PEFA	3	Tip	2	-23.20
75	PEFA	3	Tip	3	-22.92
76	PEFA	3	Mid	1	-21.54
77	PEFA	3	Mid	2	-24.46
78	PEFA	3	Mid	3	-23.66
79	PEFA	3	Cal	1	-23.77
80	PEFA	3	Cal	2	-23.71
81	PEFA	3	Cal	3	-24.76
82	WAIN	1	Tip	1	-21.71
83	WAIN	1	Tip	2	-22.36
84	WAIN	1	Tip	3	-21.92
85	WAIN	1	Mid	1	-21.12
86	WAIN	1	Mid	2	-21.73
87	WAIN	1	Mid	3	-21.26
88	WAIN	1	Cal	1	-21.22
89	WAIN	1	Cal	2	-21.17
90	WAIN	1	Cal	3	-21.30
91	WAIN	2	Tip	1	-21.12
92	WAIN	2	Tip	2	-21.25
93	WAIN	2	Tip	3	-21.30
94	WAIN	2	Mid	1	-20.63
95	WAIN	2	Mid	2	-21.02
96	WAIN	2	Mid	3	-20.83
97	WAIN	2	Cal	1	-20.66
98	WAIN	2	Cal	2	-20.90
99	WAIN	2	Cal	3	-20.57
100	WAIN	3	Tip	1	-21.33
101	WAIN	3	Tip	2	-21.35
102	WAIN	3	Tip	3	-21.41
103	WAIN	3	Mid	1	-20.84
104	WAIN	3	Mid	2	-21.47

105	WAIN	3	Mid	3	-20.94
106	WAIN	3	Cal	1	-20.55
107	WAIN	3	Cal	2	-20.63
108	WAIN	3	Cal	3	-20.60

GOEA = Golden Eagle
GGOW = Great Gray Owl
PEFA = Peregrine Falcon
WAIN = Captive Peregrine Falcon

Tip = Tip of feather
Mid = Middle of feather
Cal = Calamus of feather

The SAS System

General Linear Models Procedure

Class Level Information

Class	Levels	Values
SPECIES	4	1 2 3 4 (GOEA, GGOW, PEFA, WAIN)
FEATHER	3	1 2 3 (Indivual #1, #2, #3)
LOCATION	3	1 2 3 (Tip, Mid, Cal)

Number of observations in data set = 108

General Linear Models Procedure

Dependent Variable: RATIO

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	35	144.4572	4.1274	7.19	0.0001
Error	72	41.3191	0.5739		
Corrected Total	107	185.7763			

R-Square	C.V.	Root MSE	RATIO Mean
0.7775	-3.3789	0.7576	-22.4202

Source	Degrees of Freedom	Sum of Squares	Mean Square	F Value	Pr > F
Species	3	99.3889	33.1296	57.73	0.0001
Feather(Species)	8	14.5571	1.8196	3.17	0.0039
Location	2	1.8022	0.9011	1.57	0.2150
Location*Species	6	16.7801	2.7967	4.87	0.0003
Location*Feather(Species)	16	11.9288	0.7455	1.30	0.2218

Tests of Hypotheses using the Mean Square for Feather(Species) as an error term:

Source	Degrees of Freedom	Sum of Squares	Mean Square	F Value	Pr > F
SPECIES	3	99.3889	33.1296	18.21	0.0006

Tests of Hypotheses using the Mean Square for Location*Feather(Species) as an error term

Source	Degrees of Freedom	Sum of Squares	Mean Square	F Value	Pr > F
Location	2	1.8022	0.9011	1.21	0.3245
Location*Species	6	16.7801	2.7967	3.75	0.0160

Appendix 3 - Stable Isotope Ratio Values For Individual Raptors (Exact locations of collection sites have been kept confidential. Individuals without specific location data were not used in ecoregional analyses.)

Species	Age / Sex	Location	15N (‰)	13C (‰)	%N	%C
OSPR	Juv	Chip Lake	12.04	-24.26	16.39	47.41
	Juv	Steele Lake	12.03	-26.55	13.06	42.55
	Juv	Steele Lake	8.42	-22.04	18.89	54.18
	Juv	Fallis	13.66	-24.57	14.34	46.26
	Juv	Fallis	13.95	-24.48	13.70	41.86
	Juv	Wabaman	13.80	-24.80	17.57	52.92
	Juv	Wabaman	14.04	-24.12	13.68	43.03
	?	Cold Lake	11.89	-18.51	14.02	40.13
	Juv	AB #1	11.84	-26.45	13.34	48.45
	Juv	Wabaman	11.79	-22.47	16.39	48.80
	Adult	Chip Lake 96	13.83	-24.36	15.74	45.68
	Juv	Chip Lake 96	11.01	-22.97	15.58	49.60
	?	AB #2	10.70	-31.13	13.81	45.77
	?	AB #3	9.59	-23.75	12.92	47.87
	Adult F	High River	10.43	-26.93	13.30	44.07
	Adult F	AB #4	8.71	-22.58	15.52	48.75
	Juv F	Edson	12.28	-25.60	14.98	45.14
	Juv	Crosslake	12.44	-28.72	14.96	46.62
	?	Stoney Plain	13.32	-24.59	13.72	47.04
	Adult M	AB #5	12.35	-16.84	14.63	46.18
BAEA	?	AB '96	11.54	-21.03	12.79	40.28
	?	Kerrywood, 96	11.12	-21.17	12.92	41.52
	?	AB #1	12.28	-22.17	15.89	44.90
	?	AB #2	11.51	-21.95	15.80	45.97
	Adult M	Calgary #1	10.36	-23.25	14.58	46.35
	2-3 yr	Barrhead	11.87	-27.04	15.25	44.76
	Imm M	AB #3	13.16	-21.22	15.59	45.10
	Adult M	Calgary #2	16.19	-15.65	16.44	46.06
	3 yr	AB #4	14.54	-24.87	17.05	47.09

