Ecological and evolutionary causes and consequences of intra-population variability in foraging niche: predator and prey in a marine archipelago

by

Christopher Tod Darimont
B.Sc., University of Victoria, 2000

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Abstract

The niche concept, which provides a tractable measure of the environment encountered by organisms, figures prominently in ecological and evolutionary theory. Although neglected, valuable information may be gained by examining niche variation at hierarchies nested within its historical roots at the species level. Herein I examine intrapopulation variation in foraging niche – at the sub-population, social group, and individual levels - and investigate its ecological causes and evolutionary consequences in a predator-prey system within a marine archipelago.

I used two analytical techniques. My primary tool, stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$, coalesces the multiple dimensions of the foraging niche into two dimensions. Variation in prey remains identified in faeces served as an independent data set.

I examined how different levels of resource availability over space and time as well as competition could account for observed intrapopulation niche variation in a terrestrial carnivore (wolf, *Canis lupus*). Major shifts in resource use were associated with biogeographic region, from dominance of *in situ* terrestrial resources (deer, *Odocoileus hemionus*) on the mainland to prevalence of allochthonous (marine) resources on islands. The probability of deer remains in wolf faeces declines as a function of island isolation. Correspondingly, marine enrichment in isotopic signatures of wolves increases with isolation. Estimates of marine biomass assimilation vary from roughly 25 to 50 to 75% among mainland, inner, and outer island sub-populations respectively.

How animals select resources also can contribute to intrapopulation variability in niche. A 'resource selection' approach indicated that, when available, wolves select spawning salmon (*Oncorhynchus* spp.) over deer. Although only available during autumn, salmon contribute up to 25% of biomass assimilation in wolves over the 6 month period for which it was estimated. Moreover, previously undocumented salmon hunting by wolves I report identifies them as among a few primary biological vectors that transfer salmon from marine into adjacent terrestrial ecosystems.

I also ask whether intrapopulation variation exists at finer scales, and specifically at the individual level. Approximately 40% of total variation in 'isotopic niche' exists *within* social groups, likely a function of strong intraspecific (*i.e.* intra-pack) competition in this social carnivore. Moreover, the magnitude of inter-individual variation was significantly higher on inner islands compared with the mainland and outer islands, likely because of differences in prey species richness and interspecific competition, which likewise vary among biogeographic regions.

On a smaller spatial scale, I examined the niches of deer to ask whether microspatial variation in vegetation patterns also create conditions suitable for inter-individual niche divergence. Such variation presents a potentially central object on which natural selection can act. Using intra-generational comparisons of deer that had either survived or perished from wolf predation, I detected resource-specific fitness. Individuals with isotopic signatures that suggested they foraged in nutritionally-rich forest stands were more likely to be killed by wolves, suggesting a trade-off between predation risk and nutritional benefit. Moreover, non-survivors diverged more than survivors from median isotopic niches, suggesting selection against foraging specialization. Both selection against specialization and proposed trade-offs would maintain observed variation in niche, and possibly also traits associated with the niche. Stable isotope analysis in an evolutionary framework provides novel opportunity to integrate the ecological and selective landscapes to identify underlying ecological mechanisms of selection and provide insight into the maintenance of variability.

Variability in intrapopulation niche can be predicted by ecological and evolutionary conditions and processes in the environment. Specifically, niche variability is largely a function of habitat variability, which large and varied protected areas would

best provide. Moreover, management that aims to safeguard an 'average niche' for a population may not adequately protect diverse populations and the processes underlying such readily observed variability.

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Darimont, C. T., T. E. Reimchen and P. C. Paquet. 2003. Foraging behaviour by gray wolves on salmon streams in coastal British Columbia. Canadian Journal of Zoology **81**:349–353.

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Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2007. Stable isotopic niche predicts fitness of prey in a wolf-deer system. Biological Journal of the Linnean Society **90**:125–137.

A reprint in PDF appears as Appendix 1.5

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Acknowledgements

By necessity, 'I' appears as the dominant subject throughout this document. The reality is that 'I' am one component of the Rainforest Wolf Project, from which this dissertation grew. I am thankful to a massive team of volunteers, colleagues, mentors, friends, and family - many of whom belong to several categories - who contributed and supported me throughout the last six years. To those I have overlooked in my haste, I apologize; I hope I have let you know that you are important to me and the team in other ways.

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Chapter 1: Introduction

As a tractable and measurable character applicable to all living organisms, the concept of the niche directly or indirectly underlies most ecological and evolutionary theory. Hutchinson's (1957) notion of a n-dimensional hypervolume serves as the most commonly acknowledged articulation of the niche, in which each possible and varying component of the activity range of a species, both biotic and abiotic, comprises one of the dimensions. In animal ecology, dimensions related to foraging often are emphasized, following the 'eat or be eaten' dictum that unites organisms and provides a foundation into higher order inquiries in ecological systems (Hutchinson 1957). Importantly, the variability within dimensions, and in particular its causes and implications, provides the framework for the niche concept's prominence in theory.

At the level of the species, the niche concept is considered central to ecology (Leibold 1995, Chase and Leibold 2003). Most niche theories, which are many and varied, have focused on relationships among species. Principal among them is interspecific competition, which is the most commonly identified cause of niche differentiation among species (Case and Gilpin 1974, Armstrong and McGehee 1980). Indeed, competition has long been inferred by the magnitude of niche overlap between or among species (*e.g.* Hutchinson 1944). Evidence of ecological segregation is then invoked to explain the abundance and distribution of species in communities (Levins 1968, Vandermeer 1972, Gaffney 1975, Jackson 1981, Chase and Leibold 2003).

However valuable, if inquiry into niche variation was restricted to its historical roots at the coarse-grained species level, additional opportunities for insight into ecology would be forgone. Much of the literature on niche ecology anchors the 'Hutchinsonian niche' to the level of species. This only may be appropriate if species are ecologically and functionally homogenous assemblages of populations, which themselves are constructed of indistinguishable individuals. However inappropriate, this simplification pervades; even within literature that popularized the niche concept or measured niche breadth, most papers omitted discussion of intrapopulation variability (*e.g.* Hutchinson 1957, Colwell and Futyma 1971, Abrams 1980 *but see* Lomnicki 1988, DeAngelis and Gross 1992). Further, some have proposed that niche variation among individuals is uncommon and/or small in magnitude (*e.g.* Case 1981, Schoener 1986). Likewise, even current research overwhelmingly examines diet at the coarse-grained population level, with little or no attention to intrapopulation variation (*review in* Bolnick et al. 2003).

Alternatively, one can view the niche as a concept that most appropriately applies to individuals, which may be scaled up subsequently to higher levels of organization. Specifically, the niche clearly can be regarded as a response by individuals to complex ecological and evolutionary processes. Such a perspective was first articulated in a component of Van Valen's (1965) niche variation hypothesis. Examining the niches of mainland and island birds, Van Valen proposed that population niche expansion can occur via increased among-individual variation in foraging, such as he observed in island populations, which were released from interspecific competition. Prior to this, Levene (1953) described a theoretical and mathematical model for the maintenance of genetic polymorphisms in which different alleles are favoured in different ecological niches. Since these seminal works, evidence has accrued that demonstrates that individuals with access to similar suite of resources can vary widely in their niche. Recently, Bolnick et al. (2003) reviewed support for the 'individual niche', identifying evidence from 97 species across a broad range of taxa. In some cases, among-individual foraging niche accounted for most of the total population niche breadth.

What causes such variation in niche at the individual level? After all, optimal foraging theory would predict that every individual is united in behaving to maximize fitness, using resources to maximally accrue benefits such as net energetic gain (Stephens and Krebs 1987). What, then, causes such variation to be observed within species and populations?

A carefully considered response would propose that individuals (and subsequently sub-populations) would vary in niche as a consequence of a complex interaction between the ecological environment encountered by the individual (on which this dissertation is focused; Figure 1.1) as well as traits specific to that individual. As one example of how the ecological environment would influence niche, and returning to optimal foraging theory, is the prediction that optimal solutions would depend to large extent on the rate at which alternative resources are encountered (*i.e.* resource availability) and competition for these resources (MacArthur and Pianka 1966, Stephens and Krebs 1987). Essential to this argument is that one would expect resource availability and competition to vary considerably among sub-populations, and even among individuals within a population. But how, exactly, should resource availability vary at this intrapopulation level?

Resource availability varies, and can be a central cause of intrapopulation divergence in niche, because of underlying temporal and spatial variability (Figure 1.1). Specifically, populations and species can respond differently to temporal availability of resources (*e.g.* Werner and Hall 1976). Responses to seasonal pulses of resource abundance in particular are considered very important factors in the evolution of life histories (Boyce 1979). In chapter 3, I examine how the temporal (*i.e.* seasonal) availability of a marine resource can be reflected in niche variability among individuals in a terrestrial carnivore.

Resource availability varies not only over time but also over space. The influence of spatial variability on available foods can be related to Hutchinson's (1957) concept of the 'mosaic nature of the environment', which he cited as a significant cause of niche variation. Simply, heterogeneity at scales from the landscape (*e.g.* Angerbjörn et al. 1994) to microspatial (*e.g.* Kohda 1994) level can influence the distribution and abundance of foods offered to individuals and sub-populations, which cannot occupy the same space at the same time. Chapters 4 and 5 explore this concept and examine specifically how biogeographic heterogeneity can influence niche variation among sub-populations. Specifically, I evaluate how niches diverge between mainland and island populations in a terrestrial carnivore, as well as among island populations as mediated by island characters (especially isolation). Such resource polymorphism, commonly detected in fishes, amphibians, and birds, has not frequently been revealed in mammals (*review in* Skúlason and Smith 1995). On a smaller scale, in chapter 9, I investigate whether microspatial variation in vegetation patterns can also create conditions suitable for niche divergence among individuals (herbivores) foraging among, or even within, different forest stand types.

Spatial heterogeneity may also influence resource availability in an indirect manner by altering predator-prey dynamics in insular environments. In this way, consumers themselves may in fact affect their own resource availability. Theoretical, experimental, and observational data suggest that predators in isolated fragments can exert significant effects on prey abundance (Kareiva and Southwood 1990, Kareiva and Wennergren 1995, Dolman and Sutherland 1997, Schneider 2001, Vucetich and Peterson 2004). In chapters 4 and 5, I make inference into how island characters, especially isolation, could influence *in situ* terrestrial (*i.e.* island) resource availability by altering predator-prey relationships.

Alone, resource availability may not adequately explain observed intrapopulation variability in niche. A more detailed examination requires asking how consumers select from available prey resources. In chapter 6, I adopt a 'resource selection' approach (Manly et al. 2002) to discriminate between hypotheses that identify a marine resource as a selected or alternate resource for a terrestrial carnivore.

Determining which resources are selected over others can yield insight into the ecological relationships among consumer, prey, and the ecosystem. Particularly relevant throughout the dissertation is how materials cross boundaries among disparate ecological environments and its implications (Polis et al. 1997, Cadenesso et al. 2003a,b). Although relatively little is known on the role of biotic vectors in transporting these cross-boundary resources (Polis et al. 1997), recent work has focused on a limited number of terrestrial carnivores that transfer spawning salmon (*Oncorhynchus* spp.) from their spawning grounds into adjacent forests. Early efforts focused on identifying the direct and indirect recipients of salmon nutrients (Reimchen 1992, 1994, Cederholm et al. 2000, reviews in Willson and Halupka 1995, Schindler et al. 2003). This allocation of salmon directly and indirectly feeds multiple trophic levels through scavenging of carcasses followed by decay and subsequent fertilization of riparian vegetation (Ben-David et al. 1998, Helfield and Naiman 2001, Hocking and Reimchen 2002, Mathewson et al. 2003, Reimchen et al. 2003, Wilkinson et al. 2005). Research in this context has focused on bear (*Ursus* spp.) and mustelid vectors, which partially consume salmon and deposit carcass remains, urine and faeces throughout riparian areas (Reimchen 1992, 1994, 2000, Ben-David et al. 1998). In chapter 7, I identify a previously unrecognized vector by providing the first description of the behavioural and ecological context of salmon predation by another terrestrial carnivore.

When resources with high nutritional content (*i.e.* protein, fat, and energy) are available to multiple consumers, one may predict that competition serves as another central cause of observed intrapopulation variability in niche. I explore how such competition within and among species can affect niche divergence among individuals in a focal carnivore (Figure 1.1). Specifically, in chapter 8, I ask how sociality influences niche divergence among members of social foraging groups. Theory leads to two opposite predictions. First, if individuals forage together and encounter the same resources at the same time, one may expect little inter-individual variation in niche. Specifically, and especially if variation in resource availability exists over space (*i.e* biogeography, microspace, above) one may expect much smaller variation *within* compared with *among* social groups. In contrast, an alternate prediction would state that such proximity while foraging would lead to intense intraspecific competition (Goss-Custard et al. 1984, Giraldeau and Caraco 2000), particularly if dominance hierarchies exist and there are quality differences among resources (Radford and du Plessis 2003). Also in chapter 8, I test a component of Van Valen's (1965) niche variation hypothesis, which predicts that with reduced *interspecific* competition, niche variation increases (within a focal species). Biogeographic characters of the landscape are again important in this inquiry, as they dictate the distribution and density of potential competitors.

Whereas resource availability and competition may be central causes to observed intrapopulation variability, traits unique to individuals also influence foraging decisions. Although I only briefly explore them in a component of chapter 9, related mechanisms that would influence inter-individual niche divergence are numerous and likely conflated. Proximally, they can relate to differences in physiology and behaviour, which can be ultimately governed by age (Polis 1984, Werner and Gilliam 1984), sex (Shine et al. 1989), and morphology (Price 1987). Moreover, an individual's experience (*e.g.* Werner et al. 1981) and cultural heritage (*e.g.* Estes et al. 2003) can influence resource use. Moreover, niche variation among individuals likely also is influenced by a genetic component to resource preference, for which there is good evidence of heritability (*review in* Jaenike and Holt 1991).

Viewing the niche as a heritable trait provides opportunity to examine the evolutionary implications of variation among individuals, and by extension how such implications may subsequently be a cause of observed variability (Figure 1.1). The main focus of chapter 9 is to examine the relationship between the niche of individuals in a prey population and their survival - a common fitness measure - under the risk of lethal predation. This is a rare approach; evolutionary-ecological studies tend to examine population-level responses to predation, and in general there has been little inquiry into individual variation or its consequences, especially in the context of fitness (review in Bolnick et al. 2003; *but see* Clutton-Brock 1988, Stuart-Smith and Boutin 1995). The extent to which fitness is linked to spatial behavioural traits underlying the niche would determine how evolution of those traits and potentially also the niche itself would proceed by natural selection. Although not investigated here, selection would also be influenced by the amount of unsuccessful predation; if predation is highly efficient, there is little differential survival among phenotypes and thus slight opportunity for selection to operate (Vermeij 1982).

The primary tool for my inquiries into niche variation is stable isotope analysis (SIA). Remarkably analogous to a Hutchinsonian n-dimensional hypervolume, SIA can coalesce and reflect the niche in fewer dimensions. Combined, two isotopic signatures I used - carbon and nitrogen - can thus simplify and explore the complexity of the niche. These signatures estimate use of resources by consumers over potentially long periods (*reviews in* Peterson and Fry 1987, Rundel et al. 1989, Kelly 2000). For example, isotopic signatures in herbivores reflect those of the plants they consume (Stewart et al. 2003), which themselves vary among and within areas and species, mediated by abiotic and biotic factors. Specifically, there are well-known environmental gradients or discontinuities that are reflected in signatures; for example a large isotopic gradient exists between marine and terrestrial biomass (Chisholm et al. 1982), which features prominently in chapters 3, 5, 6, and 8. Additionally, when the isotopic composition of potential prey is known, details about individual variation in diet can be identified (Bolnick et al. 2003, Matthews and Mazumder 2004). Further, models I employ in this dissertation permit quantitative estimates of the contribution of potential food sources to dietary niche (*e.g.* Phillips and Koch 2002).

Although currently unexploited in evolutionary studies, SIA can serve an important role in the continued evaluation of the relative roles of random and deterministic processes in evolution. Especially valuable would be scenarios in which both isotopic and phenotypic variability among individuals is known and can be related to measures of fitness. Indeed some of the most noteworthy demonstrations of natural selection are supported by detailed and long-term information about the ecological theatre in which selection occurred (*e.g.* Grant and Grant 2002, Reimchen and Nosil 2002).

A secondary tool I employ is analysis of faeces. Although often perceived an aged technique, I have attempted to be creative in extracting additional 'facts from faeces' (Putman 1984, Kohn and Wayne 1997), increasing the breadth of information available from animal 'waste'. The principal contribution in this respect was a recognition that faeces contain not solely 'prey remains' but additionally individuals that were selected against by an agent of selection (*i.e.* predator); and furthermore that their traits and ecology could be compared to survivors. Such monitoring of predation can provide direct evidence for selection and its targets (Endler 1986, Shine et al. 2001).

Insights gained from this approach and others were in part aided by three philosophical perspectives upon which I relied heavily during this dissertation. First, I often pursued (and was afforded the privilege to do so) an inductive approach. Initial observations, especially in the field, led to the goal of finding out how nature works. Second, and related, I have considered myself a student of natural history, particularly at the beginning of the project. While such activity is becoming (undeservedly) marginalized in academia (Noss 1996), it provided me sufficient insight (and enthusiasm) to pose the questions I did in my study system. Third, I felt strongly about embracing traditional ecological knowledge, especially from the Heiltsuk (Haggan et al. 2006).

Relationships among focal organisms in my inquires allowed me to investigate both previously addressed and newly identified processes related to intrapopulation variability in niche. Wolf (*Canis lupus*)-deer (*Odocoileus hemionus*)-salmon (*Oncorhynchus* spp.) associations provided the model system. Owing to their large spatial requirements and elusive nature, wolves as a focal species define a system profoundly more challenging than those previously investigated in the context of niche ecology and evolution (*e.g.* Darwin's Finches [*Geospiza* spp.]; three-spined sticklebacks [*Gasterosteus aculeatus*]). Moreover, one also may predict that these carnivores may not show much departure from an ungulate-dominated niche; recent reviews concluded that although wolves can be opportunistic predators, the abundance and availability of ungulates strongly predict the distribution, behaviour, and ultimately reproduction and survival of wolves (Paquet and Carbyn 2003, Peterson and Cuicci 2003).

In my study area, however, potential niche space available to wolves (and their prey) is broad and variable, providing abundant opportunity to identify patterns of niche variation as well associated causes and consequences. If continuity of ecological and evolutionary process among taxa is indeed the norm, I would predict that processes identified in other systems should be detected readily among wolves and their prey in the study area (Figure 1.2).

British Columbia's (BC's) central and north coast, which is roughly 60,000 km^2, includes an archipelago. Islands there - that vary in size, isolation and other characters - offer natural and replicated experimental units (Gorman 1979, Williamson 1981) that differ not only in resource availability but also in potential competition. Specifically, marine resource availability varies considerably over space (biogeographic regions, home ranges of wolves) as well as time (seasonally, yearly). Moreover deer (prey) in the area have wide potential niches (Kirchhoff and Larson 1998), which allowed me to assess the evolutionary implications of niche divergence under the risk of predation.

This study area, known as the 'Great Bear Rainforest', is among the few remaining large areas on the planet only minimally modified by habitat destruction, fragmentation, and invasive species. Consequently, it is a precious academic resource (Paquet et al. 2006), harbouring one of humankind's last opportunities for studying pristine systems that are being replaced elsewhere with invasive species or managed landscapes (McKinney and Lockwood 1999).

Chapter 2 (already published) describes the study area and distribution of wolves across the BC archipelago. Chapters 3, 4, 7, and 9 - data chapters - are likewise already published. These five chapters appear in brief summary form in the dissertation and as PDFs in Appendices 1.1 to 1.5. Additional data chapters (5, 6, and 8) are written in (expansive) manuscript format. All data chapters and this Introduction contain broad discussion; accordingly, I do not provide a separate Discussion chapter. Also appearing as publication reprints in PDF are appendices 2.1 to 2.4, which are: collaborations related to this project (Bryan et al. in press [ontogenetic niche differentiation in wolves]; Paquet et al. 2006 [spatial ecology of island wolves]; Price et al. in press [mammal distribution on islands]); and a paper tangential to the dissertation's theme on niche variation (Darimont et al. 2005 [moose emigration to BC's coast]).

Figure 1.1. Causes and consequences of intrapopulation variability in foraging niche. Not an exhaustive list, this figure highlights the ecological and evolutionary conditions and processes associated with niche variation observed in the study system. In italics are processes that serve as central themes in chapters, which are identified by numbers in parentheses. Though not a central theme of the dissertation, I also list traits unique to the individual (*i.e.* sex, age, etc.) that may influence expression of inter-individual variation.

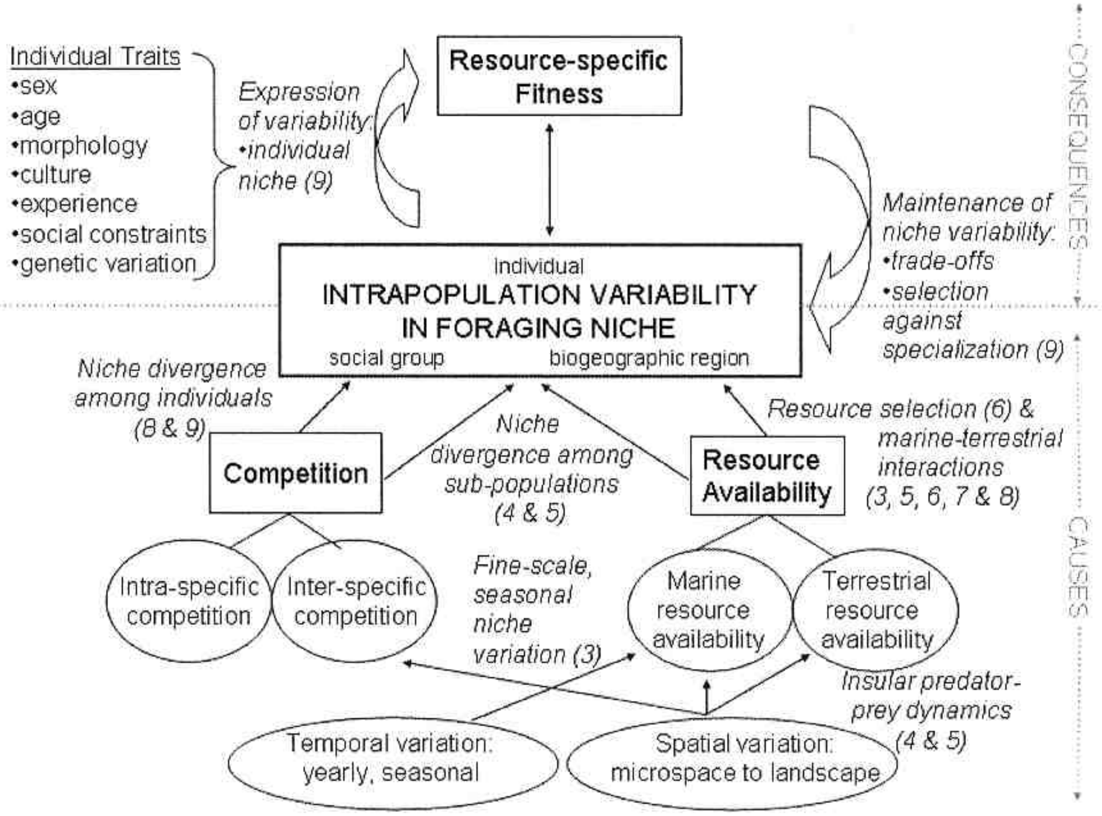
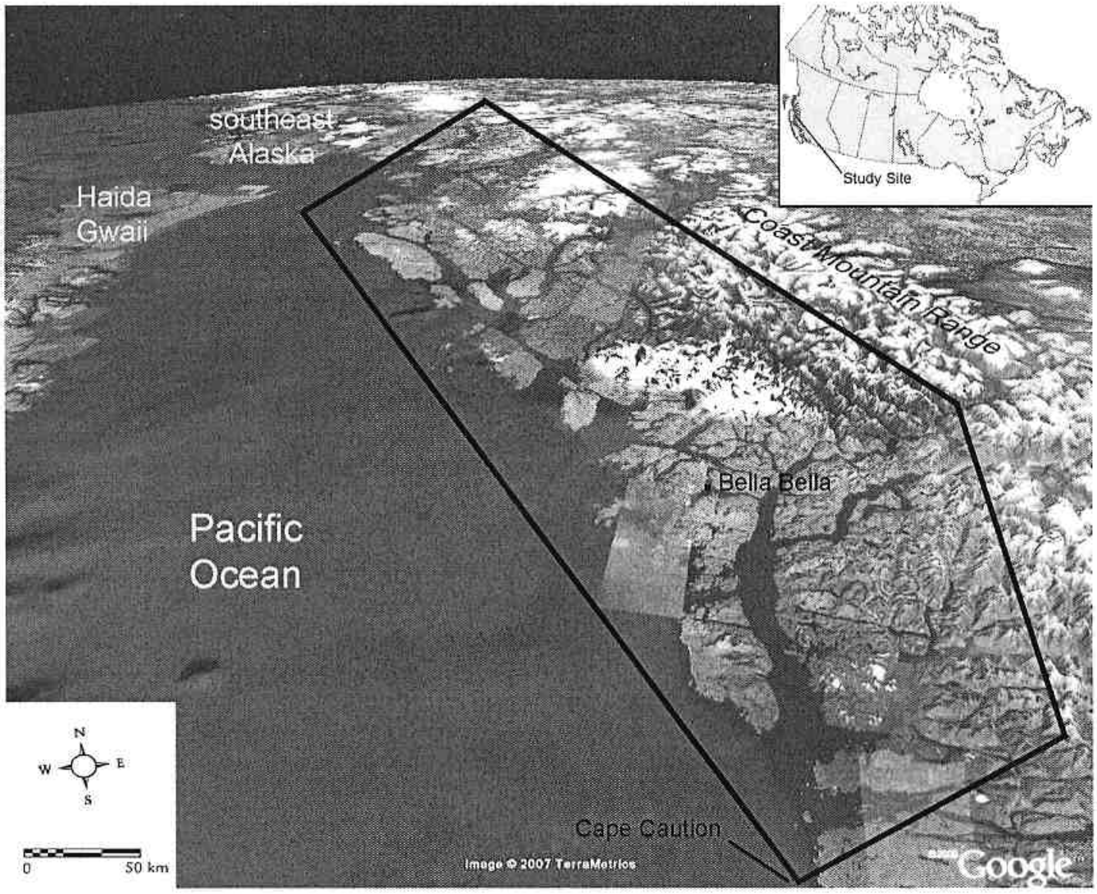


Figure 1.2. Study area on British Columbia's central and north coast. Roughly 60,000 km^2, this area is bound by Cape Caution to the south, southeast Alaska to the north, the Coast Mountain Range to the east, and the Pacific Ocean to the west. Basemap downloaded from www.earth.google.com.



Chapter 2:

Description of study area, focal system, and island distribution of focal species

Below follows a brief summary of:

Darimont, C. T., and P. C. Paquet. 2002. The gray wolves, *Canis lupus*, of British Columbia's central and north coast: distribution and conservation assessment. Canadian Field-Naturalist **116**:416–422.

A reprint in PDF appears as Appendix 1.1

2.1. Chapter Summary

British Columbia's central and north coast is a remote, nearly pristine, and rarely studied 60,000 km^2 network of islands and naturally fragmented mainland landmasses. Little scientific information is known about even the most fundamental ecological parameters, including the distribution of mammals throughout the archipelago. During summers 2000 and 2001, my colleagues and I surveyed 36 islands and 42 mainland watersheds in the area for the presence of wolves (*Canis lupus*). Wolf sign (scat, tracks, howling, and visual observations) was detected at all locations, including islands separated by approximately 7, 8, and 12-km from other large landmasses. The distribution of wolves on islands may be dynamic, with occupancy by solitary wolves or packs being ephemeral. The potential for an island to support a persistent population of wolves may depend on the presence and abundance of their main terrestrial prey, black-tailed deer (*Odocoileus hemionus*), and security from exploitation by humans. These factors likely are mediated by island isolation, area, shape, topography, and extent of logging. As described, this system defines a unique opportunity to examine processes related to island biogeography and resource availability. Additional insight can be sought with the subsequent understanding of how resource availability can vary by season, influence of marine resources, and with levels of interspecific and intraspecific competition, which varies among areas in this archipelago and adjacent mainland.

Chapter 3:

Detection of fine-scale temporal niche differentiation

Below follows a brief summary of:

Darimont, C. T., and T. E. Reimchen. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. Canadian Journal of Zoology **80**:1638–1642.

A reprint in PDF appears as Appendix 1.2

3.1. Chapter Summary

Seasonal shifts in dietary niche are widespread but our ability to detect them can be limited. Comparisons of stable isotopic signatures in metabolically inert tissue portions grown at different times may yield insight but are inadequately exploited in dietary reconstructions. I used segments of guard hair to index diet to periods of growth (*i.e.* season, periods with and without a resource). I applied this methodology to test whether wolves (*Canis lupus*) from British Columbia used marine resources, and if so, whether the bulk of enriched (marine-derived) nutrients was assimilated when salmon were available. Nine of 17 wolves were categorized as potential consumers of marine resources based on relatively enriched $\delta^{13}C$ signatures. In 5 of these 9, I detected a seasonal shift in niche; relatively more $\delta^{13}C$ and $\delta^{15}N$ was assimilated during fall compared with summer, suggesting use of salmon during fall. All 8 non-enriched samples and both controls showed no seasonal shift in diet. Using salmon when available may be adaptive given its predictability, spatial constraint, high caloric content, and lower potential costs in survival relative to hunting large mammals. This fine scale isotopic approach may permit identification of otherwise undetectable niche differentiation among conspecifics or heterospecifics.

Chapter 4:

Intrapopulation variability in niche I: the influence of biogeography on niche variation in a terrestrial carnivore

Below follows a brief summary of:

Darimont, C. T., M. H. H. Price, N. N. Winchester, J. Gordon-Walker, and P. C. Paquet. 2004. Predators in natural fragments: foraging ecology of wolves in British Columbia's central and north coast archipelago. Journal of Biogeography **31**:1867–1877.

A reprint in PDF appears as Appendix 1.3

4.1. Chapter Summary

Consumers may influence their potential niche space by affecting resource availability, particularly in isular landscapes. As one example, predator-prey dynamics in archipelagos may be influenced by fragmentation. Although little is known about these processes, an increasingly fragmented planet underscores the urgency to predict its consequences, particularly for large carnivores, which are sensitive to fragmentation. Accordingly, my aim was to examine how the foraging niche of an apex mammalian predator, the wolf (*Canis lupus*), varied across an archipelago. I sampled 30 mainland watersheds and 29 islands for wolf faeces in summers 2000 and 2001 and identified prey remains. I examined broad geographic patterns and detailed biogeographic variables (area and isolation metrics) as they relate to prey consumed. Black-tailed deer was the most common item in occurrence per faeces (63%) and occurrence per item (53%) indices, representing about 63% of mammalian biomass. Wolves consumed more deer on islands near the mainland (65% occurrence per item) than on the mainland (39%) and outer islands (45%), where other ungulates (mainland only) and small mammals replaced deer. On islands, the probability of detecting deer was influenced primarily (and inversely) by island distance to mainland (not by area or inter-landmass distance). I infer from this pattern that, under continued predation by wolves, reproduction and/or island recolonization by deer is too infrequent to provide similar availability of deer encountered in less isolated areas. Although sampling was limited in time, consistent patterns among islands suggest that this high level consumer can influence the availability of its main prey, thus influencing its own potential niche space. Additional and more intense sampling of this system over multiple years with stable isotope analysis would aid in evaluating this hypothesis.

Chapter 5:

Intrapopulation variability in niche II: biogeographic characters predict marine-terrestrial niche variation in a terrestrial carnivore

5.1. Introduction

Spatial variation at the landscape level can have considerable influence on ecological processes, and especially those related to foodweb ecology. Often in spatially heterogeneous areas, adjacent habitats can differ in available resources. Commonly, resources originating from one ecosystem are consumed by foragers inhabiting another. This flow of allochthonous materials across habitat boundaries can have significant effects not only on foodweb ecology but also on higher order processes such as community structure, as well as the behaviour and life history of consumers (Polis and Hurd 1996a, Polis et al. 1996, 1997, Jefferies 2000, Knight et al. 2005).

Marine-terrestrial interfaces present a prominent example of cross-boundary transport of resources. Shorelines offer terrestrial consumers considerable subsidies from the ocean. Coastal areas worldwide receive from 10 to 2000 kg/year/m of shoreline in organic matter via washed-up algae and carrion alone, which fuel the base of foodwebs along these coastal fringes (Polis et al. 1996).

The quantity and implications of this cross-boundary flow from the marine to terrestrial systems would relate to many characters of both the landscape (*i.e.* coastal mainland and islands) and focal organisms. Biogeographic variables such as area, isolation, and island shape would be important. For example, one would predict that island shapes with greater perimeter (*i.e.* shoreline) to interior ratio would be more permeable to marine nutrient subsidies (Polis et al. 1997). Additionally, larger islands may have greater topographic variability, and thus habitat variability, enabling them to offer consumers resources that may be scare or absent on other islands.

Larger islands, with greater catchment area, may be more likely to provide to terrestrial consumers a resource that is considered one of the most dominant marine subsidies in the Pacific region; spawning salmon (Gende et al. 2002, Schindler et al.

2003). These fishes, which migrate up terrestrial waterways, become available to myriad consumers and scavengers on land. The influence is so profound that it can influence major life history characters in many taxa, from invertebrates to large mammals (*e.g.* Ben-David et al. 1997, Hilderbrand et al. 1999, Cederholm et al. 2000, Hocking et al. 2006, Christie and Reimchen in press).

Additionally, landscape variation in heterogeneous areas can affect foodweb ecology by influencing terrestrial, or *in situ*, resource availability in fragments. Specifically, the interaction between landscape and consumer-resource dynamics can affect the availability of those resources. For example, in fragmented systems, relationships between predator and prey can depart from those observed in homogeneous landscapes. Isolation, in particular, can affect predator-prey dynamics (Kareiva and Southwood 1990, Kareiva and Wennergren 1995, Dolman and Sutherland 1997). In remote fragments, populations may be volatile, characterized by large amplitudes of both predator and prey (Taylor 1984, McCauley et al. 2000). From the perspective of the predator, one would predict that dietary breadth would increase during resource scarcity (Stephens and Krebs 1986). Under these scenarios, predators may rely to a greater extent on cross-boundary subsidies that originate in adjacent ecosystems.

Islands in marine archipelagos offer replicated natural experiments to explore patterns in how predator-prey systems respond to allochthonous (marine) and *in situ* (terrestrial) resource availability as they may relate to landscape variation. In chapter 4, I conduct preliminary examinations into the influence of island isolation, area, and their interaction on the niches of wolves (*Canis lupus*) that inhabit an archipelago in coastal British Columbia. In this initial investigation, one-time sampling of faeces indicated a greater probability of wolves departing from their primary (and terrestrial) prey item (deer; *Odocoileous hemionus*) on islands with greater isolation. Given these data, in chapter 4, I offer the working hypothesis that with increased isolation deer could not reproduce and/or recolonize fast enough to remain available to wolves at levels observed in less isolated areas. I also predict in chapter 4 that additional sampling, spanning multiple seasons and years, would identify the pattern as a steady-state: deer would not be common prey for wolves in isolation but marine foods would comprise prominent contributions to wolf diet.

An additional hypothesis to explain this pattern is that isolated islands support greater marine resources than other islands and the mainland, and the increased use of these marine foods reflects this increased availability. In chapter 4, I show that prey with which wolves replaced deer were often products of cross-boundary subsides from the ocean: smaller intertidal mammals (*i.e.* mink, *Mustela vison*; river otter, *Lontra canadensis*), birds, intertidal organisms, and early runs of spawning salmon.

Assessing patterns in niche among elusive, low-density animals with large spatial requirements over vast landscapes for several years presents tremendous logistical challenges. Faecal examinations in chapter 4 yielded preliminary patterns but offered only a temporal 'snapshot'. Here I use stable isotope analysis of wolf hair, which indexes individual diet in a chronological manner over the entire growth period of pelage, roughly half a year. Moreover, samples originated from a large and broad biogeographic range, allowing opportunity for detailed examination into predator-prey associations across levels of varied insularity and other island characters.

Although islands provide ideal model systems for studying predator-prey interactions in isolation, isolated islands often lack predators and even on less isolated islands mammalian carnivores are relatively rare (Williamson 1981, Alcover and McMinn 1994, *but see* Peterson et al. 1984). Consequently, theoretical insight into insular predator-prey dynamics is limited. The marine archipelago of coastal British Columbia and the wolf-deer system across islands, however, may provide opportunity for insight. In this chapter my objective is to test the prediction of increased use of marine resources with isolation. Also, I seek to identify whether marine or *in situ* terrestrial resource availability is more important in predicting the niches of archipelago wolves. I use island shape and island area as proxies for marine resource availability whereas I interpret any patterns related to isolation and estimated deer abundance on each island as proxies for *in situ* resource availability. I examine broad patterns in isotopic signatures in wolves among mainland and island regions and in detail investigate how these biogeographic and food resource variables can influence the foraging niche of this top predator at a marine-terrestrial interface.