	Imm M	Stoney Plain	11.39	-20.95	13.74	45.16
	Imm M	Spirit River	11.39	-24.37	14.69	47.58
	Adult F	AB #5	10.59	-22.57	14.35	47.16
	2 yr F	Stoney Lake	10.62	-18.20	14.50	46.80
	Imm F	Wagner	9.56	-17.83	15.83	46.70
	3 yr F	High River	13.55	-19.85	14.98	44.24
	Imm	Grand Prairie	11.20	-26.22	15.35	46.07
	3 yr M	Jasper	11.56	-26.13	13.29	47.75
	Imm	Conrich AB	11.60	-23.59	15.78	47.55
GOEA	?	Brazeau Dam area #1	5.88	-23.30	13.08	41.40
	?	Brazeau Dam area #2	8.06	-22.71	17.92	58.00
	?	Brazeau Dam area #3	7.65	-22.54	14.73	47.17
	?	Spirit River	8.27	-22.88	15.87	49.71
	Juv	PPT	8.82	-21.72	14.16	45.50
	Adult	PPT	6.45	-23.65	14.20	45.79
	?	AB 1a '96	5.78	-22.58	13.88	44.37
	?	AB 2a '96	4.93	-21.01	13.63	43.69
	?	AB 3a '96	9.23	-21.22	13.25	39.78
	?	Kerrywood	6.31	-21.87	12.85	42.06
	Adult M	AB PMA	4.94	-22.78	14.30	46.59
	Adult M	3 Hills	6.70	-21.81	13.44	43.47
NOHA	?	Beaverhill Lake	9.86	-23.11	15.51	48.91
	?	Kerrywood	7.11	-23.26	11.80	41.29
	Adult F	Amisk Lake	9.11	-20.61	14.29	46.65
	Juv f	AB #1	5.44	-22.70	14.29	48.05
	Juv M	Edmonton	5.56	-22.48	14.94	49.57
	Adult M	Meeting Creek	7.40	-20.66	15.59	51.20
	Adult F	Trochu	8.08	-19.38	16.09	52.72
	Juv F	Beaverhill Lake #2	9.18	-21.19	15.04	51.12
	Juv F	Winnipeg	4.88	-24.06	15.95	46.90
	Juv M	Llyodminster	5.02	-23.89	16.05	54.48
	Adult F	Leduc	6.02	-24.06	15.61	53.17
	Adult F	St. Albert	8.81	-22.91	16.47	54.57
	Adult F	AB #2	10.63	-22.76	16.73	53.35

	Adult M	Grande Prairie	11.55	-17.70	16.11	53.45
	Adult M	Seymore	8.87	-22.57	16.15	56.15
FEHA	Juv	New Place	9.09	-22.60	15.77	41.48
	Juv	Y. Coulee	8.82	-23.10	18.61	53.96
	Juv	Y. Coulee	9.21	-23.10	17.77	50.57
	Juv	West Landis #1	10.26	-22.72	18.37	50.25
	Juv	West Landis #2	9.66	-23.22	19.22	55.16
	Juv	West Landis #3	10.09	-23.05	20.56	57.16
	Juv	Tower 7 N of B21	9.27	-23.03	18.94	52.39
	Juv	SE Strawpile	7.25	-23.17	17.20	45.61
	Juv	NW Paluszak	8.27	-22.73	22.33	58.91
	Juv	Tower 14 S Cessford Rd	8.47	-22.98	13.64	42.87
	Juv	Pole 59	9.83	-22.94	17.69	49.04
	Juv	Pole 59 #2	10.27	-23.48	14.62	44.41
	Juv	Pole 66	9.61	-22.94	19.36	55.43
	Juv	Pole 69	9.90	-23.84	14.71	39.31
	Juv	Pole 71	10.48	-24.32	17.42	48.53
	Juv	Pole 73	7.20	-24.32	19.31	54.11
	Juv	Pole 77	9.41	-21.40	11.96	35.35
	Juv	Pole 78	6.74	-24.76	12.77	42.01
	Adult F	Walsh	11.67	-22.24	15.72	47.50
	Adult F	AB	10.30	-22.89	15.31	49.27
	Adult M	Dunkirk	10.68	-21.88	13.83	42.84
	Adult F	Cessford	9.28	-18.04	13.83	46.44
RLHA	?	L. Slave Lake	6.88	-24.13	15.91	48.00
	?	Spirit River #1	7.51	-22.70	15.35	45.93
	?	Tofield '96	5.96	-21.59	12.97	41.86
	?	Indus	6.90	-23.22	14.55	47.66
	Juv M	Debolt	7.53	-22.12	16.03	48.32
	Adult F	AB #1	7.12	-22.79	15.86	47.31
	Imm F	Ft. McMurray	3.52	-24.25	16.82	48.79
	Adult F	Crooked Creek	6.38	-22.25	15.46	47.44
	?	Cheyenne	7.18	-20.78	15.46	49.32
	F	AB #2	3.70	-22.02	16.93	49.25
	F	AB #3	5.81	-21.42	15.93	47.28

	Adult F	Caslon	5.62	-22.95	16.22	46.70
	Adult F	AB #4	5.46	-22.46	16.73	47.75
	Ad F	Ft. McMurray #2	5.95	-23.16	14.56	48.38
	Imm F	Edson	6.63	-22.14	15.82	47.34
	M	Edson	9.66	-22.89	15.65	50.65
	Ad M	Calgary	5.14	-23.15	16.03	47.81
	Ad F	AB	3.41	-22.95	16.61	51.82
	Imm F	Whitecourt	2.56	-24.42	15.74	49.49
	Imm F	Ft. McMurray #3	6.34	-23.87	15.93	50.12
BWHA	?	Cold Lake	5.81	-22.70	16.08	47.75
	?	Blue River	11.20	-21.20	12.86	40.29
	Adm	Wabuman	7.98	-22.12	14.01	48.47
	Juv F	Bruderheim	6.17	-23.33	15.34	50.28
	?	AB #1	7.65	-21.35	10.36	34.33
	Juv F	22 km SE Edm	5.77	-23.47	14.83	50.04
	Adult M	Sherwood Park	5.93	-24.80	15.50	53.38
	Juv F	Newall County	6.04	-28.81	14.29	47.89
	Juv M	Deerland	6.26	-23.75	12.48	50.86
	Juv F	Smith	5.63	-23.24	16.19	50.53
	Adult F	Slave Lake	7.00	-22.00	15.14	49.23
RTHA	Adult	Calling Lake #1	8.48	-24.19	13.55	41.79
	Adult	Calling Lake Trp #20	7.13	-24.57	14.96	46.57
	Adult	Gwynne	7.91	-23.79	14.63	49.23
	Juv	Gwynne	5.78	-23.05	14.49	47.73
	Adult	Hay Lakes	8.65	-23.09	15.42	45.91
	Juv	Hay Lakes	8.16	-24.75	14.18	47.57
	Adult	Looma Hwy 21	7.19	-23.90	15.21	50.83
	Juv	Looma Hwy 21	5.03	-24.71	15.49	51.58
	Juv	Rollyview	5.51	-24.80	14.47	39.46
	Adult	Rolly View	7.32	-24.37	16.18	50.32
	Juv	Rollyview	7.13	-24.57	14.28	47.94
	Adult	Ardrossan	7.37	-23.43	13.71	47.44
	Juv	Ardrossan	7.13	-24.58	15.44	51.41
	Adult	NW Wetaskiwin (4mi)	6.92	-24.00	14.64	50.08
	Juv	NW Wetaskiwin (4mi)	5.62	-24.57	16.19	50.58