5.2. Materials and Methods

5.2.1 Study Area

British Columbia's central and north coast is a remote area, mostly accessible only by boat or air. The study area is large, roughly 60,000 km^2, and delineated by the Kshwan Valley (55 ° 37' N, 129 ° 48' W) in the north and Cape Caution (51° 10' N, 127 ° 47' W) in the south. The Coast Mountains and the Pacific Ocean bound the study area to the east and west respectively (Figure 1.2). Most low elevation forest in this nearly pristine region is classified as the Coastal Western Hemlock biogeoclimatic zone (Pojar and Mackinnon 1994). Potential prey base for wolves is diverse, including black-tailed deer, mountain goat (*Oreamnos americanus*), moose (*Alces alces*), beaver (*Castor canadensis*), black bear (*Ursus americanus*), river otter (*Lontra canadensis*), plus smaller mustelids, rodents, and birds. Five species of spawning salmonids (*Oncorhynchus* spp.), crustaceans, molluscs, and marine mammals are also available to wolves. Main prey groups, however, as revealed in over 3200 faeces collected over all seasons over 3 years across the landscape, are deer, salmon, and marine mammals (chapters 4, 6, Bryan et al. in press [appendix 2.1]).

5.2.2. Sample collection and preparation for isotopic analyses

This is the same coast-wide dataset of isotopic samples I examine in chapter 8. It includes, too, samples from the Bella Bella 'core study area' I use in chapter 6. During spring and summer 2001 to 2004, coast-wide sites were sampled non-randomly but were well distributed throughout the entire study area (Figure 1.2). At each location, the team surveyed beaches, estuaries, and forests of the beach fringe, often on wildlife trails. We also surveyed logging roads when encountered, circumnavigated beaver ponds, and walked forest ridgelines. Surveys rarely extended greater than 5 km inland. For information on 'core study area' sampling, which followed a similar protocol, see chapter 6. On these surveys, I collected wolf hair that had been shed in resting sites on or near established transects (chapter 6) or at homesites (reproductive areas). I assume each sample originated from one wolf as they were exclusively found in day beds and, on many occasions, I sampled sites directly after viewing individual wolves.

I used tissue types and sampling protocols that were most appropriate to answer the questions I posed. Wolves have one annual moult that begins in late spring when the old coat sheds and a new coat grows until late fall (Young and Goldman 1944). Therefore each sample represents an integrated record of diet for roughly half the previous year's foraging. Thus, samples represented diet in years 2000 to 2003. Over the same period, I also sampled hair from potential wolf prey, which were extracted from wolf faeces I collected. Scats were autoclaved, soaked and washed in hot soapy water to remove residue. Finally, I also collected equal samples of both sexes and species from 16 recently senesced spawning pink and chum salmon (*Oncorhynchus gorbuscha* and *O. keta*), which form the majority of salmon available to the area's wolves. I sampled only tissue from salmon heads because wolves primarily consume this body part (chapter 7).

To prepare hair, I sonicated samples (between 10 and 30 strands each) in distilled water, then soaked them in 2:1 chloroform:methanol solution for approximately 24 hours to remove oils and debris. I then dried hair at 60^0 C for at least 48 hours. Salmon tissue was homogenized in a blender, then desiccated in a drying oven for 2 weeks before sample preparation. I powdered the dried hair and salmon tissue in a Wig-L-Bug™ grinder (Cresent Dental Co, Chicago, Ill). Approximately 1-mg was sub-sampled for continuous-flow isotope ratio mass spectrometry analysis at the stable isotope facility, University of Saskatchewan, using a Europa Scientific ANCA NT gas/solid/liquid preparation module coupled to a Europa Scientific Tracer/ 20 mass spectrometer. Isotopic signatures are expressed in delta notation (δ) as ratios relative to PeeDee limestone (carbon) and atmospheric N_2 (nitrogen) standards as follows:

$$\delta X = [(R_{sample}/R_{standard}) - 1] * 1000,$$

where X is ^{13}C or ^{15}N, and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Units are 'parts per mil' (ppm), or commonly expressed as $^0/_{00}$. Note that carbon signatures in this dissertation (and many other studies) are negative, reflecting their relative isotopic depletion compared with the PeeDee belemnite standard (limestone from the PeeDee Formation in South Carolina; derived from the Cretaceous marine fossil *Belemnitella americana*).

To estimate precision, I drew on a closely related isotopic dataset on hair from deer. These samples were collected by the same researchers, prepared by the same technician and ran on the same mass spectrometer by the same operator during the same year. Thirteen replicates on separate mass spectrometer runs showed precision averaging 0.05 (+/- 0.04 SD) $^{0}/_{00}$ for carbon and 0.06 (+/- 0.05 SD) $^{0}/_{00}$ for nitrogen.

5.2.3. Statistical Analyses

I explored patterns in isotopic data from wolves as they may relate to three areas associated with general habitat differences: mainland, inner islands, and outer islands (chapter 4; see also Figure 1.2). I defined inner islands as those directly adjacent to the mainland and outer islands as those that are not, irrespective of distance to mainland (chapter 4). Because deer have wide dietary niches and are the primary prey of wolves in the area, I also examined isotopic signatures of deer in these three biogeographic regions. This tests the hypothesis that any changes in isotopic signatures among wolves of these regions could be related to changes in deer signatures (or the underlying plant food web).

In the same biogeographic framework I investigated seasonal changes in isotopic niche to inquire if salmon use differs among the same three regions. Assuming wolf pelage grows at a relatively constant rate, the base portion of guard hairs would reflect most recent dietary assimilation (fall) whereas the tip portion would reflect summer diet (chapters 3). In wolves that received $\delta^{13}C$ and $\delta^{15}N$ enrichment primarily from salmon, one would expect coupled enrichments of these isotopes in hair that grew during fall salmon runs (base) relative to hair that grew during summer (tip; when salmon are absent; chapter 3). In chapter 6, I provide evidence that this technique yields an accurate measure of salmon use by wolves.

Identifying which ecological variables best explain the extent of marine resources in wolf diet may give insight into underlying process above and beyond general biogeographic patterns. Accordingly, I used Akaike Information Criteria (AIC) to evaluate the strength of support for competing models that explain how different combinations of biogeographic and food resource parameters may affect isotopic signatures of wolves. Using each island as a case ($n = 11$), I necessarily limited candidate variables, focusing on: distance to mainland (MDIST); an estimate of each island's relative deer abundance (DEER); island area (AREA), and shape (SHAPE). This last variable reflects how much shoreline is available for a given island area, which may provide a reasonable proxy for marine mammal and intertidal resource availability. Shape index was calculated in GIS as:

(0.25*Perimeter)/sqrt. (Area),

where 0.25 accounts for square pixel shape (Paquet et al. 2006 [appendix 2.2]). Smaller shape index values represent rounder islands (with less shoreline per given area). For details about the DEER model, which estimates relative deer abundance and can be applied at the island level, see chapter 6 and Paquet et al. (2006 [appendix 2.2]).

From these variables of interest, I formed exploratory *a priori* hypotheses to explain how these biogeographic and food resource features would affect the mean $\delta^{13}C$ signatures of wolves on each island. I selected $\delta^{13}C$ as the dependent variable because it is a better indicator of marine versus terrestrial source of biomass accumulation than $\delta^{15}N$ (Tieszen and Boutton 1988). Specifically, any measure using $\delta^{15}N$ would include not only source processes but also those related to trophic position (DeNiro and Epstein 1981, Minigawa and Wada 1984).

Candidate models were partly based on earlier data from this system of how marine enrichment (or departures from deer diet) increases with isolation (chapters 4, 8). Accordingly, each candidate models included MDIST. Candidate models took a general linear form (GLM), weighted by the square root of the number of wolves sampled on each island. I pooled data across years because there is little variation in isotopic data among years (chapter 8). Multicollinearity diagnostics suggested only weak to moderate interdependencies among predictor variables (Variance Inflation Factors range: 1.297 to 10.26; note that only values over 15 suggest a possible problem with collinearity; SPSS Inc., Chicago, USA).

For each model, I calculated AIC, adjusted for small sample sizes (AIC_c), following the formula: $AIC_c = n \log(o^2) + 2K + 2K(K + 1)/(n - K - 1)$, where $o^2 = \text{Sum}(e_i^2/n)$, K is the number of parameters (including intercept and error term), n the numbered of islands and e_i the residuals for each candidate model (Burnham and Anderson 1998, p. 63). I then evaluated ΔAIC_c to select best approximating model(s) and make appropriate inference. Although a threshold of 4 is commonest, to increase inference I also used $\Delta AIC_c < 5$ to describe an alternative top model set (see Results). Finally, I summed Akaike weights (ω_i) across top model sets for each variable to rank them by importance (Burnham and Anderson 1998). Each candidate model had errors that were normally distributed (Kolmogorov-Smirnov Z tests, all $P > 0.05$). All statistics were estimated using SPSS 11.0 (SPSS Inc., Chicago, USA).

For increased resolution into food resource use, specifically identifying what prey are used and their relative importance across biogeographic regions, I used isotopic mixing models. These models work by assessing similarity in isotopic composition among the consumer's tissues and its food sources (after adjustment for fractionation - or changes in signatures - during digestion, metabolism, and assimilation) to provide an index of the relative importance of each item in the consumer's diet. Mathematically, these are 'linear mass balance mixing models' that quantify the fractional contribution of elemental mass from each food source to a consumer's diet (Phillips 2001). Phillips' models are comprised of three equations and three unknowns (f_X, f_Y, and f_Z), which can be solved to determine the contribution of each food source to diet, given the linear independence of the equations (natural variations in C and N isotope ratios are generated by different biochemical and ecological processes, likely satisfying this assumption). The mass balance equations are:

$$\delta^{13}C_M = f_X\,\delta^{13}C_{X'} + f_Y\,\delta^{13}C_{Y'} + f_Z\,\delta^{13}C_{Z'} \qquad (1)$$

$$\delta^{15}N_M = f_X\,\delta^{15}N_{X'} + f_Y\,\delta^{15}N_{Y'} + f_Z\,\delta^{15}N_{Z'} \qquad (2)$$

$$fX + fY + fZ = 1 \qquad (3)$$

where M is the 'mixture' (*i.e.* consumer tissue) and X, Y, and Z are the sources (*i.e.* food groups). In equations 1 and 2, the fractions of each source add to the value of the mixture; isotopic values of food sources have already been adjusted to account for trophic fractionation (designated as such by the prime (') symbol). In equation 3, total fractions must add to unity.

This standard mixing model was subsequently improved to account for how variations among the sources in elemental concentrations for the two isotopes may affect the source proportions derived for the two elements. Philips and Koch (2002) developed a 'concentration-weighted linear mixing model' ('IsoConc') allowing for each element of a source's contribution to be proportional to the contributed mass times the elemental concentration in that source. In sensitivity analyses, varying the N concentration of only one source had large and differing effects on the estimated contributions of each source, and was demonstrated using a case study of bears (*Ursus* spp.) feeding on salmon, moose (*Alces alces*), and plants. The estimated biomass contribution of salmon from the concentration-weighted model was significantly different than that calculated with the original model (Philips and Koch 2002).

Given that potential prey groups for wolves also differ in elemental concentrations (see Results; Table 5.1), I used IsoConc (Philips and Koch 2002). I considered three prey item groups for wolves: deer, salmon, and 'marine mammal' group, which included seals (*Phoca vitulina*), river otters (*Lontra canadensis*) and mink (*Mustela vison*). I grouped these three animals because they typically have marine diets, have isotopic signatures not significantly different from one another (data not shown), and because they are the most common 'tertiary' prey taxa recovered in wolf faeces after deer and salmon (chapters 4, 6, Bryan et al. in press [appendix 2.1]).

For increased insight, I also used an 'IsoError' model, another iteration of the basic linear mixing models that allows variability in the food sources and consumers to be recognized in mixture estimates (Phillips and Gregg 2001). Whereas IsoConc yields only a point estimate of the contribution of each food source, IsoError provides measures of variability. The model provides these estimates for consumer diets using the following inputs: mean, sample sizes, standard deviation, and correlations (between isotopic signatures within each source) of three prey 'endpoints' and the mixture.

Isotopic values in prey remains, which were extracted from wolf faeces, were corrected for digestion effects prior to model input. Previously, I had found that digestion of prey hair by wolves caused a marginal but consistent enrichment in isotopic signatures across four trials in which I sampled hair from deer pre- and post-digestion by wolves (*i.e*, on prey carcasses and in wolf scat respectively). Mean shifts in $\delta^{15}N$ and $\delta^{13}C$ were + 0.84 (+/- 0.66 SD; range 0.30 to 1.66) and + 0.49 (+/- 0.15 SD; range 0.28 to 0.61) respectively (chapter 9). These grand means thus were subtracted from faecal hair samples (prey) to correct for digestion effects.

5.3. Results

5.3.1 General biogeographic patterns in isotopic signatures

Wolves showed clear biogeographic patterns in isotopic signatures, which increased with greater isolation from the mainland. Both carbon and nitrogen signatures in wolf hair increased significantly from mainland to inner to outer islands ($\delta^{13}C$ ANOVA; $F_{2,75} = 24.97$, n = 78, P < 0.001; δ15N Kruskal-Wallis test; $\chi^2 = 33.00$, n = 78, df = 2, P < 0.001). In contrast, deer signatures, representative of the terrestrial foodweb, remained similar among these biogeographic regions ($\delta^{13}C$ ANOVA; $F_{2,71} = 0.66$, P = 0.518, Figure 5.1; δ15N ANOVA; $F_{2,71} = 0.164$, P = 0.849, Figure 5.2).

Marine influence, as indexed by mean $\delta^{13}C$ signatures of 11 sampled packs inhabiting islands, increased linearly with isolation (r = 0.76, n = 11, P = 0.007, Figure 5.3). Similarly, $\delta^{15}N$ increased with greater island isolation (r = 0.68, n = 11, P = 0.022). The relationships between isolation and mean isotopic signatures were not evident after the removal of the (most isolated) Dundas Island datapoint ($\delta^{13}C$; r = 0.47, n = 10, P = 0.170, Figure 5.3 inset; $\delta^{15}N$; r = 0.36, n = 10, P = 0.310).

Biogeographic patterns were not as strong in seasonal shifts in wolf diets among regions. There was only marginal increases in fall enrichment from the mainland to the outer islands in both isotopes ($\delta^{13}C$ ANOVA, $F_{2,75} = 2.20$, n = 78, P = 0.121; $\delta^{15}N$ ANOVA; $F_{2,75} = 2.00$, n = 78, P = 0.142, Figure 5.4).

Using individuals as cases, patterns of correlation between carbon and nitrogen marine enrichment differed among biogeographic regions. $\delta^{13}C$ versus $\delta^{15}N$ slopes increased significantly from mainland to inner and outer islands (ANCOVA; Adjusted R^2 model = 0.95; LOCATION x $\delta^{13}C$ interaction $F_{2,75} = 21.20$, n = 78, P < 0.001). Significantly less enriched nitrogen is assimilated with enriched carbon on the mainland compared with islands (Figure 5.5).

5.3.2. Effects of island isolation, area, shape, and deer abundance

Finer scale analysis with additional biogeographic and food resource parameters yielded only marginally more insight into the processes underlying observed patterns. Using AIC, the only model in the top set, defined by $\Delta AIC_c < 4$, was one that included

MDIST only, suggesting that the overwhelming influence in the isotopic patterns among identified variables was due to isolation. Extending the top model set to those with $\Delta AIC_c < 5$ yielded little additional information. Each other parameter occurred once with MDIST but no parameter coefficients other than for MDIST were significant (Table 5.3). Summing Akaike weights over this top model set revealed that MDIST was at least 14 times more important in predicting isotopic signatures than any other parameter. Conducting this analysis again, but excluding Dundas - the most isolated island - yielded identical model ranking and similar weighting.

Subsequent univariate analysis showed no patterns with DEER, AREA, or SHAPE (data not shown). Plotting residuals of $\delta^{13}C$ over isolation, however, revealed a subtle pattern related to island area. Specifically, higher residual scores were related to the greater log (island area) ($r = 0.61$, $n = 11$, $P = 0.045$).

5.3.3 Results of isotopic mass-balance models

Output from IsoConc and IsoError models yielded similar estimates of prey consumption by wolves, and showed biogeographic patterns concordant with raw isotopic data. Contributions from terrestrial sources (*i.e.* deer) decreased from the mainland to islands while the contributions from salmon and marine mammals increased (Figure 5.6). Wolves from all islands combined consumed at least twice the biomass of marine foods compared with mainland conspecifics. Salmon and marine mammals accounted for only about 25% of biomass assimilation for mainland wolves. On the inner islands, however, these prey contributed about half of the biomass. On the outer islands, both models suggested that roughly 75% of biomass was derived from salmon and marine mammals (Table 5.4).

5.4. Discussion

Principal concepts of landscape ecology – spatial variation in habitat, boundary effects, and landscape connectivity – also can be central to food web ecology (Polis et al. 1996a). Herein, I explicitly explore these links by identifying biogeographic patterns in the niche of a top predator in the foodweb of a marine archipelago. Moreover, examining the influence of several variables allowed me to discriminate among possible hypotheses regarding ecological processes underlying these patterns. Before discussion of these patterns and processes, I explore how these data also yield insight into the life history of wolves of coastal BC.

5.4.1 Marine Wolves

Given current understanding of the life history of wolves, a terrestrial predator, one may not expect extensive use of marine resources. Across their holarctic range, wolves have been described as ungulate specialists, with close ecological and evolutionary associations with these hoofed prey for hundreds of thousands of years (Paquet and Carbyn 2003, Peterson and Cuicci 2003). Recent but limited research has shown that wolves, however, when sympatric with salmon likely do depart from an ungulate-dominated diet and potentially consume this marine resource to a considerable degree (Szepanski et al. 1999, chapters 2, 4, and 7). Moreover, in chapter 6, I show that wolves actually select salmon over deer, consuming the marine resource as a function of its availability while not responding to deer abundance. Data presented here show increased temporal and spatial breadth of this association with salmon, as well as identify marine mammals as similarly frequent prey items. Collectively, salmon and marine mammals on average comprise more than half of assimilated biomass for island wolves.

Considering this marine food consumption, coupled with their archipelago habitat that necessitates frequent swimming (chapter 2, Paquet et al. 2006 [appendix 2.2], *personal observation*), BC's coastal wolves share many characters with a terrestrial ursid - Polar Bears (*Ursus maritimus*) - that many consider a 'marine mammal'. With the perspective that evolutionary transitions from terrestrial (back) to marine life histories occur gradually, one could consider these coastal members of Canidae behind Polar Bears, which themselves are behind 'fully marine mammal' mustelids (*i.e.* river otter; sea otter; *Enhydra lutris*) on a continuum. Additional discussions on the process of resource-associated population divergence follow in the *Implications* section below.

5.4.2 General biogeographic patterns in isotopic signatures

Fundamental changes in the isotopic niches of wolves occurred across the landscape. δ^{13}C and δ^{15}N signatures increased from the mainland to inner islands to outer islands. These increases were the result of marine enrichment. Differences in isotopic pools or signatures in prey across the landscape do not offer a plausible explanation; across the same regions, the signatures of deer did not change. And although data were insufficient to test, there is limited reason to believe that salmon or marine mammal signatures would differ either. If changes in marine mammal signatures underlie the variability in wolf signatures, one would in fact predict the opposite pattern of that observed. Specifically, in general one would predict less intertidal invertebrate biomass on the mainland compared with islands, given that bottom-up influences that promote intertidal productivity are greater on islands compared with mainland areas, and wave-exposed compared with sheltered areas (Menge et al. 2000 *and references therein*). If the case in this study area, this would lead to the prediction of higher trophic level consumption (and $\delta^{15}N$ signatures, which increase at each trophic step) in mainland otter and mink. This would have an effect of elevating $\delta^{15}N$ signatures in their consumers (wolves) on the mainland, thus masking the effect of increased enrichment with isolation.

Models such as IsoConc and IsoError provide estimates of niche only as accurate as their inputs. I found, however, that these two models yielded concordant and plausible estimates of how niches varied across the landscape. Specifically, mean wolf signatures from each area largely fell within the (narrow) mixing triangle defined by deer, salmon, and 'marine mammal' prey groups. Only the estimated range of salmon contribution to the diet of mainland wolves included negative values in the IsoError procedure. Collectively, this suggests that the simplification of isotopic niche space used in models was reasonable. Indeed, decisions underlying the simplification were informed by faecal data from the same population (chapters 4, 6; Bryan et al. in press [appendix 2.1]). Moreover, estimates of prey signatures were likewise derived from field sampling the prey population (and targeted tissue types in the case of salmon), not from literature, which is often the case.

Regardless of the accuracy with which the models may adequately simplify sub-population level niche, one would expect departures by individuals from food niches composed of one of the three identified food groups. In this biodiverse area that offers dozens of terrestrial and marine prey species to apex predators, among other items I have observed the remains of sea lions (*Zalophus californianus*), goat (*Oreamnos americanus*), porcupine (*Erethizon dorsatum*), moose (*Alces alces*), black bear (*Ursus americanus*), beaver (*Castor canadensis*), smaller rodents, birds, and intertidal animals in the faeces of BC wolves (chapters 4, 6, Bryan et al. in press [appendix 2.1]). Moreover, I also have observed wolves feeding on stochastic resources, particularly those from the ocean such as beached humpback whales (*Megaptera novaeangliae*) and giant Humboldt squid (*Dosidicus gigas*). Astonishingly, I have heard a credible account of several wolves that were scavenging on (top of) a bloated and floating humpback whale that was entangled in a fishing net near Bella Bella.

Although alone these items have not occurred in more than 5% of faeces examined in my other examinations, faecal data cannot identify how important items may be to some individuals. These rare items in fact could be frequently consumed by certain individuals and/or during certain times. Such broad potential niches, especially in a context of reduced interspecific (and/or high intra-specific competition) provide conditions that promote individual dietary specialization (Van Valen 1965, Roughgarden 1972, Grant and Price 1981, Estes et al. 2003, chapter 8). For visual interpretation of how some of these items may influence the signatures of wolves, I plot isotopic data from additional mammalian prey items I sampled, plus Todd's (1999) data on Humpback whales. Items isotopically more distant to the mixing triangle would have the greatest effect on influencing wolf signatures, given equivalent consumption frequencies (Figure 5.6).

These mixing models also permitted estimates of marine biomass (C and N) contributions to diet. Combining salmon and marine mammal groups into a single marine contribution permits a simple index of niche divergence among regions; marine input to diet varied from roughly 25% to 50% to 75% among mainland, inner, and outer islands, respectively.

Further, these models coupled with additional analysis of isotopic data revealed several additional patterns relating to how marine contributions from salmon and marine mammals varied across regions. First, models estimated that in every region, marine mammal contribution to wolf niche was greater than salmon. Although in chapter 6, I show that wolves select salmon as a positive function of its availability, its tertiary standing among prey groups here reflects the time window that the whole hair samples provide, which spans about 6 months, or roughly 3 times the period in which most salmon are available to wolves. In contrast, marine mammals are available throughout the year.

These data aid in explaining earlier results of Szepanski et al. (1999), who also used isotopic mixing models to estimate prey consumption by wolves, sampled in nearby southeast Alaska. Although these authors included only salmon as possible marine prey, they postulated that other animals, and particularly seals, likely also would have contributed to enriched isotopic signatures. If the niches of wolves from coastal BC and southeast Alaska are similar, they are likely correct, and this consideration underscores value in including all potential prey groups in mixing models. Likewise, it highlights the value of an additional and independent dataset (*i.e.* faeces) to identify the potential niche space of populations (see chapter 6).

Marine mammals appear to be common food resources not only for BC coastal wolves but also other mammalian carnivores in coastal areas. In Glacier Bay, Alaska, harbour seals (mostly pups) comprised almost one-third of prey consumed by a wolf group during summer (Meiklejohn 1994). Likewise, Klein (1995) commonly observed harbour seal remains in the faeces of formerly captive wolves, which were introduced to Coronation Island, southeast Alaska. Coyotes (*C. latrans*) also consume marine mammals; in Washington State, a harbour seal mortality study identified coyote predation as the primary cause of death for pups, accounting for nearly 20% of deaths (Steiger et al. 1989). Rose and Polis (1998) identified the remains of sea lions, dolphins (*Delphinus delphis*), and two whale species in the scats of coyotes from coastal Baja, Mexico.

Another pattern I detected departed from that observed by Szepanski et al. (1999). Whereas biogeograhic patterns were clear and strong among BC regions, these authors found no significant differences in isotopic signatures (or salmon consumption estimates) between coastal mainland and island wolves, even with large sample sizes (n = 62 and 101 for mainland and island wolves, respectively). In fact, δ^{13}C signatures were marginally *higher* in mainland wolves. Also, whereas I found higher variation on islands (this study, chapter 8), Szepanski et al. (1999) showed the opposite trend. Notably, however, we ascribe it to the same underlying process. In areas where deer availability is suspected to be lower, isotopic means and variability in wolves are higher, reflecting more frequent departures from a terrestrial, deer-dominated diet. The differences between studies is that Szepanski et al. (1999) cite low deer densities on the mainland, whereas - although I do not provide data for mainland deer densities - I suggest that deer availabilities may in fact decrease on islands with greater isolation from the mainland (see below). Another reason for these differences between results may be related to logging intensity and history; the Alaskan study area has hosted logging at far great rates and over longer periods. There is good evidence that such habitat modification leads to declines in deer over time (chapter 2). If logging occurred more on the mainland compared with islands of southeast Alaska, this could underlie the differences. Also, island systems in their study were generally not as isolated as those I studied.

The second emergent pattern in this chapter relates to how prey taxa through which wolves become marine enriched differed across regions. From the mainland to inner islands, additional marine enrichment was derived from proportionately more salmon than marine mammals in diet, whereas marine mammals were responsible for more of the additional marine biomass contributions on the outer islands (Table 5.4). This is what one would expect as salmon spawning habitat becomes marginal on the flatter outer coast, whereas marine mammal availability becomes greater along the nutrient-rich outer island coastlines.

5.4.3. Effects of island isolation, area, shape, and deer abundance

In chapter 4, I predict that the ecological conditions I deduce from one-time sampling of faeces could represent a steady state: over time wolves regulate deer on isolated islands to low abundance, regardless of other island characteristics. Here stable isotopic data, which indexes diet over roughly 6 months, from multiple individuals of 11 social groups over four years adds evidence to support this hypothesis. Irrespective of estimated habitat for deer, as well as island size or shape, with greater isolation wolves depart from deer diet, consuming greater proportions of marine resources.

Although patterns in intrapopulation niche variability are clear, the processes behind such patterns are complex and difficult to identify. That wolves depart from a diet dominated by deer with greater isolation may be a function of less deer availability (*in situ* resources) or more allochthonous resource availability (marine resource subsidies).

The data presented here argue for the former, as isolation alone is by far the best predictor of wolf niche, much better than variables that would provide proxies for marine resource availability.

More resources from the ocean should be available to wolves on larger islands and those with increased perimeter to area ratio. Greater catchment areas on larger islands are more likely to support runs of spawning salmon, and increased shoreline should make marine prey from intertidal organisms to beached whales more available to wolves. Despite these predictions of greater availability, there is little evidence that island size and shape predict the niche of island wolves.

How, then, would isolation affect the niches of wolves? Are fewer deer supported by outer island habitats, or do wolves themselves limit numbers of deer on islands? One method of estimating availability is applying a model used by Paquet et al. (2006 [appendix 2.2]), which predicts the relative abundance of deer from topographic slope. Islands varied little in estimates of deer availability, and I found no relationship with marine resource use. One caveat of this model, however, is that the data to construct it were collected on the mainland and inner islands only (study area for chapter 6). For any number of reasons, the capability of outer islands to support deer as a function of its topography may differ, and may in fact be less.

Another, and parsimonious, explanation for a reduced capability for outer islands to support deer is a 'top-down' process. The pattern of marine influence (and departures from deer-dominated diet) was overwhelmingly related to isolation. MDIST, or distance to mainland, alone accounted for nearly half the variation in $\delta^{13}C$ signatures of wolves. The details of the process could relate to reduced dispersal ability of deer prey. Regardless of an island's carrying capacity for deer, predators may deplete populations in isolated fragments if colonization is limited. Specifically, greater distances to mainland can reduce immigration rates by deer, predisposing island populations to sustained predation by wolves (chapter 4). If this is correct, the consuming wolves are themselves influencing resource availability, and thus affecting their potential niche space.

Although examinations of large mammalian predator-prey systems in isolation are extremely rare, others have presented similar data and offered similar explanations. On 540 km^2 Isle Royale, separated from the mainland by over 40 km, fluctuations of wolves and moose (*Alces alces*) have been extreme over the 50 years since colonization by wolves (Peterson et al. 1984, Peterson and Page 1988, Vucetich and Peterson 2004). Closer to BC, in adjacent southeast Alaska, Klein (1996) documented his observations following the release of formally-captive wolves on 73 km^2 Coronation Island, 900-m from another landmass. After reaching a peak of 13 wolves in four years, the population fell to one. During this time, Klein's informal observations suggested that deer numbers had declined significantly. Examination of wolf faeces over this period suggested a departure from deer to smaller terrestrial mammals, seals, and intertidal organisms (Klein 1996). The last wolf was shot in the late 1960s, ending the experiment, and the deer population has since rebounded (Person et al. 1996).

If Klein's (1996) information and the data presented here and in chapter 4 are representative, combined they provide evidence for top-down effects by wolves that affect this predator's own niche. Although its challenging to sample large carnivores and their prey over time, future studies that sample islands to estimate numbers of predator and prey, while monitoring foraging habits, before and after wolf colonization, could provide additional evidence to evaluate this working hypothesis.

Another method to test this hypothesis is to employ dendrochronology. If deer numbers cycle down following depletion by wolves and up following wolf emigration, one may expect this pattern reflected in vegetation over time, apart from effects associated with climate. On Isle Royale, McClaren and Peterson (1994) examined tree rings in balsam fir, *Abies balsamea.* Growth rates were related to independently estimated wolf and moose densities over more than 30 years. Decreased growth was observed when wolf numbers were low and moose numbers high, and vice versa. This provided good evidence that wolf predation reduced herbivory on saplings, supporting a trophic cascade model (McClaren and Peterson 1994).

The wolf-prey system on BC's coast, however, differs from areas without marine subsidies. Specifically, in areas with allochthonous resource availability, consumer abundance is not necessarily solely a function of *in situ* productivity (Polis et al 1996a, 1997, Jefferies 2000). For example, marine-subsidized coyotes maintain 4-5 times higher densities on the coast compared with inland populations in Baja (Rose and Polis 1998).

If this is the case in coastal BC, I suspect that marine subsidies could contribute to sustained low deer numbers on isolated islands.

The pattern of increased marine influence on wolf niche with greater island isolation also fits predictions regarding competition for salmon across the regions. In chapter 6, I demonstrate that when available, wolves select salmon over deer. One may expect wolves to consume more salmon on islands compared with the mainland, where they likely compete with grizzly bears. On outer islands, competition would be further reduced due to an absence of black bears (see chapter 8 for more detailed discussion).

5.4.4. Implications of divergent niches among biogeographic regions

The existence of such divergent niches among sympatric populations has several ecological, evolutionary, and conservation implications. Among ecological consequences, the different suite of prey consumed on islands may be associated with different social ecologies of wolves on islands. Data here, and from chapter 8, suggest much more inter-individual variation in foraging patterns compared to mainland conspecifics, which may reflect a looser social network. Indeed, increased consumption of marine prey, which are generally smaller than deer, is consistent with individuals foraging alone. Second, data from island wolves suggest considerable use of salmon; given that they are the primary mammalian vectors of this marine resource into terrestrial systems on many islands, one would expect profoundly different and as of yet unexplored patterns in distribution of salmon-derived nutrients (see chapters 6, 7 for discussion).

Evolutionary implications of divergent niches among biogeographic regions may be several. First, and particularly if mixing of individuals between mainland and island populations is low, one would expect that marine-oriented island wolves have morphological (*i.e.* colouration best suited for hunting along shorelines), physiological (*i.e.* digestive physiology), and other adaptations for preying on a different suite of food resources than mainland conspecifics. One also may expect immune system or behavioural adaptations that reflect a greater exposure to diseases of marine origin. Salmon poisoning disease (*Neorickettsia helminthoeca*), in particular, may be relevant (see chapter 7 for discussion). Marine mammals, too, are a known reservoir of viral diseases to terrestrial mammals (Prato et al. 1974). In a few weeks at least 300 sled dogs

(*Canis lupus familiaris*) in one area of Alaska died of canine distemper (*Morbillivius* spp.), which was linked to Siberian seals (*Phoca sibirica*) that carried the closest identified strain. Likewise, marine-enriched wolves would likely bear increased levels of salmon-born contaminants for which they have no evolutionary history; higher levels of persistent organic pollutants are associated with greater salmon consumption in grizzly bears of coastal BC (Christensen et al. 2005).

Additional evolutionary implications of these data on niche variation relate to the potential of population divergence. Resource polymorphisms, for which these highly divergent niches among sub-populations qualify, are thought to play a major diversifying force, potentially contributing to population sub-division and even incipient speciation (*review in* Skúlason and Smith 1995). Like here, in many cases, reduced inter-specific competition and empty niches are associated with niche expansion within populations. For example, when they co-occur in lakes, pumpkinseed sunfish (*Lepomis gibbosus*) and bluegill sunfish (*Lepomis macrochirus*) occupy discrete niches; pumpkinseeds specialize on snails in shallow water while blue-gills are planktivorous generalists in open water. Robinson et al. (1993), however, found that where pumpkinseeds existed without bluegills, they had differentiated into two morphs - the typical form, which consumed snails, and an open-water morph with modified gill arches, which fed on zooplankton. This intrapopulation niche divergence, although commonly detected in fishes, amphibians, and birds, has not frequently been revealed in mammals (*review in* Skúlason and Smith 1995), but one would predict that the same processes would apply across taxa.

If niche divergence among biogeographic regions is in fact associated with adaptive morphological, physiological, and behavioural differences, one also may expect a similarly divergent population structure among these regions (*e.g.* mainland versus islands). In theory, a cline in environmental characters can generate genetic differentiation (Doebeli and Dieckmann 2003). Even in large mammals with high dispersal capability, there is an emerging literature on genetic differentiation associated with ecological differences, not solely geographical distance. Examples include data from arctic fox (*Alopex lagopus;* Dalén et al. 2005), cougar (*Puma concolor;* McRae et al. 2005), coyotes (*Canis latrans*; Sacks et al. 2004), and lynx (*Lynx lynx* and *L. canadensis*; Rueness et al. 2003a,b). Perhaps the best example of associated divergence in diet and genetic structure within sympatric large mammal sub-populations is between resident (fish-eating) and transient (marine mammal-eating) killer whales (*Orcinus orca;* Hoelzel et al. 1998).

In wolves, recent analyses have identified population subdivision related to: 1) climate and vegetation clines across a west-east axis of North America (Geffen et al. 2004), 2) hunting specialization on migratory caribou (*Rangifer tarandus*) versus non-migratory prey in northern British Columbia, Yukon, and Nunavut (Carmichael et al. 2001), and 3) climate, habitat types, and diet composition in Eastern Europe (Pilot et al. 2006). This third study was particularly important as sample sizes were large and they found concordant results in both mitochondrial and microsatellite markers. Moreover, climate and vegetation patterns explained over 40% of the genetic variation in mitochondrial DNA over and above that explained by geographical distance. Notably, in the area in which it was possible to assess, foraging niche was associated with genetic distance; 20% of the variation was predicted by the frequency of red deer (*Cervus elaphus*) in wolf diet.

Similar processes may occur on smaller spatial scales, even in this highly mobile carnivore. The working hypothesis that ecological differences among areas (reflected in their niche) can facilitate microevolutionary process behind population subdivision has received preliminary support in this system of coastal BC wolves. Preliminary analysis of microsatellite data (10 loci) from 5 social groups in coastal BC show that island versus mainland occupancy is a better predictor of genetic distance among groups than linear distance among them (Erin Navid, University of Calgary, *personal communication*).

Regardless of possible genetic differentiation, such ecological divergence among subpopulations, especially considering the small spatial scale and high mobility of the animal, should be recognized as important in conservation debate. I agree with Crandall et al. (2000) that so-called ‘evolutionarily significant units’ or high priority conservation units within a species should draw heavily on ecological diversity. In short, the focus of managers should include the preservation of functional diversity rather than solely historical legacy, detectable with neutral genetic markers. Indeed, ecological and functionally divergent populations may not be those with a long history of isolation.

The recent evolutionary history of wolves along British Columbia and Alaska, however, is unknown, but these data on niche may add insight into existing working hypotheses. The most widely accepted suggestion, based on inference from systematics derived from skull measurements, designate wolves of coastal BC and Alaska as isolated members of *C. l. nubilis* - a group that includes populations from central Canada and Minnesota (Nowak 1996). This classification is consistent with speculation that wolves re-colonized the Pacific Northwest from continental North America after the Wisconsin glaciers receded, following the northern expansion of deer less than 10,000 years ago (Klein 1965).