	Adult	Redwater	8.49	-21.00	17.11	46.52
	Juv	Redwater	7.91	-23.08	16.41	51.10
	Juv	W of Chipman (4mi)	9.30	-21.22	14.38	39.02
	Juv	Millet Hwy 2a	4.91	-25.27	19.89	55.25
	Adult	SE Edm 1 st and 23 ave	11.51	-22.77	14.17	50.07
	Juv	SE Edm 1 st and 23 ave	8.39	-24.33	15.45	49.58
	Juv	W Edm 142 St	8.21	-25.53	19.71	53.68
	Adult	Gibbons	7.44	-24.61	14.67	46.59
	Juv	Gibbons	5.90	-25.18	14.67	45.16
	Adult	Bittern Lake	8.66	-23.99	13.22	40.79
	Juv	Saunders Lake #1	6.43	-25.30	13.81	44.79
	Juv	Saunders Lake #2	6.49	-24.04	14.86	47.14
	Juv	Saunders Lake #3	7.65	-25.13	16.55	52.24
	Juv	Spirit River	6.59	-23.95	11.90	36.75
	Adult	Rycroft	5.74	-23.43	16.07	45.85
	Adult	Sher Park Petro Way	8.19	-23.35	21.35	65.96
	?	Rose (Hanna Region)	7.93	-22.54	14.39	45.55
	Juv	Bruderheim #1	9.04	-24.10	15.39	50.31
	Juv	Bruderheim #2	7.20	-24.20	15.86	51.29
	Juv	Bruderheim #3	6.66	-24.25	12.23	39.86
	Juv	Holden	11.03	-22.60	10.93	37.26
	Juv	Gene	8.79	-22.56	14.38	51.14
	Adult F	S AB	6.49	-22.42	14.57	51.57
	Juv F	Rainbow Lake	2.77	-23.96	15.02	54.80
	?	Slave Lake	2.71	-22.61	13.29	35.71
	Adult F	High Level	6.39	-21.65	12.11	33.24
	Juv F	Ft. McMurray	4.83	-25.64	16.51	57.35
	Juv M	Cold Lake	4.86	-21.33	18.66	55.06
	Juv M	S AB	5.62	-21.39	17.27	53.75
	Juv F	Nojack	5.56	-21.70	20.03	62.93
	Juv F	Black Diamond	7.47	-23.20	18.81	59.56
SWHA	Adult	Redwater	9.17	-21.62	18.23	50.92
	Juv	Redwater	5.58	-24.81	22.44	64.30
	Juv	SE Edm	6.80	-25.30	15.54	45.74
	Juv	SE Edm 75 st & 55 ave	4.72	-24.55	16.22	43.30
	Juv	Linbrook	7.06	-23.91	13.72	42.66

	Juv	NW Beaverhill Lake	7.24	-24.94	17.09	44.53
	Juv	6 km NW Volmer	6.45	-24.90	18.98	50.23
	Juv	Manning Freeway	7.80	-24.87	15.63	47.44
	Adult	Leduc Hwy 39	9.77	-23.44	17.98	47.47
	Juv	Leduc Hwy 39	4.97	-23.40	12.02	37.78
	Juv	ESE McLoskey	9.74	-22.31	14.09	41.32
	Juv	W. Gordon #1	9.17	-23.22	20.05	56.74
	Juv	W. Gordon #2	9.36	-22.96	19.89	50.72
	Juv	W. Gordon #3	9.23	-23.04	15.04	45.70
	Juv	Shelterbelt	8.47	-22.39	11.48	37.20
	Juv	SE Stifle	10.30	-22.74	17.78	52.31
	Juv	E. Landis	11.61	-21.12	19.53	51.87
	Adult M	SE Edm	7.41	-20.40	12.89	40.10
	Adult M	Leduc	12.11	-25.60	14.82	47.33
	Adult F	SE Edm #2	8.01	-24.25	13.59	42.28
	Adult M	S Edm #1	7.16	-23.55	11.78	37.93
	Adult M	S Edm #2	7.01	-23.02	13.21	41.68
	Adult F	W. Edm #1	6.19	-20.06	14.28	46.83
	Adult F	E. Edm	9.18	-20.14	14.42	46.53
	Adult F	SE Edm #3	7.37	-20.68	14.40	50.16
	Adult F	Mannville	7.45	-20.43	13.88	43.18
	Adult F	W. Ed #2	6.83	-23.66	14.65	48.05
COHA	Adult	Redwater	8.29	-23.58	14.84	43.23
	Juv	Redwater	5.50	-23.37	15.90	56.38
	Adult	Sturgeon River Gibbons	8.09	-21.20	12.53	41.90
	Adult	Redwater	7.51	-23.43	14.05	45.07
	Juv	Redwater	7.14	-24.82	12.72	48.35
	Juv M	10 km S Ardrossan #1	6.97	-22.87	17.06	55.63
	Juv F	10 km S Ardrossan #2	10.74	-23.55	17.98	47.89
	Juv	10 km S Ardrossan #3	6.48	-24.13	19.29	52.69
	Juv	Antler Lake #1	5.75	-23.96	16.76	53.27
	Juv	Antler Lake #2	4.98	-23.61	18.13	54.89
	Juv	Antler Lake #3	5.09	-23.73	19.34	56.74
	?	Edmonton #1	10.91	-22.09	11.93	36.69
	?	Edmonton #2	4.80	-22.80	13.71	40.18
	?	Elk Island	7.66	-22.91	16.13	47.32