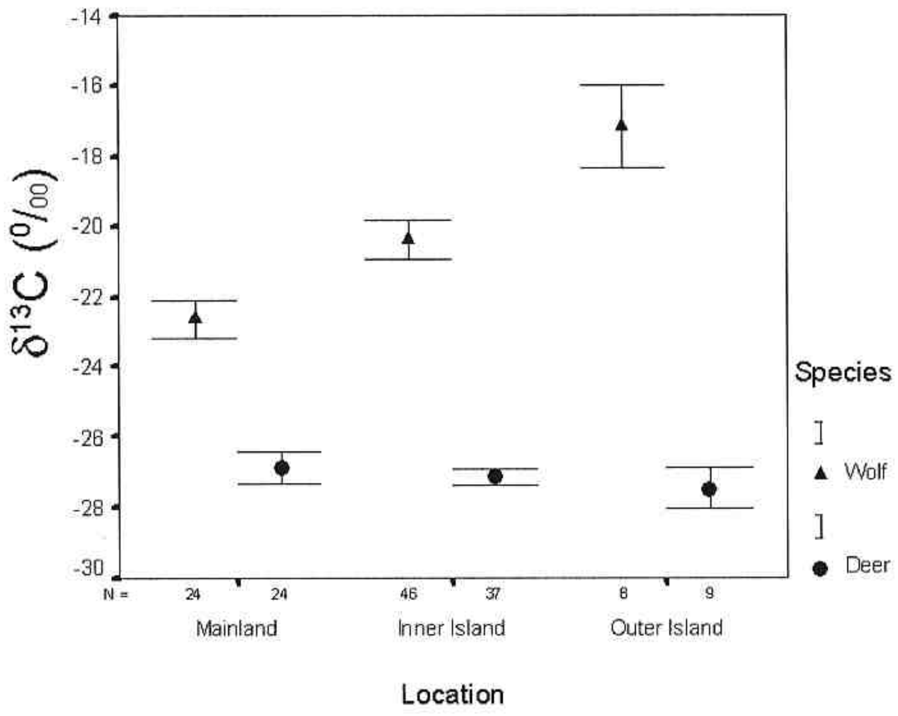
That deer, as the implied primary prey of wolves, figure prominently in the interpretation of this recent evolutionary history can be challenged with the current data, especially given the context of other evidence. As an alternate hypothesis, wolves may have persisted on a series of ice-free refugia on the coast during the Wisconsin glaciation. In another large mammal with high trophic needs and a marine niche - black bears (*Ursus americanus*) - mitochondrial DNA (mtDNA) identified distinct coastal and continental lineages, which may have been isolated from each other for 360,000 years (Byun et al. 1997, 1999, Reimchen and Byun 2005). These authors suggested this was likely the result of pre-glacial differentiation owing to geographic isolation and the preservation of distinct mtDNA lineages in coastal glacial refugia.

That island wolves can incorporate 50 to 75% of their protein from marine sources suggests that they too could have persisted in refugia, even in the absence of deer. Indeed, the outer islands I sampled were adjacent to the continental shelf area that multiple lines of evidence suggest were relatively productive tundra-like ecosystems, which could have functioned as ice-free refugia (Fladmark 1979, Warner et al. 1982, Josenhans et al. 1997). Moreover, the remains of several plausible prey items, both terrestrial and marine, with confirmed glacial dates have now been collected in southeast Alaska and Haida Gwaii, which are both adjacent to this area. Wiggens (2005) itemizes these as hoary marmot (*Marmota caligata*), ringed seal, northern sea lion (*Eumetopias jubatus*), red fox (*Vulpes vulpes*), and arctic fox (*Alopex lagopus*). These physical data provide unambiguous evidence for the presence of a refugium that supported mammals. Moreover, Wood et al. (1994) used protein electrophoresis to identify a genetic lineage of sockeye salmon (*O.*

nerka) associated with a refugium origin. Additionally, the remains of brown bear, another high trophic level mammal, have been recovered on Prince of Wales Island, southeast Alaska, and date back to 35,000 BP, predating the peak of the last glaciation (Heaton and Grady 1993). Given the presence of such prey and similarly high trophic level mammals, wolves too may have been present in these refugia, particularly if they could have persisted on a marine-dominated diet.

Irrespective of uncertainty in their recent evolutionary history, wolves of coastal British Columbia face a near future in which marine resources on which they likely depend face continued and new threats. Many Pacific Northwest salmon stocks have declined dramatically and continue to do so, due to modification of spawning habitat by logging and over-exploitation by the fishing industry (National Resources Council 1996, Harvey and MacDuffee 2002). Additionally, oil and gas development in the waters immediately adjoining the outer coastal islands has been recently proposed. Evidence gathered after 20 years of research on the effects of the Exxon Valdez oil spill indicates that there are still considerable negative effects on ecosystem processes and across many taxa (*reviews in* Peterson 2000, Peterson et al. 2003). Terrestrial carnivores, especially those that have considerable marine niches like island wolves, would be highly vulnerable to a similar catastrophic event.

Figure 5.1. $\delta^{13}C$ isotopic signatures in wolves (*Canis lupus*) and deer (*Odocoileus hemionus*) (and 95% CI) from mainland, inner (adjacent to mainland), and outer islands. Wolves have more enriched isotopic values with greater isolation. In contrast, deer show no difference among biogeographic regions, suggesting elevated signatures in wolves are the result of marine-derived enrichment and not isotopic variability (*i.e.* enrichment) at the base of the food web. Samples collected in coastal British Columbia, 2001 to 2004.



Figures 5.2. $\delta^{15}N$ isotopic signatures in wolves (*Canis lupus*) and deer (*Odocoileus hemionus*) (and 95% CI) from mainland, inner (adjacent to mainland), and outer islands. Wolves have more enriched isotopic values with greater isolation. In contrast, deer show no difference among biogeographic regions, suggesting elevated signatures in wolves are the result of marine-derived enrichment and not isotopic variability (*i.e.* enrichment) at the base of the food web. Samples collected in coastal British Columbia, 2001 to 2004.

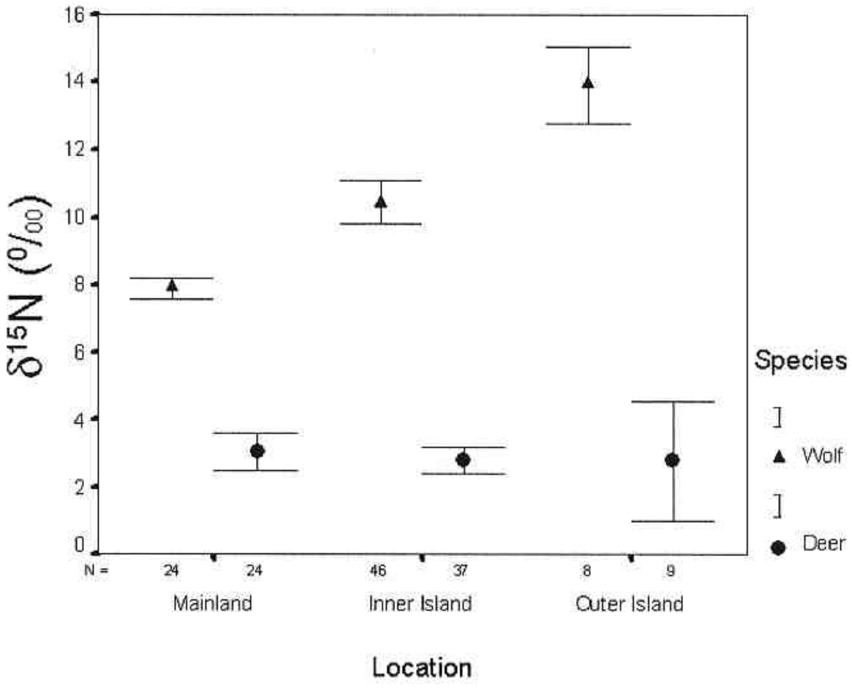


Figure 5.3. Mean $\delta^{13}C$ signatures of wolf (*Canis lupus*) social groups as a function of their island's distance to mainland. Isotopic signatures derived from wolf hair collected in coastal British Columbia, 2001 to 2004. Inset shows dataset that excludes Dundas Island.

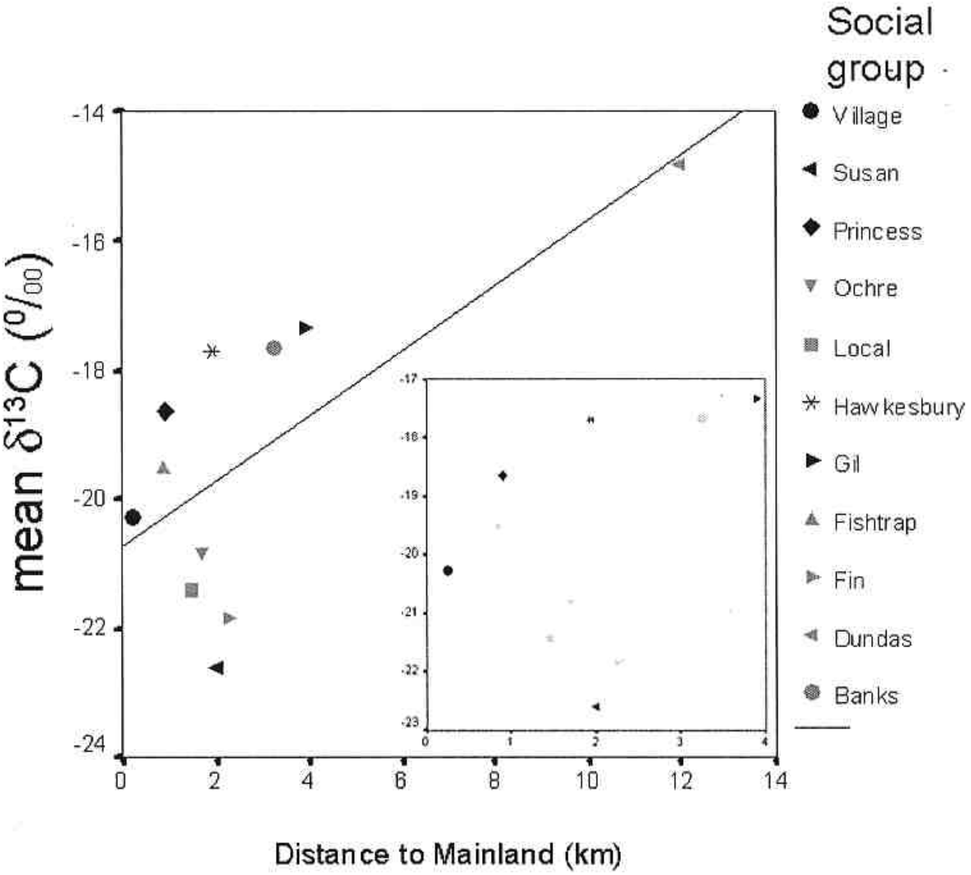


Figure 5.4. Mean seasonal isotopic enrichment (fall minus summer values; and 95% CI)) in $\delta^{13}C$ and $\delta^{15}N$ signatures of wolves (*Canis lupus*) from mainland, inner, and outer island areas of coastal British Columbia. Hair samples (n = 78) collected 2001 to 2004.

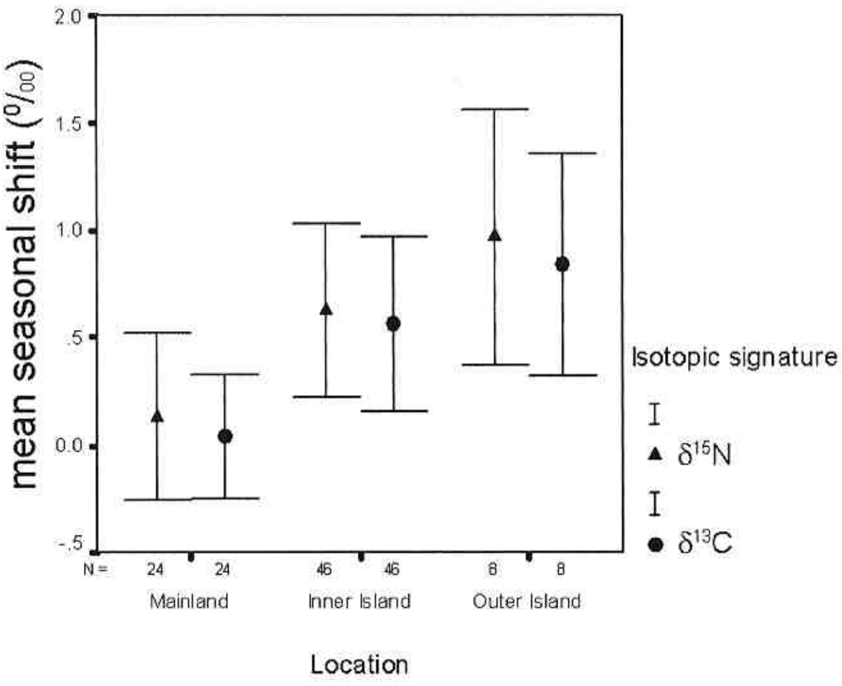


Figure 5.5. Correlation between $\delta^{13}C$ and $\delta^{15}N$ in wolf (*Canis lupus*) hair collected on the mainland (n = 24), inner islands (n = 46), and outer islands (n = 8) of coastal British Columbia, 2001-2004. Bivariate correlations were 0.66, 0.96, and 0.98 for mainland, inner and outer islands respectively (all $P < 0.001$). The slope from mainland wolves was significantly less than island samples, suggesting less use of salmon in total marine enrichment (see Discussion).

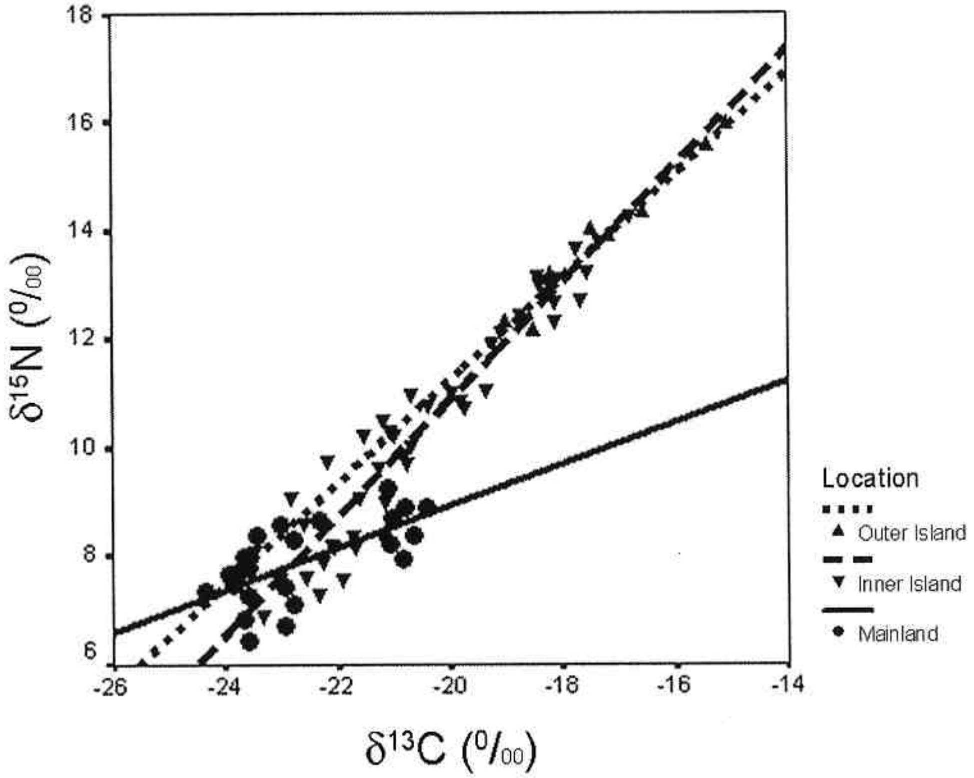


Figure 5.6. IsoError isotopic mixing triangle. Shown are mean (and SE) $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures of wolves (*Canis lupus*, n = 24, 46, and 8 for mainland, inner, and outer islands respectively) and their commonest prey taxa. Marine mammal prey are seals (*Phoca vitulina*; n = 9), river otters (*Lontra canadensis*; n = 4), and mink (*Mustela vison*; n = 6), which had isotopic signatures that were not significantly different. Salmon were 8 pink (*Oncorhynchus gorbuscha*) and 8 chum (*O. keta*). Deer (n = 66) are *Odocoileus hemionus*. Wolf data from whole hair samples. Salmon data derived from

recently senesced individuals. Other prey values derived from hair recovered in wolf faeces. Prey endpoints in mixing triangle represent expected values of wolves consuming exclusively that prey group. Prey signatures corrected for fractionation. All samples collected 2001 to 2004 in coastal British Columbia. I also plot additional mammalian prey items for which I have data (means and SE), plus Todd's (1999) data on Humpback whales (*Megaptera novaeanglia,* 'M') from the Atlantic Ocean, which likely have similar signatures to those inhabiting BC waters (Todd, *personal communication*). A = moose (*Alces alces*, n = 3), C = beaver (*Castor canadensis*, n = 15), E = porcupine (*Erethizon dorsatum,* n = 5), O = goat (*Oreamos canadensis*, n = 10), R = rodents (*Sorex monticolus,* n = 24; *Peromyscus maniculatus*, n = 11; *Clethrionomys* spp., n = 1), U = black bear (*Ursus americanus*, n = 17).

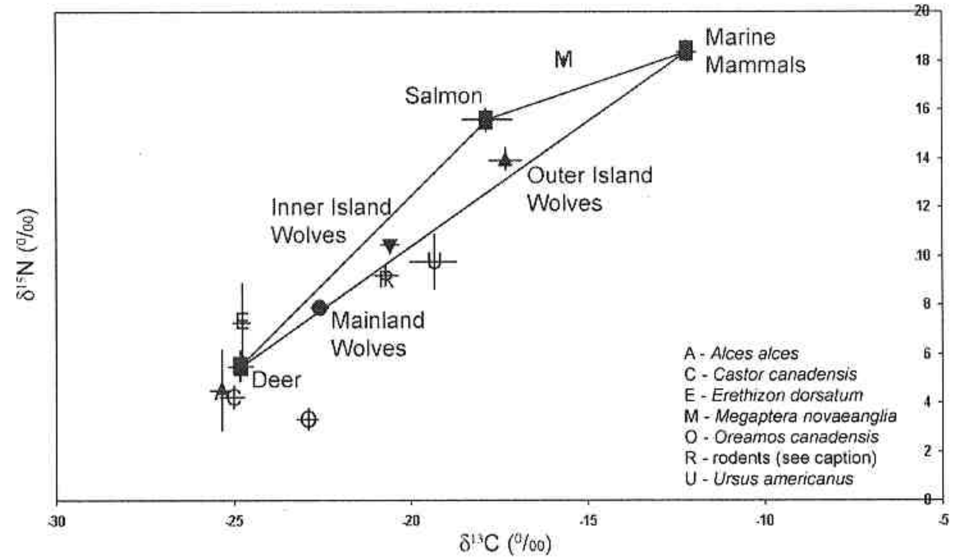


Table 5.1. Input data used for IsoConc and IsoError isotopic models (Phillips and Koch 2002, Phillips and Gregg 2001). [a] %C and %N values of muscle tissue calculated from USDA Nutrient database (NDB) catalogue code NDB 17164 for deer (*Odocoileus* spp.) and NDB 35071 for marine mammals (represented by ringed seal, *Phoca hispida*). %C and %N values of salmon head tissue, which wolves selectively consume over muscle tissue (chapter 7), derived from my isotopic dataset. [b]Fractionation caused by prey hair passing through digestive system of wolves, estimated from captive and wild feeding trials (chapter 9). [c]I assumed identical signatures between (sampled) hair and muscle tissue (that wolves consumed) of prey (Tieszen and Boutton 1988, Hobson 1995, Roth and Hobson 2000, Urton and Hobson 2005). [d]Prey tissue-wolf hair fractionation values (Δ) from the only canid for which these data exist; red fox; *Vulpes vulpes*; Roth and Hobson (2000, see also Urton and Hobson 2005). [e]'Marine mammal' prey were harbour seals (*Phoca vitulina*; n = 9), river otters (*Lontra canadensis*; n = 4), and mink (*Mustela vison*; n = 6), which had isotopic signatures that were not significantly different. [f]Salmon species were pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*), the species that provide the most spawning biomass to the area's vertebrate consumers.