	?	Orloff Rd Calling Lake	7.43	-22.54	14.28	42.58
	?	AB #1	5.11	-21.14	14.11	47.18
	Juv	AB 1A '96	10.89	-21.38	12.75	39.31
	Adult	Beaverhill Lake 96	10.87	-22.00	13.30	42.50
	?	NW Lacombe	10.35	-23.02	13.85	42.37
	?	Kerrywood	6.09	-21.03	14.39	44.75
	Juv	AB 2a '96	6.01	-21.61	14.43	45.36
	Juv F	Antler Lake 96	8.73	-22.03	13.95	45.94
	Adult	Antler Lake 96	8.61	-22.28	14.32	47.40
	Adult	Redwater 96	7.58	-21.02	19.91	67.59
	Juv #946	Redwater 96	7.38	-23.24	18.20	69.90
SSHA	?	Calling Lake	7.72	-22.10	15.35	43.88
	?	Beaverhill Lake	8.61	-21.52	13.37	45.10
	Juv	S. Edm	3.67	-20.66	13.69	42.91
	Adult F	Devon	7.98	-23.30	13.73	42.84
	Adult	1a '96	5.60	-22.60	14.19	44.20
	Adult F	2a '96	9.09	-22.39	14.33	43.49
	?	Kerrywood '96	7.40	-23.12	14.18	43.73
	Adult M	AB #1	7.28	-21.40	10.96	34.32
	Adult F	Calgary	7.28	-21.49	15.01	46.31
	Adult F	Nanton	6.61	-21.40	14.55	45.96
	Juv M	3411 103 ave Edm	7.09	-22.46	13.08	43.08
	Juv	Athabasca	7.68	-22.54	15.43	48.78
	Juv	Red Deer	6.66	-24.75	14.62	46.75
	Adult F	Ft. Assinaboine	6.09	-21.45	16.08	50.03
	Adult F	Calgary	6.03	-21.38	14.38	46.70
	Adult F	Canmore	5.44	-22.51	14.89	49.13
	Adult F	Edmonton	7.35	-22.16	15.70	49.45
	Adult M	Calgary	5.40	-21.95	14.54	46.10
	Adult M	Cochrane	9.87	-15.11	13.65	48.36
	Juv M	Calgary	6.28	-22.17	15.02	48.07
NOGO	Adult	8 mi N Opal	6.11	-25.20	11.70	40.70
	Adult	Calling Lake	7.21	-20.51	13.48	42.09
	Adult	Daygrass Lake	7.90	-22.04	14.94	49.73
	Adult F	Hinton R27 T51	7.50	-20.07	17.63	48.30

	Adult	Hinton R27 T50 Sec 34	4.83	-22.66	13.65	43.52
	Adult	Hinton nest #2	7.45	-21.02	15.67	47.19
	Juv	Hinton nest #2	3.89	-21.00	14.96	48.36
	Juv M	Sylvan Glenn	4.79	-25.84	13.78	47.19
	Juv	Sylvan Glenn	9.54	-23.00	16.28	47.87
	Adult	Hinton nest #1	7.33	-24.27	17.20	44.15
	Juv	Hinton nest #1	6.33	-22.17	15.05	48.47
	Adult	Hinton Wild Hay	6.34	-21.18	16.80	46.74
	?	AB #1	6.61	-24.11	15.86	48.06
	Juv	AB #2	7.77	-23.77	12.35	44.49
	Juv	AB #3	7.59	-23.66	10.97	37.41
	Juv	AB #4	8.13	-25.02	15.87	48.24
	Juv	AB #5	7.71	-23.91	13.89	46.27
	Juv	AB #6	5.32	-20.85	14.14	44.09
	Juv	Bonneville '96	8.25	-23.43	12.88	40.92
	Juv	Buffalo Lake '96	6.21	-21.78	15.02	45.26
PEFA	Juv '95	Edmonton AGT	10.62	-15.76	17.46	47.88
	Adult '95	Shelter Pt	11.28	-22.83	14.38	46.38
	? '94	Shelter Pt	10.80	-21.54	13.54	44.71
	? '95	Alison Bay	10.83	-23.53	15.17	50.32
	?	Fiddler Pt	11.88	-23.21	16.20	51.39
	Adult'95	AB #1	10.45	-23.95	14.93	48.23
	Adult 95	AB #2	10.04	-23.18	13.12	43.43
	?	Boyer Island	9.80	-18.68	-	-
	?	Grouse Cape	9.70	-18.81	-	-
	Adult '94	Halfway Island	8.20	-22.11	-	-
	Adult '95	Halfway Island	10.93	-23.18	15.34	49.17
	Adult 96	Halfway	10.22	-24.08	12.42	39.45
	?	AGT	9.36	-23.64	-	-
	Juv 96	Hamilton	9.58	-23.68	14.74	46.40
	Adult 96	Hamilton	11.06	-20.99	15.15	46.16
	Juv 96 F	Halfway #1	8.95	-23.97	14.30	43.19
	Juv 96 F	Halfway #2	8.09	-23.97	15.55	46.28
	Juv 96	Lemon Is #1	7.02	-24.04	16.08	45.23
	Juv 96	Lemon Is #2	7.74	-24.14	15.16	45.49
	Juv 96	Peace #3 #1	8.47	-22.96	15.28	43.52

	Juv 96	Peace #3 #2	8.41	-22.91	14.90	43.05
	Juv 96	Peace #3 #3	8.85	-22.78	16.17	46.98
	Juv	Lower Klewi F	7.57	-23.24	16.02	46.52
	Juv	Lower Klewi m	7.75	-23.61	15.80	45.91
PRFA	?	Longstreak	10.94	-21.91	15.30	45.92
	?	N Red Deer	9.93	-22.42	17.02	51.14
	?	Red Deer	8.45	-24.31	16.49	44.39
	Juv	Landslide	7.54	-22.44	16.80	47.20
	Juv	Side Hob Bow	9.87	-21.80	15.94	44.61
	Juv	Golf Course	10.56	-16.23	15.28	43.16
	Juv	Touge Creek	5.59	-23.56	20.66	55.58
	Juv	Bassano Dam #1	9.00	-24.58	16.46	54.29
	Juv	Bassano Dam #2	9.38	-23.39	20.20	50.19
	Juv	Fairbrother	6.69	-23.10	17.48	48.93
	Juv	Nowton Coulee	7.90	-24.27	15.76	47.88
	Juv	Coult Dairy	9.05	-22.17	16.72	47.23
	Juv	Coult Dairy #2	8.16	-22.87	18.17	50.43
	Juv	AB #1	6.09	-24.16	19.27	49.29
	Adult	J Campbell #1	9.47	-23.32	12.96	39.00
	Adult	1st Porcupine	9.69	-23.98	15.65	46.77
	Adult	J Campbell #2	10.33	-23.71	13.25	38.40
	Adult F	AB #2	13.42	-15.83	15.50	49.09
	Adult M	Enchant	7.43	-22.90	15.48	48.62
MERL	Juv	W Edm 149st White Mud	7.89	-19.52	17.11	53.82
	Juv	W Edmonton 15418 81ave	7.95	-19.43	15.85	46.28
	Adult	Borden Park Edm	10.07	-21.19	15.15	44.83
	?	Boreal Foothills #1	9.04	-15.86	13.90	43.32
	?	Boreal Foothills #2	5.89	-21.95	15.59	45.68
	?	AB #1	5.94	-21.38	16.86	53.17
	?	AB #2	10.16	-19.05	22.70	66.36
	?	AB #3	5.82	-23.94	14.82	42.04
	?	AB #4	8.88	-21.22	18.03	50.91
	?	AB #5	11.88	-20.46	13.88	39.16
	?	Spirit River	6.97	-22.42	15.75	46.43

	?F	Calgary 79	11.02	-21.65	12.11	39.63
	?	Kerrywood '93	5.45	-21.56	13.23	43.66
	?	AB 1a 96	11.03	-18.45	12.75	41.21
	?	AB 2a '96	10.06	-18.16	13.33	42.57
	?	AB 3a '96	13.02	-20.65	12.67	41.52
	?	AB 4a '96	10.41	-20.12	13.55	42.12
	?	Kerrywood	6.67	-21.71	13.36	42.85
	?	Ft. Vermillion	8.14	-21.18	13.20	41.58
	Adult F	Mt Pleasant, Edm	9.32	-21.15	13.82	44.60
	Adult F	Borden Park, Edm	10.55	-18.31	13.77	43.08
	Adult F	Beechmont Cem.	9.93	-20.56	12.94	44.61
	Adult F	E. Edm	8.57	-21.52	14.58	46.35
	Adult M	Mt Pleasant	9.45	-20.31	14.55	47.80
	Adult M	155st Edm	10.80	-21.17	13.21	44.38
	Adult M	Beechmont Cem.	9.22	-19.11	12.62	42.08
AMKE	Juv	Steele Lake	5.77	-22.10	14.18	45.81
	Adult	RR 222 N of 643	13.20	-20.88	15.48	47.32
	Juv	Big Lake	9.10	-23.70	13.97	44.04
	?	AB #1	7.84	-23.74	14.34	43.81
	?	AB #2	6.15	-22.74	12.78	41.85
	?	AB #3	9.36	-20.54	15.38	49.27
	?	Ft Smith	8.70	-23.25	12.62	44.54
	Adult F	Evansburg	7.50	-22.84	13.13	42.53
	Adult	Gordon's	5.87	-23.35	12.34	38.31
	?	Indus #1	7.89	-20.97	11.12	42.10
	?	AB 1a '96	8.27	-22.57	13.05	40.92
	?	Indus #2	6.99	-21.79	13.63	43.21
	Adult F	Crosslake	10.30	-15.69	20.12	35.17
	Adult M	Rochester	8.06	-24.94	19.93	64.11
	Adult F	Big Lake 96	9.74	-23.62	11.18	35.51
	Adult M	Red Deer	7.99	-23.76	12.62	38.76
	Adult M	AB #4	5.80	-24.53	11.18	39.88
	Adult M	Crosslake	9.81	-15.53	15.38	42.58
	Adult M	Stoney Plain	4.27	-16.42	13.62	47.42
	Adult M	Gibbons	7.22	-23.95	11.60	39.89

	Adult F	Steele Lake #1	6.98	-24.02	13.82	44.46
	Adult F	Steele Lake #2	10.13	-15.18	13.00	43.26
GHOW	Adult	Calling Lake Trp 15	8.92	-26.07	14.57	39.77
	Adult	Calling Lake Trp 9	7.01	-24.08	17.22	52.17
	Adult	Calling Lake Trp 11	9.28	-22.49	15.89	42.24
	Adult	Calling Lake Trp 20	11.30	-20.78	14.43	39.59
	Juv	Hinton R24 T52	7.39	-22.45	14.36	43.85
	Adult	Hinton R24 T52	10.41	-23.65	16.07	47.83
	Adult	Sherwood Park	8.72	-25.25	14.40	44.73
	?	Spirit River #1	6.97	-25.04	14.30	45.18
	?	Spirit River #2	6.96	-23.27	14.18	44.19
	?	Spirit River #3	7.37	-24.40	15.74	49.48
	?	Spirit River #4	8.53	-24.82	15.18	47.97
	?	Spirit River #5	9.36	-23.49	16.17	49.39
	?	Spirit River #6	5.87	-24.96	14.56	46.15
	?	Spirit River #7	10.14	-23.75	14.92	44.85
	?	18 km E Rochester	6.91	-24.39	14.06	42.62
	?	Leduc	9.40	-23.60	14.29	39.79
	Juv	SE Edm	8.88	-24.57	14.04	43.75
	Juv	Redwater	7.96	-23.35	13.44	43.24
	Adult	Redwater	8.63	-24.00	13.49	43.49
	Adult	1 km s Redwater	8.86	-23.62	13.61	44.67
	Adult	SE Edm	10.50	-23.39	12.70	41.96
	Juv	1 km s Redwater	7.14	-24.02	14.28	45.81
	Juv	Redwater #1	6.45	-23.50	13.81	44.79
	Adult	Redwater	6.84	-23.44	13.27	44.07
	Juv	Redwater #2	7.86	-23.97	11.80	37.19
	Juv	Josephburg	7.46	-23.28	13.52	45.66
	Juv	Gibbons	8.09	-24.44	14.80	45.48
	Adult	Josephburg	8.06	-23.82	13.88	43.31
	Juv	Jasper Park Lodge	8.97	-22.07	13.09	44.29
	Adult	Jasper Park Lodge	8.45	-23.52	14.89	47.25
	Juv	Gibbons	8.03	-23.92	12.57	42.97
	?	Kerrywood #1 96	10.71	-21.94	16.31	48.46
	?	Kerrywood #2 96	9.39	-24.93	13.81	47.21
	?	Kerrywood #3 96	10.08	-22.50	15.42	45.43