Prey species (source)	**Element (X)**	**% by mass[a]**	**Mean δX (SD)**	$\Delta_{\text{hair in scat-hair}}$[b]	$\Delta_{\text{hair-tissue}}$[c]	$\Delta_{\text{tissue-wolf hair}}$[d]	**δX used in models**
Deer	carbon	51.8	-27.1 (0.9)	-0.5	0.0	+2.6	-25.0
(n = 66)	nitrogen	13.8	2.9 (1.2)	-0.8	0.0	+3.4	5.5
Marine mammals[e]	carbon	52.7	-14.2 (1.3)	-0.5	0.0	+2.6	-12.1
(n = 19)	nitrogen	13.9	16.0 (1.4)	-0.8	0.0	+3.4	18.6
Salmon[f]	carbon	42.9	-20.5 (2.9)	n/a	n/a	+2.6	-17.9
(n = 16)	nitrogen	9.8	12.1 (1.1)	n/a	n/a	+3.4	15.5

Table 5.2. Isotopic values of 'mixture' (wolf; *Canis lupus*) for IsoConc and IsoError models (Philips and Koch 2002, Phillips and Gregg 2001). Hair samples collected on the mainland, inner islands, and outer islands of British Columbia's coast, 2001 to 2004.

Location	**Element (X)**	**Mean δX**	**SD**
Mainland	carbon	-22.6	1.3
(n = 24)	nitrogen	7.9	0.7
Inner Islands	carbon	-20.4	1.9
(n = 46)	nitrogen	10.4	2.1
Outer Islands	carbon	-17.2	1.4
(n = 8)	nitrogen	13.9	1.4
All Islands	carbon	-19.9	2.1
(n = 54)	nitrogen	11.0	2.4

Table 5.3. Top model set ($\Delta AIC_c < 5$; see methods) to predict marine resource use ($\delta^{13}C$ in hair) by wolves (*Canis lupus*) from 11 island packs sampled in 2001 to 2004 in coastal British Columbia. Shown are model structure, ΔAIC_c, and Akaike weight (ω_i). MDIST is island distance to mainland. DEER is island's relative deer abundance, estimated from a model derived from deer pellet group data. AREA is island area. Shape is a measure of shoreline to interior ratio; larger values for more complex shorelines. Shown also are parameter coefficients, (standard errors), and model R^2. $^{**}p < 0.01$, $^{*}p < 0.05$. n = 11 islands.

Model Form	ΔAIC_c	ω_i	β_0	MDIST	DEER	AREA	SHAPE	R^2
β_0 + (MDIST)	0.00	0.77	-20.744** (0.478)	0.483* (0.168)				0.48
β_0 + (MDIST) + (DEER)	4.38	0.09	-21.181** (0.700)	0.504* (0.172)	0.070 (0.080)			0.53
β_0 + (MDIST) + (AREA)	4.82	0.07	-20.872** (0.540)	0.482* (0.174)		0.005 (0.001)		0.50
β_0 + (MDIST) + (SHAPE)	4.87	0.07	-19.552** (1.489)	0.502* (0.178)			-0.389 (0.689)	0.50

Table 5.4. Estimates of biomass contributions (%) from three prey groups (deer; *Odocoileus hemionus*; salmon; *Oncorhynchus* spp., and marine mammals; *Phoca vitulina*, *Lontra canadensis*, and *Mustela vison*) to wolf (*Canis lupus*) diet during period of wolf hair growth. Data derived from models IsoConc (Phillips and Koch 2002) and IsoError (Phillips and Gregg 2001). For input parameters, see Tables 5.1 and 5.2. Shown are point estimates for IsoConc and estimates of **mean**, (SD) and [95% confidence interval] for IsoError.

		IsoConc			**IsoError**	
Location/ Prey	**Deer**	**Salmon**	**Marine Mammals**	**Deer**	**Salmon**	**Marine Mammals**
Mainland (n = 24)	76.1	6.5	17.3	**82.2** (4.7) [72.9 - 91.5]	**-1.7** (14.5) [-8.6 - 27.1]	**19.5** (9.9) 0 - 34.4
Inner Islands (n = 46)	52.7	19.0	28.2	**60.1** (7.4) [45.3 - 74.8]	**9.2** (21.5) [0 - 51.6]	**30.6** (14.1) [2.9 - 51.6]
Outer Islands (n = 8)	24.6	25.5	49.9	**31.9** (12.3) [7.0 - 56.8]	**16.4** (36.5) [0 - 89.4]	**51.7** (24.2) [3.1 – 100]
All Islands (n = 54)	48.3	20.2	31.5	**56.0** (7.8) [40.6 - 71.4]	**10.1** (22.7) [0 - 54.6]	**33.9** (14.9) [4.6 - 63.2]

Chapter 6:

Resource selection: terrestrial carnivore selects seasonal marine resource over terrestrial resource

6.1. Introduction

Ecological boundaries are ubiquitous, ranging from subtle transitions such as benthic-to-pelagic zones in lakes to abrupt borders between ocean and terrestrial domains. An understanding of how boundaries and associated processes influence the interacting ecosystems, however, is poorly developed (Cassenasso et al. 2003a). Interest often lies in the role of boundaries as barriers between disparate systems. Boundaries are often permeable, though, allowing exchanges of materials, energy, and organisms among areas (Cadenesso et al. 2003 a,b).

Physical or biotic vectors transport these resources across boundaries. Water and wind are principal physical vectors, moving organisms, detritus, and nutrients by advection or diffusion. For example, on a global scale, flooding and winds carry aquatic vegetation with biomass an estimated 4.5 times greater than *in situ* terrestrial productivity in receiving areas (Polis et al. 1997). In contrast, biotic vectors are animals that consume foods in one area and deposit the remains (*i.e.* carcass residue, faeces, nitrogenous wastes) into another (Polis et al. 1997). These materials in turn become incorporated into the receiving system's nutrient dynamics and foodweb.

Ecologists interested in foodwebs, however, have largely neglected to examine how biotic vectors affect foodweb structure and dynamics across a spatially structured environment (Polis et al. 1997), though notable exceptions exist. Nesting seabirds for example deposit nitrogen- and phosphorus-rich guano into terrestrial environments (*e.g.* Polis and Hurd 1996a and references within). In the Gulf of California, when combined with adequate precipitation, these marine-derived contributions can increase primary productivity by over an order of magnitude compared to islands lacking nesting colonies (Polis et al. 1997). These subsidies have cascading effects; insects are roughly three times more abundant on these islands, and populations of their predators – spiders and lizards – are similarly increased (Polis and Hurd 1996b, Polis et al. 1997).

Ecologists have recently turned to another system of marine subsidy mediated by a biological vector, and notable information regarding ecological processes and consequences have emerged. Specifically, spawning salmon (*Oncorhynchus* spp.) are transferred from water bodies to adjacent shorelines by terrestrial carnivores. Although river otters (*Lontra Canadensis;* and flooding activity) contribute (Ben-David et al. 1998), critical to this process is the behaviour of bears (*Ursus* spp.), which partially consume salmon and deposit carcass remains, urine, and faeces throughout riparian areas (Reimchen 1992, 1994, 2000). Early research focused on identifying the direct and indirect recipients of salmon nutrients (Reimchen 1992, 1994, Cederholm et al. 2000). This allocation of salmon by bears directly and indirectly feeds multiple trophic levels through scavenging of carcasses followed by decay and subsequent fertilization of riparian vegetation (Ben-David et al. 1998, Helfield and Naiman 2001, Hocking and Reimchen 2002, Mathewson et al. 2003, Reimchen et al. 2003, Wilkinson et al. 2005).

Ecological characters such as the distribution and behaviour of biological vectors determine the ecological consequences that follow transfer of nutrients across boundaries. At a watershed level, Reimchen (2000) noted that higher quality (larger and fresher) salmon were transferred further into the forest by fishing bears on Haida Gwaii. Hildebrand et al. (1999) estimated that 96% of marine-derived nitrogen (from salmon) consumed by adult female bears at an Alaskan watershed is excreted as urine, and much of this is distributed on the trail network. With complementary results, Wilkinson et al. (2005) showed higher salmon-enriched isotopic signatures in lanky moss (*Rhytidiadelphus loreus*) on bear trails compared to random areas in the Clatse watershed in coastal British Columbia (BC). The difference was particularly evident above a waterfall which blocked spawning salmon, demonstrating the transfer of nutrients over longer distances within a watershed. In the same watershed, the distribution of bear trails and preferred feeding sites combined contributed to a clumped distribution of nitrogen added to the riparian forest (Wilkinson et al. 2005). Similar ecological implications likely exist on larger spatial and temporal scales; Hildebrand et al. (1996) estimated that grizzly bears (*U. arctos*) incorporated 33-90% of their diet from salmon last century in the massive but now extirpated bear-salmon system in the Columbia River drainage, and presumably also distributed the carcass remains, urine, and faeces associated with this foraging. If bears are the primary and most widely distributed vector linking salmon to terrestrial environments, one largely may predict the ecological consequences (*i.e.* nutrient transfer) based alone on these and similar studies of bear-salmon interactions.

Another widespread and large terrestrial carnivore has been linked to spawning salmon but the nature and geographical scope of the relationship is not well understood. Although scattered, there are older, brief, and tangential notes of salmon as a food resource for wolves (*Canis lupus*), none of which have described salmon as a frequent prey (Young and Goldman 1944, Mech 1977, Mech et al. 1998). Recently, however, in wolves of coastal and interior Alaska, Szepanski et al. (1999) noted marine-enriched isotopic signatures in wolves, and associated evidence indicated the dominant source was likely spawning salmon. In chapter 3, I sample chronologically-segmented portions of guard hair from wolves of coastal and interior BC to demonstrate that seasonal marine isotopic enrichment occurred during periods of salmon availability, providing additional evidence of salmon consumption. Subsequently, I observed one social group in coastal BC capturing salmon, partially consuming them, and distributing the remains on land (chapter 7). Most recently, a one-time survey detected the presence of salmon in roughly 7% of wolf faeces collected over an area greater than 40,000 km^2 in coastal BC, though sampling occurred largely before salmon become available during autumn (chapter 4). Finally, in chapter 5, isotopic data from wolves sampled over multiple years across the entire BC coast suggested salmon contributed up to 25% of biomass assimilation over the 6 month growth period of sampled hair. Collectively, these observations suggest that wolves could also be a common predator and biological vector of salmon. What remains unknown is an understanding of the larger ecological context of salmon predation by wolves, and by extension inference into the geographical and ecological scope of this interaction that links ocean and land.

If predation on salmon by wolves is frequent and widespread, this would describe a wolf-prey relationship that departs from dominant patterns defining this terrestrial carnivore. Recent reviews concluded that although wolves are flexible and opportunistic predators, the abundance and availability of ungulates - or hoofed animals - in an area determines the distribution, behaviour, and ultimately reproduction and survival of wolves (Paquet and Carbyn 2003, Peterson and Cuicci 2003). Consistent with conclusion, Szepanski et al. (1999) inferred that marine-enriched signatures in mainland coastal wolves (presumably from salmon) were related to lower ungulate densities in mainland areas relative to islands, suggesting a functional response by wolves from deer as main prey to salmon as alternate prey. Such a hypothesis suggests that wolves select deer over salmon, and only switch to salmon under conditions of lower deer availability. An alternate hypotheses, and based on data and discussion in chapters described above, posits that when sympatric with salmon - a relatively predictable, nutritious, safe, and spatially-constrained resource - wolves would select this marine food over deer, thus seasonally disrupting the tight association with between wolves and ungulates.

Herein, I test these competing hypotheses by determining 'resource selection' (Manly et al. 2000) by wolves in multiple packs over four years across a landscape that varies in relative availability of ungulates and salmon to 8 social groups. Specifically, I test whether salmon use is a function of its availability. Determining which resources are selected over others provides fundamental life history information and can yield insight into the ecological relationships among consumer, prey, and the ecosystem.

6.2. Materials and Methods

6.2.1 Study area

A detailed ecological description of the general study area can be found in chapters 2 and 5. In a roughly 3300 km^2 subset of the total coast-wide study area, I collected wolf hair and faecal samples from wolves in a 'core study area' centered on Bella Bella (52^0 10' N, 128^0 09' W). About 800 km^2 is ocean, which separates several mainland landmasses and six main islands ranging in size from about 50 to 400 km^2 plus several smaller islands (Figure 6.1).

6.2.2. Data Sets

I used faecal and isotopic data from wolves to estimate resource use. Faeces allow precise identification of prey, typically to the level of species (Ciucci et al. 1996). If collected over multiple seasons in known areas of use by wolf social groups, these scat samples permit detection of intrapopulation and seasonal variability in foraging behaviour.

Stable isotope data (the ratios of carbon and nitrogen stable isotopes in animal tissue) provide an independent data set. Isotopic signatures in consumer tissue are related to diet and provide an alternative method to estimate food use (chapter 1). $\delta^{13}C$ signatures are enriched relative to diet only negligibly (DeNiro and Epstein 1978) and have been used to indicate relative contribution of isotopically distinct carbon sources, such as relatively enriched marine versus relatively depleted terrestrial foodwebs (*i.e.* Chisholm et al. 1982). Marine foods also are elevated in $\delta^{15}N$ but an enrichment of 3-5 $^{0}/_{00}$ at each trophic step (DeNiro and Epstein 1981, Minagawa and Wada 1984) obscures differentiation between isotopically distinct food sources, but provides indication of trophic level. The discrete behaviour of both isotopes allows for a cross-referenced analysis of diet. Metabolically inert tissue such as hair used in this study reflects diet only during growth and retains this information in a chronological manner.

6.2.3 Sample collection and analyses

During spring (May/ early June), summer (late July), and fall (late September/early October) of 2001 to 2003, wolf faeces were collected from areas in which our research team has closely monitored the activity of eight social groups since 2000. The team sampled the same three to seven sites per pack in every season across all years in which packs were sampled. In 2001, we sampled the home ranges of four groups, and in 2002 and 2003, we added four more to total eight each season. Sites were well-distributed within home ranges and selected to be areas with greater probabilities of detecting wolves and their sign, based on our previous experiences in the area as well as that of our Heiltsuk First Nation field colleagues. Sites were primarily wildlife trail networks and beach fringes of river valleys, but also included road systems and power-line right-of-ways. About half the sites in each pack's territory were areas in which salmon were present during the fall spawning season. The same research team (and typically the same individuals) sampled the same sites each season and year. Faeces can decompose rapidly in this wet environment (Wallmo et al. 1962, *unpublished data*). Thus, I considered each collection representative of the season in which it was collected. I stored scats in plastic bags and froze them until analysis at the University of Victoria.

Sorting and identification of prey remains in faeces followed the protocol described in detail in chapter 4. Briefly, samples were autoclaved, then soaked and rinsed in water within a 1 mm mesh sieve until only hair, bone fragments, and other macroscopic components remained. Mammalian prey were identified by referring to dichotomous keys, and by comparing hair in faeces with voucher samples with a dissecting microscope (magnification 20 - 40X; Mathiak 1938, Mayer 1952, Stains 1958). Non-mammalian prey, such as fish, bird, and marine invertebrates, were identified by bones, teeth, feathers, and shell fragments. Birds and small rodents (*i.e.* smaller than beaver) were not identified further than class and order respectively.

To eliminate inter-observer variability, only one person identified prey remains, and only after a lengthy training period (~ 60 hours). I estimated her precision by having an independent volunteer select 141 scats (~ 6 %) for her to resample, as well as administer and score the results. The primary prey item was consistently identified in 139 (98.6%).

During spring and summer 2001 to 2004, I also collected wolf hair that had been shed in resting sites on or near established transects (above) or at homesites (reproductive areas). Chapter 5 details the collection and preparation of samples from wolves and their prey for isotopic analysis.

6.2.4 Statistical Analyses

Although sample sizes (of individual wolves) may be marginal compared with other systems, I suspect I sampled a considerable proportion of this core study area population, especially via isotopic analyses. Summer pack sizes (including pups) averaged roughly 9, which would total about 36 and 72 resident wolves for 2000-1 and 2002-3 respectively. For years 2000 to 2003, I sampled 17, 11, 21, and 11 wolf hair samples, which would represent roughly 47, 31, 29, and 15% of the resident population respectively.

To assess variability in resource use and availability among social groups, I first estimated their home ranges using data on sightings, which I entered into a Geographic Information System (GIS). After hundreds of hours of field time, which included direct observations, videography, and photography, differences in pelage and other morphological characters allowed me to easily and repeatedly identify at least one member of each social group over the 4 years of study. I used ArcView 3.2 to plot re-sightings of these individuals and used the 'Home Range' application to estimate 95% kernel home ranges. The kernel method is particularly suited to the presentation and quantitative determination of 'activity densities' within the ranges. This method mathematically converts the position coordinates into areas with varying probabilities of use and presents these graphically (Worton 1987, Hooge et al. 1999). Although sample sizes larger than 30 re-locations (*i.e.* re-sightings) are stated as minimum for accurate home range estimates from which statistical comparisons of home range use (e.g. among years, habitats, groups etc.) can reliably be conducted (Worton 1987), data limitations constrained the utility of my estimates. Samples sizes ranged from only one individual per pack re-sighted at all pack locations over all years (Ochre Pack) to three individuals re-sighted many times per season at all pack locations in each of all four years (Fishtrap Pack).

A preliminary genetic data set showed population sub-division consistent with that identified via the re-sighting method above. Ten microsatellite loci extracted from at least 30 wolf faeces collected in 2003 within four of the putative home ranges were examined by a collaborating graduate student. Samples were more similar to those collected within their putative home range compared with those sampled in other home ranges (Erin Navid, University of Calgary, *personal communication*).