	?	Kerrywood #4 96	8.06	-23.51	15.22	46.17
	?	Kerrywood #5 96	10.61	-23.23	11.82	40.81
	?	Kerrywood #6 96	8.45	-23.20	14.59	46.32
	Juv F	Jasper	8.58	-21.48	15.30	47.75
	Juv M	Ft. McMurray #1	11.79	-22.20	12.51	48.46
	Adult M	Edson	7.04	-23.62	14.09	48.34
	Juv M	Ft McMurray #2	4.76	-22.11	14.41	47.02
	Adult F	Lethbridge	12.83	-23.25	13.09	45.96
	Adult M	Athabasca	7.26	-22.10	13.82	48.42
	Adult F	Nobleford	10.35	-22.55	14.22	46.64
	Adult F	Cardston	7.59	-22.85	14.03	45.98
	Adult F	Tilley	6.76	-23.37	14.44	47.57
	Adult F	Athabasca	8.57	-24.28	14.49	46.40
	Adult M	Jasper	6.25	-21.81	15.24	48.65
	Adult F	Ft McMurray #3	6.26	-24.01	15.00	48.05
	Adult F	Lethbridge #2	9.55	-24.22	14.80	46.43
	Juv F	Brooks	10.07	-20.65	15.54	48.82
	Adult M	Lethbridge #3	12.81	-20.61	15.05	47.76
	Adult F	Nobleford #2	10.21	-19.52	13.61	47.07
	Adult F	Picture Butte	12.67	-21.01	13.06	44.17
	Adult F	Grand Cache	6.07	-25.05	14.36	49.82
	Adult F	Lethbridge #4	13.65	-20.27	15.48	47.61
GGOW	Adult	6 km E Rochester	6.83	-25.70	19.41	58.79
	Adult	Niton	7.63	-23.43	13.96	47.76
	?	N of Bow River #1	6.81	-25.39	14.45	45.11
	?	N of Bow River #2	6.35	-25.55	13.79	47.33
	?	N of Bow River #3	9.29	-24.11	13.65	41.96
	?	N of Bow River #4	7.43	-24.64	12.92	45.43
	?	N of Bow River #5	6.56	-23.46	14.87	48.25
	?	Spirit River #1	10.30	-21.54	15.31	50.25
	?	Spirit River #2	9.63	-21.16	12.95	48.73
	?	Calling Lake Trp 17	8.43	-22.78	16.97	51.94
	?	Rocky Mtn House #1	8.34	-24.34	14.08	43.85
	?	Rocky Mtn House #2	7.84	-23.88	14.94	47.54
	Adult M	Rochester	8.00	-24.05	11.67	44.76
	Adult M	Smith	8.88	-23.66	16.44	55.65

	M	Spirit River	8.30	-23.90	11.94	45.68
	Adult M	Hondo	5.85	-22.50	13.21	43.25
	Adult F	Smith	8.33	-23.37	13.62	44.02
	F	Ft. Assinaboine	6.29	-22.92	13.96	45.11
	Adult F	Ft. Vermillion #1	8.72	-23.26	12.76	41.92
	Adult F	High Level	7.75	-23.44	13.09	42.24
	Adult F	Ft Vermillion #2	9.48	-24.06	13.85	44.55
BAOW	?	Calling Lake #1	6.67	-21.34	15.19	42.26
	?	Calling Lake #2	7.81	-20.80	18.38	53.56
	?	Calling Lake #3	4.81	-20.84	15.97	53.37
	?	Calling Lake #5	7.33	-23.79	18.36	54.60
	?	Calling Lake #6	6.31	-23.66	19.47	56.37
	?	Sherwood Park #1	9.10	-19.66	16.21	47.96
	?	Sherwood Park #2	5.46	-21.18	17.14	49.12
	?	Orloff Lake	7.71	-20.14	15.27	50.53
	?	Hinton R27 T51	7.82	-21.35	15.31	51.48
	Juv	Canmore	6.93	-23.47	14.60	48.95
	?	Canmore IV	7.26	-24.38	14.31	45.10
	?	Drayton Valley	5.02	-19.80	15.01	49.58
	?	Spirit River #1	5.64	-22.42	14.18	52.77
	Ad F	Spirit River #2	5.99	-21.38	15.36	48.51
	?	Sexsmith	7.54	-20.14	14.22	48.06
	Adult F	Solomon Cr. Hinton	7.88	-20.38	14.37	47.42
	Adult	Sexsmith '96	7.30	-21.99	13.57	44.53
	?	Calling L. 96	6.79	-22.79	14.75	45.77
	?	Kerrywood 96	8.89	-21.48	14.74	47.68
	Juv	Rochester 96 #1	6.26	-24.35	21.41	64.76
	Juv	Rochester 96 #2	6.23	-23.82	18.80	55.64
NSOW	Adult	Opal RR222	10.58	-22.08	15.23	52.72
	?	AB #1	6.93	-23.99	14.11	47.08
	?	AB #2	9.13	-23.13	12.69	43.67
	?	AB #4	10.08	-25.73	12.85	37.40
	?	AB #5	7.10	-22.25	19.56	55.27
	?	Spirit River	8.85	-22.20	15.52	52.66
	Juv	AB #1	6.54	-23.78	13.58	47.72