I used faecal data to identify dietary items and breadth as well as general patterns of foraging but focus on isotopic data to test hypotheses of resource selection. I report occurrence per faeces (O/F) index for comparison with published literature but use the occurrence per item (O/I) index in statistical tests because the former can be problematic because it exceeds unity when summed (*i.e.* some faeces contain multiple prey items; Kohira and Rextad 1997). O/F is the frequency by which an item occurs among all *faeces*, whereas O/I is the item's frequency among all *items* identified in all faecal samples. For additional comparison to literature, I also estimated mammalian biomass consumed using a regression equation created by Weaver (1993): $Y = 0.439 + 0.008\ X$, where Y is the estimated biomass of prey consumed per faecal sample and X is the mass of prey. Although masses may differ among age and sex classes, and wolves may kill unequal ratios of these classes, I used mean masses of adults reported in Cowen and Guiguet (1975) and Banfield (1981), and assumed a 1:1 sex ratio. For deer, however, I distinguished between adults and fawns for biomass calculations using diagnostic hair diameter and colour characters, which are useful until the autumn (Scott 1979). I assigned fawn weight as 25% that of adults. By necessity, biomass estimates excluded non-mammalian prey (n = 404 of 2692 items identified).

I analysed isotopic data from whole guard hairs as well as segments grown during summer and fall, calculating any seasonl shift by subtracting summer from fall isotopic signatures (see chapter 5 for details). Briefly, in wolves that received $\delta^{13}C$ and $\delta^{15}N$ enrichment primarily from salmon, one would expect a 'seasonal shift' or positive values ('enrichments') of these isotopes in hair that grew during salmon availability in autumn (base) relative to hair that grew during summer (tip). I also present data from un-segmented, whole hair samples to assess marine contribution to diet throughout the summer and fall.

I tested for general patterns and intrapopulation variability in niche among social groups using general linear models with faecal and isotopic data. All dependent variables were normally distributed and variances typically homogeneous among groups. To compare to wolf signatures, I also show isotopic values from prey, the hair of which were corrected for digestion effects (see chapters 5, 9).

To gain insight into resource selection, I examined availability and use of primary terrestrial and marine resources at the pack level, a hierarchy at which I could estimate these parameters. I used a Weighted Least Squares General Linear Model (GLM), which specifically examined how the availability of the primary terrestrial prey (DEER) and marine prey (SALMON) influenced the use of salmon by wolves (Manly et al. 2002), and included year (YEAR) as a random term. I weighted the models according to the square root of the sample size (of wolf hair) used to compute average isotopic signatures for each pack year.

I used the average $\delta^{13}C$ 'seasonal shift' of each pack in each year as the dependent variable (n = 15) and proxy for salmon use for several reasons. First, $\delta^{13}C$ is a much better tracer of dietary 'source' (*i.e.* marine versus terrestrial) than $\delta^{15}N$, which also reflects trophic position (Vander Zanden et al. 2000). Second, if wolves use salmon, they should show elevated $\delta^{13}C$ signatures in the fall grown hair compared to summer-grown hair, which would produce the 'seasonal shift'. Third, and as expected, $\delta^{13}C$ seasonal shifts were strongly related to the occurrence of salmon in faeces (O/I salmon) of the same packs during the same year (see Results). I did not use O/I salmon directly to estimate salmon use because it may be sensitive to sampling bias; sample size varied among pack and fall seasons (n = 9 to 132 scats). Also, faecal data can be biased by spatial effects (*i.e.* locations where samples were collected and the resources present). Hair, in contrast, accompanies wolves throughout the season and incorporates many months of foraging behaviour. Additionally, isotopic data spanned four years while I had scat data for only three. $\delta^{13}C$ seasonal shift data were normally distributed (Kolmogorov-Smirnov Z test; $P = 0.35$).

To estimate deer availability (DEER), I ran a model developed from deer pellet sampling in the study area (Paquet et al. 2006 [appendix 2.2]). This model was derived from 110 transects, each 1 km, comprised of 50 continuous 1 X 20 m belt plots, designed specifically for sampling deer in coastal temperate forests (Kirchhoff 1990). Using these data, equations can be derived that predict relative deer density based on ecological and landscape features on the assumption of a positive relationship between numbers of pellet groups and numbers of deer (Rowland et al. 1984). Using GIS, we extracted ecological data such as topographic slope, forest cover, and aspect along transects from 30 x 30 m pixels. In our dataset, the most parsimonious of best-performing models used solely topographic slope to estimate relative deer abundance. Observed pellet-group densities were normalized to account for representation of available slopes and sampling bias. Using a curve-fitting regression method (SPSS 11.0, SPSS Inc., Chicago, USA), a curvilinear function was created that describes the relationship between observed pellet-group density and slope that was highly predictive ($R^2 = 0.87$). This was then converted to a spatial probability layer, which in theory could range from 0 to 1, calculated and expressed in one hectare polygons, in ArcView 3.2 using the following equation:

$$\text{Relative pellet-group density (probability)} = -0.0007X^4 + 0.0184X^3 - 0.1639X^2 + 0.5355X - 0.3125,$$

where X is the slope category, ranging from 1 to 9 in five degree increments. Slope class 1 included slopes 0 to 4.99, and 9 from 40 to 44.99. Maximum probabilities of detecting deer pellets occurred at moderate slopes, between 10 and 15 degrees. For each 95% kernel home range, I calculated the average density (probability) to use as a proxy for deer availability.

To estimate salmon availability (SALMON), I extracted salmon 'escapement' data from the Pacific Salmon Escapement Database (nuSEDS), maintained by Fisheries and Oceans Canada (www.dfo-mpo.gc.ca) for each year for each pack home range, and converted to biomass using published weights for each species (Groot and Margolis 1991, Hocking 2006; Table 6.1).

I formed exploratory *a priori* hypotheses to explain how these measures of resource availability would predict resource use. From these hypotheses, I developed a simple set of candidate GLM models, restricted to combinations of one to three of the identified parameters (DEER, SALMON, YEAR) and 2-way interaction terms. For interaction terms, I reasoned that one variable's effect (*i.e.* SALMON) on resource use may depend on the effect of another (*i.e.* DEER). For each model, I calculated Akaike Information Criteria (AIC), adjusted for small sample sizes (AIC_c), following the formula: $AIC_c = n \log(o^2) + 2K + 2K(K + 1)/(n - K - 1)$, where $o^2 = \text{Sum } (e_i^2/n)$, K is the number of parameters (including intercept and error term), n the numbered of 'pack years' and e_i the residuals for each candidate model (Burnham and Anderson 1998, p. 63). I then evaluated ΔAIC_c to select best approximating model(s) and make appropriate inference, using $\Delta AIC_c < 4$ to describe the top model set. Finally, I summed Akaike weights (ω_i) across the top model set for each variable to rank them by importance (Burnham and Anderson 1998). Each candidate model had errors that were normally distributed (Kolmogorov-Smirnov Z tests, all $P > 0.05$). Tests were performed using SPSS 11.0 (SPSS Inc., Chicago, USA).

6.3. Results

6.3.1. Resource availability

Availability of deer and salmon resources differed among wolf social groups. Average probabilities of detecting deer pellets across 95% kernel home ranges (proxy for relative deer densities) varied from 0.06 to 0.26 (CV among packs = 0.40). More variance existed in salmon availability among 'pack years', which ranged from approximately 1 to over 220 metric tones per year (CV among groups = 1.01).

Availability of salmon not only would be influenced by total biomass available but also by use of salmon-bearing watersheds within each home range, which differed among groups. During autumns 2000 to 2003 (and to present), I frequently observed wolves or their sign (scats, tracks, bedding sites) at one or several of the salmon-bearing watersheds of all packs, except the Mosquito group (see Figure 6.1 for Mosquito home range). Although my survey effort for each group would be roughly similar (given equivalent numbers of transects, plus one to several additional watershed visits), I did not observe Mosquito pack members during salmon runs at either of the two sampled (of three total) salmon-bearing creeks in their home range, including the largest. In fact, this watershed (Neekas) yielded a 2000 to 2003 average of 179.9 tonnes of salmon per year. This represents 81% of the salmon biomass in the home range, and alone doubles the total biomass available to any pack.

Faecal collection data are also consistent with these failures to observe wolves or much of their sign at Neekas during salmon runs. Although I collected few scats in total for this group, the proportion at Neekas, and especially during the fall when salmon were available, was very low or nil; I collected only 2 faeces from the Neekas during autumns 2003 and none in 2002. Also, the total number of faeces from Mosquito wolves collected during fall declined in both years (Figure 6.2), suggesting these animals were foraging in locations other than my sampling sites during the salmon runs.

6.3.2. Resource Use

Faecal data (n = 2203 scats) indicated that the foraging niche of coastal wolves throughout all seasons was broad, but that only a few items dominated diet. Wolves consumed at least 11 species of terrestrial and marine prey plus vegetation and inter-tidal organisms. Terrestrial organisms accounted for roughly 75% of items recovered in scats and was dominated by deer, which occurred in 85% of all faeces, representing nearly 70% of all items identified and nearly 90% of mammalian biomass consumed (Table 6.2). Although only available in the fall, salmon remains comprised the second most frequent prey item in the whole dataset, occurring in over 12% of faeces and representing more than 10% of items. Additional marine prey, seal, river otter, and sea lion comprised other main prey categories, collectively representing roughly 10% of faeces, items, and biomass (Table 6.2).

At a population level and during the fall, wolves consistently diverged from a spring and summer diet dominated by deer. Among years pooled, population-level deer O/I was significantly lower in the fall (ANOVA; $F_{2,21} = 26.54$, $P < 0.001$; Tamhane's T2; fall compared with spring and summer; both $P < 0.001$, Figure 6.3). This difference was also significant in individual years (ANOVAs; all $P < 0.005$).

This pronounced seasonal dietary shift to declining use of deer in the fall was strongly related to use of salmon. Using as a case each 'pack year', there was a strong inverse relationship between the O/I of salmon and O/I deer during the fall ($r = -0.77$, $n = 20$, $P <0.001$, Figure 6.4).

There was considerable convergence in general population-level patterns of foraging between scat data and isotopic data, which also showed population-level variability in foraging that was related to marine influence. Whole hair $\delta^{13}C$ values ranged from -24.4 to -16.8 (mean = 21.4, SD = 2.0), and $\delta^{15}N$ ranged from 6.4 to 14.3 (mean = 9.5, SD = 2.1). Marine-derived isotopic enrichment of both isotopes was tightly coupled; $\delta^{13}C$ and $\delta^{15}N$ were strongly positively correlated ($r = 0.95$, $n = 60$, $P < 0.001$; Figure 6.5).

Three analyses revealed that most marine-derived isotopic enrichment was incorporated during the fall and was associated with salmon. First, average pack values for whole hair $\delta^{13}C$ can be predicted by the seasonal shifts in $\delta^{13}C$ in the same hair ($r = 0.540$, $n = 15$, $P = 0.038$). Second, most individuals occupied an area of isotopic niche space defined by coupled enrichment in both $\delta^{13}C$ and $\delta^{15}N$ during the fall ($\chi^2 = 56.13$, df = 3, $n = 60$, $P < 0.001$, top right quadrat in Figure 6.6). Third, I examined cases for which I had for the same social group both salmon O/I data for the fall (n range: 9 to 92; mean = 54.0 scats) and $\delta^{13}C$ signatures from wolf hair grown during that same year (n range: 1 to 6, mean = 3.4 hair samples). Associations between fall O/I salmon and mean $\delta^{13}C$ 'fall seasonal shift' values for each pack year were strong and positive. Social groups that had higher O/I salmon in the fall showed greater marine $\delta^{13}C$ seasonal enrichment during the same autumn (r = 0.78, n = 10, P < 0.008, Figure 6.7). O/I salmon during fall was less strongly correlated with $\delta^{13}C$ signatures in whole hair strands (r = 0.51, n = 10, P = 0.134).

At the pack level, other marine prey did not have a detectable influence on isotopic signatures. Average whole hair and seasonal shift in $\delta^{13}C$ and $\delta^{15}N$ were not related to other marine contributions to diet; O/I seal, O/I otter, or both O/Is combined in summer or fall showed no relationship with residuals (data not shown; all P > 0.300). Likewise, residuals from regressing seasonal shifts in $\delta^{13}C$ over O/I salmon in the fall were not associated with these variables (data not shown; all P > 0.330).

Social groups varied in marine resource use as assessed by both faecal and isotopic measures. In a General Linear Model, weighted by the square root of the number of items in all scats in each pack season, O/I salmon during autumn varied among packs (P = 0.051, Figure 6.3). In similar designs, but weighted by the number of hair samples used to compute averages for each pack year, $\delta^{13}C$ signatures in un-segmented wolf hair differed among packs (P = 0.034). These differences were also detectable, and approached significance, in seasonal marine enrichment for $\delta^{13}C$ (P = 0.059).

Variability in resource use among packs in the context of resource availability yielded information about resource selection by wolves. Fourteen out of fifteen 'pack years' showed a strong association between salmon use (fall $\delta^{13}C$ shift) and salmon availability; one 'pack year' showed an anomalous pattern. Regardless, multiple analyses with and without this case showed that wolves use salmon as a function of salmon availability.

Using all cases, including the anomalous datum from the Mosquito Pack, SALMON and YEAR accounted for much of the variation in seasonal shift in $\delta^{13}C$, occurring in three and two of the four top models respectively, and occurring by themselves in the two top models between which there was little difference in AIC weight. DEER and DEER x SALMON terms were less predictive, occurring once in the third model (Table 6.2a). Summing weights among top models ranked SALMON ($\Sigma\omega_i$ = 0.61) and YEAR ($\Sigma\omega_i$ = 0.44) similarly, whereas DEER and DEER x SALMON were ranked much lower (both $\Sigma\omega_i$ = 0.14). Examination of parameter coefficients, however, reveals that SALMON has a strong and significant effect only in the third model. A bivariate plot of marine enrichment and SALMON reveals how the outlier datum (Mosquito Pack 2002) influenced these results (Figure 6.8).

SALMON became a much better predictor in a dataset that excluded the Mosquito Pack 2002 datum. SALMON occurred in all three top models, and alone in the top model, which outperformed other models considerably with an AIC weight of 0.61 (Table 6.2b). Summing weights across top models placed SALMON ($\Sigma\omega_i = 0.85$) roughly six times higher than YEAR ($\Sigma\omega_i = 0.15$) and nine times higher than DEER ($\Sigma\omega_i = 0.10$).

A third and final evaluation of models used the Mosquito Pack 2002 datum but excluded Neekas salmon biomass from the home range's SALMON estimate, and likewise revealed that SALMON was the best predictor of marine enrichment in wolf diet. Again, the best of four top models included only SALMON (and the intercept) and was clearly a preferred model ($\omega_i = 0.57$, Table 6.2c; Figure 6.9a). SALMON ($\Sigma\omega_i = 0.75$) outranked YEAR ($\Sigma\omega_i = 0.23$) and DEER ($\Sigma\omega_i = 0.09$) by factors of about 3.3 and 8.3 respectively.

Across all three evaluations, SALMON was a much better predictor of marine enrichment than DEER. There were consistently positive associations between salmon availability and marine enrichment; SALMON parameter coefficients were always positive, and were significant in seven of nine occurrences.

Although limited, opportunities to examine replicate years from the same pack revealed additional support for salmon availability as the best predictor of salmon use (Figure 6.9a). The best example was Mountain pack data over two years that differed considerably in salmon availability; use of salmon was higher in the year with greater salmon. This also occurred with Fishtrap pack over two years, though to a much lesser degree. The case is less clear with the Village Pack for which I had all four years of data; a regression through all four points would yield a negative slope, but one through three would yield a positive slope. Mystery Pack data were more difficult to interpret. Although there was only negligible variability in SALMON estimates, there was notable variation in isotopic signatures among the four sampled years. The variation, however, centered around zero (*i.e.* negligible seasonal marine enrichment), in contrast to other packs the mean seasonal shifts of which were always positive.

DEER, in contrast, was a poor predictor of use of salmon by wolves (Figure 6.9b). This variable occurred in only three of all top (11) models and had only one significant parameter coefficient, which was positive. This result occurred in the first analysis that included the full dataset. A DEER x SALMON parameter occurred in one of the top models, with a negative and significant coefficient (Tables 6.2a-c).

Yearly variation accounted for more variance than DEER but less than SALMON. Across the three evaluations, YEAR consistently outranked DEER in summed AIC weights by factors ranging from 1.5 to 3.1.

Upon inspection of data after AIC procedures, I observed that another association between SALMON and mean seasonal shifts in $\delta^{13}C$ could be described. This univariate relationship may also be expressed in quadratic form, with a marginally improved strength ($r = 0.74$, $n = 15$, $P = 0.009$, Figure 6.10).

6.4. Discussion

6.4.1. General discussion

Many systems receive intermittent or pulsed food resources across ecosystem boundaries, which decay in abundance over time. Because, by definition, there are long inter-pulse durations between resource abundance, theory predicts that few consumers will be specialists on the pulsed resources. Instead, generalist consumers should be most likely to respond (Ostfeld and Keesing 2000).

Wolves have not been described as generalists but rather specialists on ungulate prey. Across their holarctic distribution, wolves have been identified as predators with close ecological and evolutionary associations with ungulate prey (Paquet and Carbyn 2003, Peterson and Cuicci 2003). With this perspective, it follows that any departure from a diet dominated by ungulates would occur only during times or in areas of low ungulate availability.

Recent but limited research has shown that wolves, however, when sympatric with salmon likely do depart from an ungulate-dominated diet and potentially consume this marine resource to a considerable degree (Szepanski et al. 1999, chapters 3,4, and 7). Details of the ecological and geographic context, however, have not been adequately examined. Herein, I demonstrate that a population on average selects salmon during autumn over their primary ungulate prey. Specifically, wolves use salmon as a function of its availability, regardless of deer availability. This information about resource selection (Manly et al. 2002) not only departs from theories regarding temporal resource subsidies but also provides essential life history knowledge about wolf-prey systems and accounts for how this predator-prey relationship would affect higher-order ecological process, namely nutrient transfer across the boundary of land and sea.

Consistent with prevailing conclusions about wolf-prey systems, for most of the year coastal wolves are indeed closely tied to their ungulate prey. Deer remains were detected in 85% of over 2200 faeces collected across all seasons and years, representing nearly 70% of all items identified and nearly 90% of mammalian biomass consumed. During the autumn, however, an alternate predator-prey system emerged with previously undocumented ecological detail.

When salmon became available seasonally, I observed a population-level shift in niche as indicated by two independent datasets. The most general evidence is the distribution of isotopic signatures in whole hair samples, which showed a continuum of marine enrichment (Figure 6.5).

Some of this marine enrichment may occur via consumption of marine prey other than salmon. Indeed, as revealed in scats, all packs used detectable but modest levels of seal and otter throughout the year (yearly averages for both species combined were < 20% in any pack; Figure 6.3). I failed, however, to find any relationship between the use of these highly enriched marine prey items as revealed by faecal analysis and the isotopic signatures of the consuming wolves at the pack level. This is additional evidence that seal and otter, though consistently consumed among packs and years, comprised modest contributions to diet for this sub-population, comprised of mainland and inner island wolves (*c.f.* outer island wolves in chapter 5).