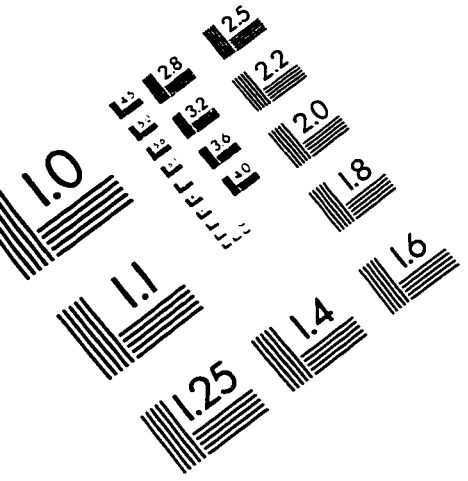
	?	Lynx	9.93	-23.23	13.87	49.62
	Juv	AB #2	7.25	-24.19	14.72	50.77
	Juv	AB #3	7.19	-23.69	15.30	49.70
	?	AB #4	8.17	-22.60	10.24	42.37
	?	Kerrywood 96	7.48	-22.36	14.40	42.65
	?	Calgary fm Kerrywood	7.89	-25.17	13.40	45.74
	?	AB 1a	5.75	-19.95	15.85	48.75
	?	AB 2a	4.08	-23.20	13.36	41.46
	?	AB PMA #1	5.12	-21.99	14.79	43.93
	?	AB PMA #2	7.95	-20.27	16.07	47.26
NHOW	Juv M	Edmonton Longman Bldg	7.52	-24.43	13.83	45.56
	? M	Slave Lake 96	6.88	-23.54	15.24	44.84
	Adult F	Peace River	6.77	-23.95	15.56	46.63
	Juv F	Hines Creek	6.58	-21.83	15.16	45.43
	Adult F	White Court	8.22	-22.47	14.76	46.32
	Adult M	AB #1	7.21	-22.94	13.07	45.47
	Juv F	AB #2	6.49	-23.27	15.73	46.51
	Adult M	AB #3	9.24	-21.18	14.95	46.78
	Juv	AB #4	6.73	-22.92	15.01	47.31
	F	AB #5	5.74	-23.37	16.20	47.93
	Juv F	Flatbush	8.83	-24.40	14.66	51.63
	M	AB #6	7.88	-22.53	15.78	47.76
	Juv M	Flatbush	5.81	-23.26	18.35	56.36
	Adult F	Rocky Mtn House	5.47	-21.95	13.13	39.02
	Juv M	Whitecourt	7.68	-24.37	15.08	49.09
SNOW	?	AB #1	2.49	-21.94	13.44	51.66
	?	AB #2	5.10	-21.65	13.41	51.21
	?	AB #3	4.55	-22.09	15.05	48.09
	?	AB #4	4.54	-22.73	15.02	51.85
	?	Ft. Vermillion #1 96	2.32	-23.56	15.47	47.39
	?	AB 1a 96	3.90	-24.25	16.13	46.74
	?	AB 2a 96	2.79	-22.34	13.92	44.87
	?	AB 3a 96	4.12	-23.56	13.15	43.79
	?	Kerrywood 96	4.76	-23.82	16.61	49.32

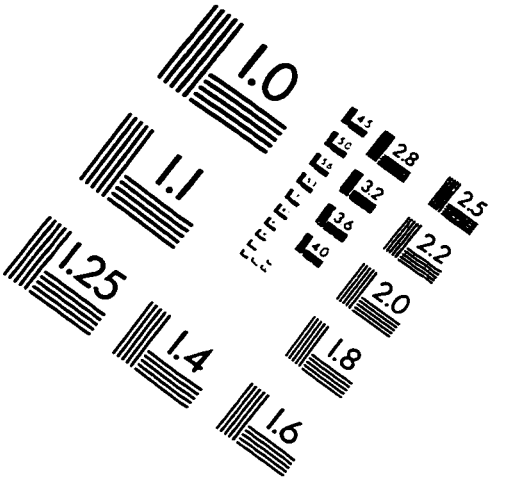
	?	Ft. Vermillion #2 96	5.21	-23.19	15.40	44.14
	Imm F	AB #5	1.89	-24.09	14.17	47.31
	Adult M	Athabasca	6.15	-22.77	15.27	48.89
	Adult F	AB #6	5.07	-21.64	13.91	47.60
	?	AB #7	2.17	-24.37	16.61	49.52
	Adult F	Calgary	6.12	-23.16	14.85	48.55
	Adult F	Beaverlodge	4.18	-21.65	13.69	47.10
	Adult F	Ft. McMurray	4.17	-23.64	14.79	47.67
	Adult F	Beaumont	2.75	-22.34	15.28	47.33
	Imm M	AB #8	5.34	-23.44	15.35	47.21
	Imm F	Drumheller	3.28	-23.67	14.06	45.58
BUOW	Juv	Peak #44	11.23	-23.43	14.38	49.63
	Juv	Peak #43	11.49	-22.94	16.03	48.72
	Juv	Stifle #10	11.59	-23.10	13.16	48.72
	Juv	Stifle R #50	12.60	-22.88	16.78	47.65
	Juv	Stifle R #38	6.70	-24.34	16.33	43.58
	Juv	Stifle N #34	6.32	-22.62	17.08	46.88
	Juv	Stigle S #49	10.93	-21.43	13.46	45.50
	Juv	Boet #48	10.84	-24.30	13.44	51.50
	Juv	Chris #55	11.07	-22.77	18.42	55.74
	Juv	Dillon #15	11.23	-22.66	18.83	55.65
	Juv	Hanna #88	12.34	-19.76	19.46	51.30
	Juv	Penke #52	10.79	-23.30	17.11	47.55
	Juv	Past #46	7.47	-22.47	16.54	45.70
	Juv	Buffalo	9.31	-22.31	17.28	48.20
	?	S. Alberta #1	9.21	-21.36	14.74	47.25
	?	S. Alberta #2	11.64	-20.89	16.75	52.14
	?	S. Alberta #3	10.60	-19.92	14.62	47.32
	?	S. Alberta #4	10.58	-20.25	14.78	51.66
	Adult	Sommerfeld #1, SK	10.74	-20.49	14.83	47.21
	Adult	Gotheil #1, SK	12.14	-21.30	14.38	45.94
	Adult F	Beck #3, SK	15.01	-22.27	13.67	46.25
	Adult M	Golf course #1, SK	8.81	-21.02	14.11	46.14
	Adult F	Milestone #1, SK	11.19	-21.52	11.30	34.85
	Adult F	Mauer #3, SK	11.43	-22.23	10.64	32.64

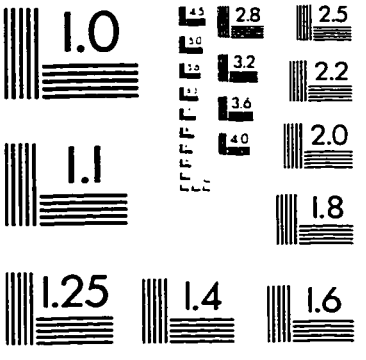
LEOW	Juv	1 mi N Redwater	7.17	-22.81	16.50	52.12
	Juv	Redwater	7.52	-23.52	15.28	52.21
	Adult	Opal Lake	6.44	-	-	-
	Juv	Opal Lake	6.43	-23.33	16.04	50.20
	?	Cold Lake	5.37	-22.98	16.10	44.20
	Adult	Egremont	7.15	-21.43	13.57	48.17
	?	Kerrywood 96	10.29	-23.19	13.27	42.92
	Ad	Edm	6.67	-24.08	18.17	59.15
	?	Lac La Biche	8.91	-23.28	16.95	59.64
	Juv	Lacombe	9.92	-22.83	20.50	62.45
	Adult M	Redwater	7.75	-22.48	18.82	62.39
	Adult M	Calgary	7.49	-21.38	19.85	65.21
	Imm F	Camrose	8.91	-22.73	20.52	64.57
	Adult M	Edgerton	8.84	-23.60	18.20	60.21
	Adult M	Stettler	8.81	-22.13	18.62	64.21
	Adult F	Two Hills	9.77	-21.46	19.35	65.29
	?	Ellerslie	8.01	-23.35	20.75	63.16
SEOW	?	Spirit River	7.34	-24.27	13.81	46.06
	?	AB #1	7.94	-23.19	13.60	44.50
	?	Hay Lakes	9.87	-22.48	14.82	46.64
	Juv M	AB #2	11.47	-22.69	15.94	45.07
	Adult M	Edmonton	5.30	-25.01	14.92	47.82
	?	Grantmyer	7.90	-21.66	15.08	51.95
	?	Spruce Grove	8.04	-22.88	14.38	48.07
	Adult F	AB #3	6.06	-24.55	13.63	46.74
	Adult M	Brooks	10.80	-21.65	15.55	48.48
	Adult M	Strathmore	11.49	-23.25	13.97	45.97
	Adult F	Canmore	7.79	-22.61	13.23	47.19
	Juv F	Calgary	8.86	-22.88	12.96	46.64
	Adult M	AB #4	10.75	-21.51	15.31	46.91
	?	Sherwood Park	7.97	-23.12	14.11	47.90
	?	AB #5	8.13	-25.32	14.73	50.09
	?	AB #6	8.23	-24.83	14.80	47.35
NPOW	?	W of Red Deer	5.45	-23.65	12.04	42.43
	Ad	AB #1	5.70	-21.02	14.63	49.74

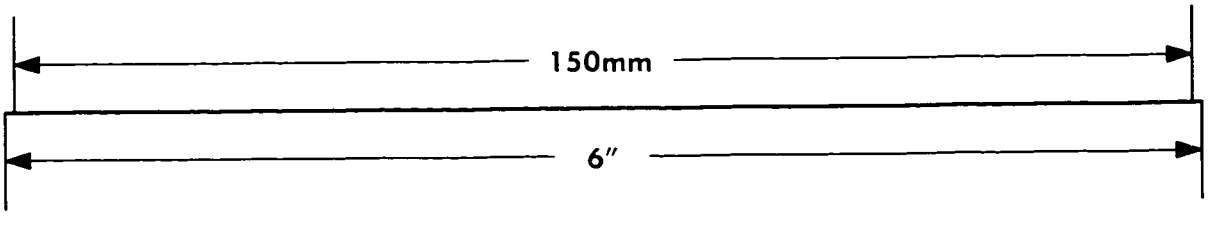
	Adult M	Cochrane	5.28	-21.10	15.37	50.50
	Adult F	Grande Cache	7.05	-20.81	15.00	49.28
	Adult m	Caroline	6.49	-23.11	14.46	48.94
	Adult M	AB #2	4.77	-21.85	-	-
	Adult F	AB #3	8.59	-20.07	15.30	50.89
BOOW	Imm	Edm, Whtmd & 53 St	8.04	-25.17	14.05	45.50
	?	Beaver Lodge	6.73	-23.56	15.00	47.77
	?	Innisfail	8.82	-22.19	15.28	46.77
	?	AB #1	10.65	-20.95	15.81	47.67
	?	Kerrywood 96	6.37	-24.34	13.62	42.90
	Adult F	Nordegg	7.69	-22.44	15.78	46.37
	?	Grande Cache	7.39	-21.21	15.34	46.47
	?	AB #2	5.38	-25.05	15.38	46.97
	Adult	AB PMA	6.61	-23.11	15.01	46.20
	Adult	AB PMA#2	9.64	-24.23	12.71	46.55
	Juv	AB #3	6.09	-23.16	14.20	46.72
	Adult	Rocky Mtn House	8.60	-25.38	13.77	49.03

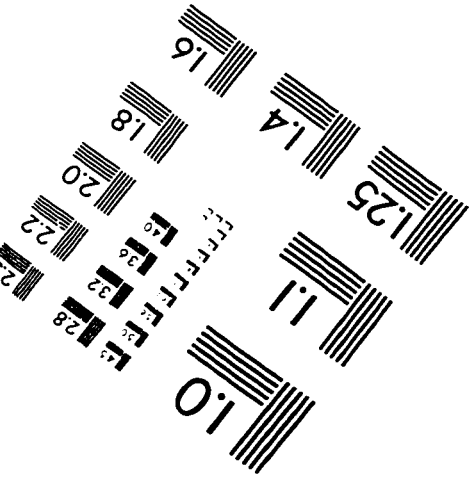
IMAGE EVALUATION
TEST TARGET (QA-3)

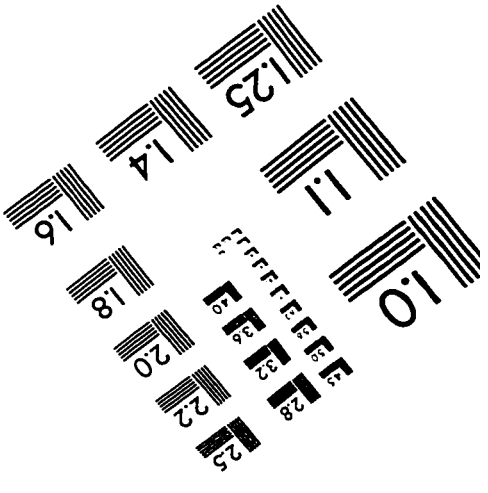












APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989