In contrast, multiple lines of evidence suggest that salmon form the primary marine prey for this population. First, chronologically-segmented tissue showed that most wolves incorporated more marine-derived carbon and nitrogen during fall, when salmon were available (Figure 6.6). Consistent with this, isotopic enrichment in hair segments grown during fall predicts the isotopic signatures in the whole hair strand. Third, as an important cross-reference, associations between the occurrence of salmon in fall faeces and isotopic seasonal shifts were strong and positive. Notably, this suggests that the intra-hair methodology developed in chapter 3 is an accurate proxy for salmon consumption. And across all years, seven of eight packs showed direct evidence of salmon consumption in autumn scats, and at O/F levels averaging from roughly 20 to 60% (Figure 6.3).

Why is there this range in salmon use by wolves? A resource selection approach can differentiate between hypotheses that would describe salmon as 1) an alternative resource to which wolves turn in conditions of ungulate scarcity and 2) a selected resource that is consumed as a function of its availability (Manly et al. 2002). My data support the latter hypothesis; over multiple analyses SALMON clearly outperformed DEER (and YEAR and interaction terms) in predicting use of salmon, and by itself formed a highly predictive (and parsimonious) model (Tables 6.2a-c, Figure 6.9a,b).

Although not a highly important variable, there was variation in salmon use among years. This could represent a myriad of conditions that may change from year to year, including climate (and its influence on deer vulnerability), changes in pack size and membership, competitive conditions (see below), and sampling biases.

How I estimated the availability of deer to wolves may have obscured an effect of this variable. Manly et al. (2002) reminded readers to carefully consider the difference between *availability* and *abundance*. The model I used yielded an estimate - and a coarse one - of relative deer *abundance* across a large landscape. I suspect that the abundance of deer is difficult to precisely or accurately estimate due to influences of climate, disease, and predation by wolves and other carnivores, all of which would vary across time and space. Actual numbers of deer that were accessible and vulnerable to wolves (*i.e. available*) could have differed from my estimate of *abundance*. If the two measures are not related, I may have failed to detect a relationship between deer availability and use of salmon. This relates to an important distinction in semantics. 'Resource selection' is a process by which an animal chooses a resource, whereas 'resource preference' is the likelihood that a resource will be chosen if offered on an equal basis with others (Johnson 1980).

Although the accuracy of my measure of salmon availability is not known, I did detect a strong and positive association between its availability and use. The reasons why a particular resource is selected is not directly revealed by the estimated preference or avoidance, but is a starting point for investigation; many factors contribute to resource selection, among them natural selection and competition (Manly et al. 2002).

6.4.2. Adaptive explantation for selection of salmon

While this wolf-prey association departs from a 'wolf-ungulate' model, it is consistent with adaptive explanations based on safety, nutrition, and energetics. Selecting benign prey such as salmon over potentially dangerous ungulate prey follows general predictions of foraging theory (Stephens and Krebs 1986). While hunting ungulates, wolves commonly incur serious injuries (*e.g.* Pasitschniak-Arts et al. 1988) and death (Stanwell-Fletcher 1942, Frijlink 1977, Nelson and Mech 1985, Mech and Nelson 1990, Weaver et al. 1992).

In addition to safety benefits, salmon also provides enhanced nutrition over deer. Although comparable in protein, salmon provide roughly 30% more fat than deer for the same mass (Table 6.3). This is likely an underestimate, as wolves selectively consume the lipid-rich heads of salmon (chapter 7). Also, in this tissue, wolves may benefit from ingestion of docosahexaenoic acid, an omega-3 fatty acid, which is essential for nervous system function, can be obtained only from diet, and occurs in high proportion in brain and optic tissue (Horrocks and Yeo 1994, Connor et al. 2001). Moreover, owing to its high fat content, salmon offers more than four times the energetic content per unit mass (Table 6.3).

This greater energetic content is especially relevant in the context of net energetic return from foraging (Stephens and Krebs 1986). For an equivalent energetic intake, wolves are compelled to travel far less for salmon as they typically do to secure vulnerable ungulate prey (*e.g.* Musiani et al. 1998). Salmon are a unique resource for wolves in that they are spatially constrained.

6.4.3. Processes that may constrain use of salmon

These safety, nutritional, and energetic benefits conferred in a spatially-constrained prey would promote competition with other predators, and several lines of evidence I outline below suggest that this also may influence resource selection by wolves. Brown (*U. arctos*) and black (*U. americanus*) bears have been observed in several competitive interactions with wolves over resources (Rogers and Mech 1981, Ballard 1982, Hornbeck and Horesji 1986, Adams et al. 1995), including salmon (Smith et al. 2003a; *personal observation*).

Such competitive interactions would be most intense under conditions of high resource density. One may reasonably estimate potential competitive intensity as linear lengths of streams and salmon density (tonnes/km). These metrics, however, had no influence on any measure of salmon consumption by wolves (data not shown) at a pack level, which integrates values from each stream in the home range. Individual creeks, however, vary in salmon density. Neekas, where wolves apparently visited infrequently during salmon runs in my observation years, hosts a salmon density about 2.5 times greater than the watershed closest in salmon density (Clatse Creek in Mountain Pack home range) and over 12 times greater than the third (Quartcha Creek in Big Country home range). Given this pattern, there may be a threshold salmon density in watersheds above which wolves avoid interacting with bears (such as the Neekas). Additional watersheds with high salmon densities would aid in testing this hypothesis.

Similarly, there may be a competitive effect on a larger spatial scale. Across the landscape, one may predict that bear densities would be correlated with salmon densities. It follows then that home ranges with greater salmon biomass may contain more bears, which would promote disproportionately greater competition compared with areas of more modest salmon availability. The quadratic form of the relationship between salmon biomass and use by wolves (Figure 6.9), which decays at higher salmon densities, is consistent with this hypothesis. This may be a tenuous hypothesis, however, as four of the data points that anchor the quadratic originate from the same valley sampled over multiple years. Additional and more refined research that examines competition among bears and wolves at the landscape scale could provide more insight.

In addition to competition, other processes likely limit the use of salmon by wolves. This may resolve an apparent paradox: if wolves select salmon over deer, why do packs with high salmon availability not exclusively consume this resource? First, wolves may be compelled to partition their diet, perhaps requiring a particular suite of micronutrients in deer or avoiding the accumulation of others in salmon. Disease may also play a role. In chapter 7, I suggest that wolves may target the heads of salmon to minimize the probability of 'salmon-poisoning disease', caused by *Neorickettsia helminthoeca,* which concentrate in the viscera of salmon. In high quantities, this parasite is fatal to canids (Knapp and Millemann 1970). In addition to limiting salmon use across the study area, this may limit use of specific runs. Perhaps, in larger watersheds such as Neekas, the population dynamics of the disease agent and its vectors and hosts operate differently; this might yield a larger parasite load per salmon. Third, there may be some limits imposed by territoriality. For example, there may be opportunity costs to focusing on a spatially constrained resource in not patrolling other areas of territories. Fourth, variability in salmon use may not only be influenced by its availability but also idiosyncratic behaviour of individual wolves and packs in this long-lived animal. For example, historical and negative encounters in the Neekas with human predators or bears may reduce the probability of use in the future, even across generations. Finally, isotopic *detection* of salmon use may be constrained by my methodology. Had we collected faeces up until the end of salmon availability (*i.e.* December for coho), I might have detected a greater proportion of salmon remains over the whole fall period. Also, the extent of $\delta^{13}C$ shift may have a threshold if salmon are actually available during growth of the 'summer' or tip segment of guard hair, which would reduce the realised seasonal enrichment.

6.4.4. Ecological implications

Regardless of potential limitations to consumption, frequent and widespread predation of salmon by this apex carnivore has higher-order ecological implications, similar to other ecological processes initiated by wolves in other systems. On Isle Royale in Lake Superior, for example, McLaren and Peterson (1994) showed that balsalm fir (*Abies balsmea*) productivity was directly related to wolf predation of moose (*Alces alces*). Thirty years of dendrochronological analyses revealed two cycles of tree ring growth that was suppressed during high moose densities, which followed low wolf densities.

Researchers have monitored similar ecosystem responses following the absence and subsequent reintroduction of wolves to Yellowstone National Park and area, which modified densities and behaviour of elk (*Cervus elaphus*). During the absence of wolves, elk over-browsed, which lead to declines in growth and recruitment of riparian Aspen (*Populus tremuloides*) in Yellowstone National Park (YNP; Ripple and Larsen 2000, Fortin et al. 2004) and Willow (*Salix* spp.) in southwestern Montana (Ripple and Beschta 2004b). Consequences for the greater ecosystem were pronounced and summarized by Ripple and Beschta (2004a): loss of riparian function, declines in beaver, and negative effects for a suite of other species that depend on riparian foodwebs. Notably, much earlier, Aldo Leopold foresaw these effects, stating, "…Yellowstone has lost its wolves and cougars with the result that elk are ruining the flora, particularly on the winter range" (Leopold 1949, p.196). Following reintroductions of wolves, identification of so-called 'trophic cascades' are emerging, among them reduced browsing intensity and altered herbivore spatial behaviour, new recruitment of woody browse species, and increases in beaver density (Ripple and Beschta 2003, 2004b, Smith et al. 2003b).

Hebblewhite et al. (2005) found similar evidence in Banff National Park, where wolves recolonized several decades after the last extirpation in the area. In areas where wolves were excluded from recolonizing and elk populations remained high (in a human-dominated refugium from wolf predation), aspen and willow recruitment declined under high browsing intensity. Beaver lodge density was also significantly lower than in areas with wolves (and less elk). Also, these authors surmised that elk herbivory had an indirect and negative effect on riparian songbird diversity and abundance (Hebblewhite et al. 2005).

In another continental area, researchers have noted additional ecosystem effects facilitated by wolf predation, one providing nutrients to other species. Not able to consume elk in a single feeding, wolves indirectly provide a considerable proportion of carcasses to a diversity of scavengers, including coyotes (*C. latrans*), bears, and ravens (*Corvus corax*) in YNP. Wilmers et al. (2003) demonstrated that packs of intermediate size lose the most carrion to scavengers, and notably that carrion supply is relatively constant across the winter and primarily dependent on wolf demographics. In contrast, before wolf reintroduction, the availability of carrion was concentrated in the late winter and related to abiotic conditions (*i.e.* snow depth and temperature). Wilmers et al. (2003) concluded that by transferring access to carrion from the highly productive late winter to the less productive early winter and from highly productive years to less productive ones, wolves provide a temporal subsidy to scavengers.

In coastal BC, wolves also provide a nutrient subsidy, one not only of similar ungulate carrion but also of marine nutrients, and notable differences exist between these two processes. First, remains of salmon typically are not defended by wolves (*personal observation*), and thus the carrion is likely more readily provided to other users. Over almost a hundred observed captures, mean handling time before wolves abandoned carcasses (after consuming only the head) was just 72 seconds (chapter 7). In addition to potential parasite burden associated with tissue other than heads, the energetic costs of any defense would exceed those of acquiring another salmon. Second, because carcasses are relatively small and able to be more readily dispersed, more individual (vertebrate) scavengers likely gain access to salmon compared with one large (ungulate) carcass of similar mass. As a consequence, this subsidy is likely distributed over a larger area (through multiple subsequent scavengers and detritivores - individuals and species). Finally, the resource subsidy - salmon - is one transported across a boundary of land and sea.

This marine resource subsidy also differs from that provided by bear vectors in salmon systems. In contrast to wolves, which often forage among or near family members, carcass transport by bears is thought to be mediated by intra-specific competition. As a consequence, one may expect different spatial patterns of nutrient subsidy. Reimchen (2000) observed that about 80% of salmon were transferred up to 100 m into the forest, with larger and fresher male carcasses transported further. In contrast, in 70% of observed transport events by wolves, carcasses were deposited on estuarine grasses, within a few metres of the creek (chapter 7). Moreover, tissue content in abandoned carcasses differs between those provided by wolf and bear vectors. Bears target brains and eggs, and under conditions of relatively low salmon abundance then subsequently consume musculature. In contrast, wolves predominantly target the heads of salmon. As a consequence, more tissue (of greater energetic content) is available to scavengers of wolf-provided carcasses.

The most notable difference between wolves and bears is the distribution of these vectors across the landscape. In general, brown bears of coastal BC are found on the mainland, and in low densities and frequencies on inner islands. Black bears commonly inhabit mainland and inner islands, and are largely absent on outer islands. In contrast, wolves can interact with spawning salmon on the mainland, and on all islands, including those most isolated (chapters 2, 8, Paquet et al. 2006 [appendix 2.2]). As a consequence, wolves may be the primary biological vector on some islands.

This difference in distribution has considerable ecological implications, including increasing and altering the 'resource shed' into which salmon are transported. Such differences *within* a species of another marine vector, the river otter is informative. Ben-David et al. (2005) examined the consequences of intrapopulation variability in foraging and scent-marking behaviour in river otters, which distribute marine nutrients from inter-tidal fish and crustaceans to terrestrial latrine sites. Different behaviours among social, non-social, and female otters lead to markedly different distribution and quantities of marine nitrogen and phosphorus inputs to latrine sites. The same may hold on a larger scale throughout BC's archipelago in which islands vary in the presence and relative densities of bear and wolf vectors.

6.4.5. Conclusions

Information about resource selection provides information about long-term resource use of populations in the past, present, and future. Consequently, several ecological, evolutionary, and conservation processes become relevant. Selection of salmon by wolves and the adaptive explanations I present argue for a historical association between the two that has been shaped by natural selection. At present, this association has immediate ecological implications not unlike those observed in the well-studied carnivore-wildebeest (*Connochaetes* spp.) migrations in Africa's Serengeti (Sinclair and Arcese 1995). For example, such flow of allochthonous subsidies can influence disease and bio-contaminant transmission, competition among users, population dynamics of consumers and alternate prey, and nutrient transfer (see also chapter 5). Finally, the future and nature of this (remaining but formally geographically widespread) wolf-salmon association remains uncertain, given the threats posed to salmon including overexploitation by fisheries, destruction of spawning habitat, and exotic salmon aquaculture that collectively have lead to coast-wide declines over the last century and threaten the future of this precious ecological resource (Harvey and MacDuffee 2002, Finney et al. 2003, Gresh et al. 2000).

Figure 6.1. 'Core study area' near Bella Bella in which wolves (*Canis lupus*) were sampled for hair and faeces on the central coast of British Columbia, 2000 to 2004. Wolf pack home ranges were estimated as 95% kernels based on re-sightings of individual wolves.

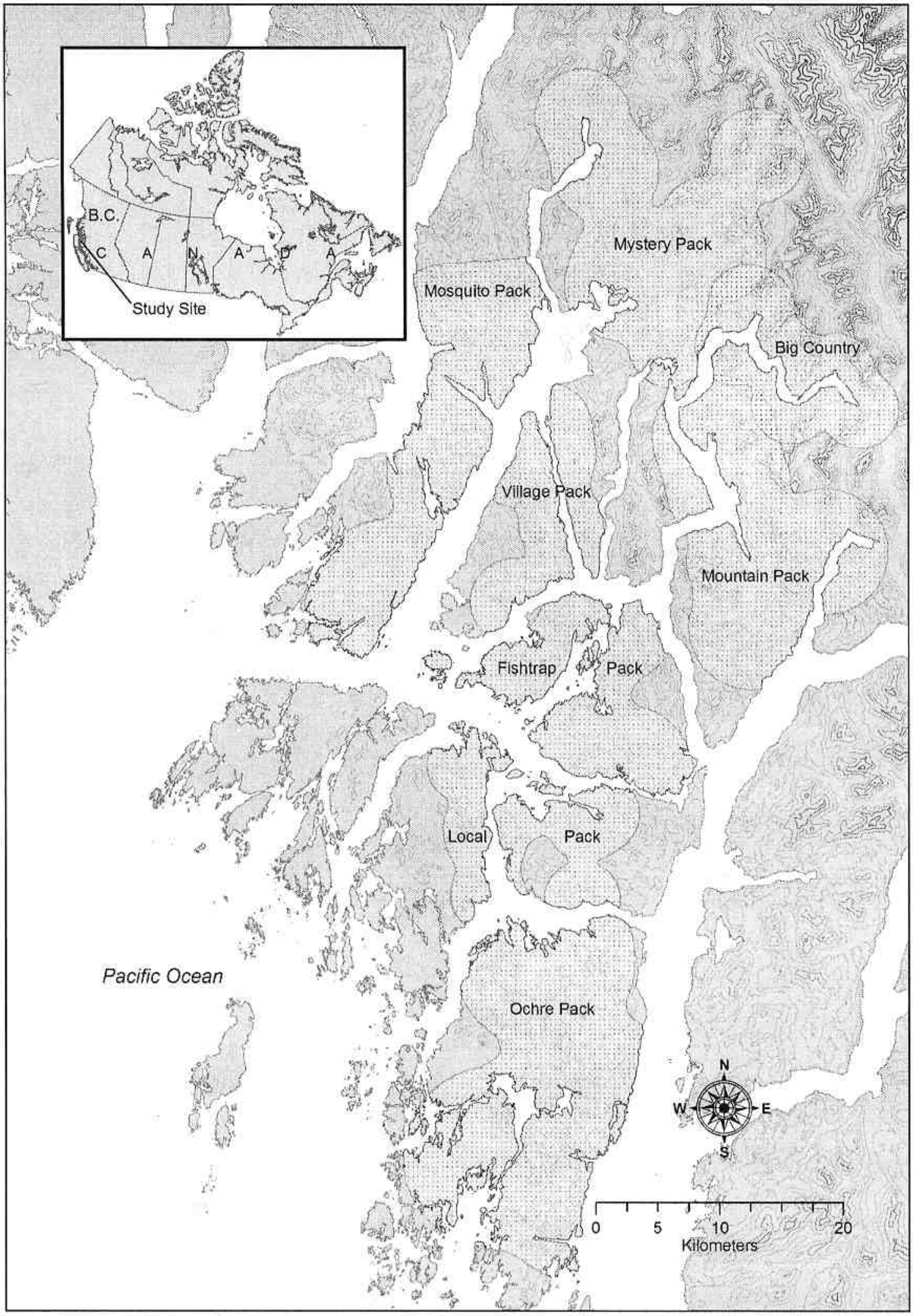

B.C.
C
A
N
A
D
A
Study Site
Mystery Pack
Mosquito Pack
Big Country
Village Pack
Mountain Pack
Fishtrap
Pack
Local
Pack
Ochre Pack
Pacific Ocean
N
W
E
S
0
5
10
20
Kilometers

Figure 6.2. Number of wolf (*Canis lupus*) faeces collected in the three Mosquito pack sampling sites in 2002 and 2003. Tankeahs and Neekas are salmon-bearing watersheds whereas the logging roads transverse the Don Peninsula (on which the territory is located; Figure 6.1).

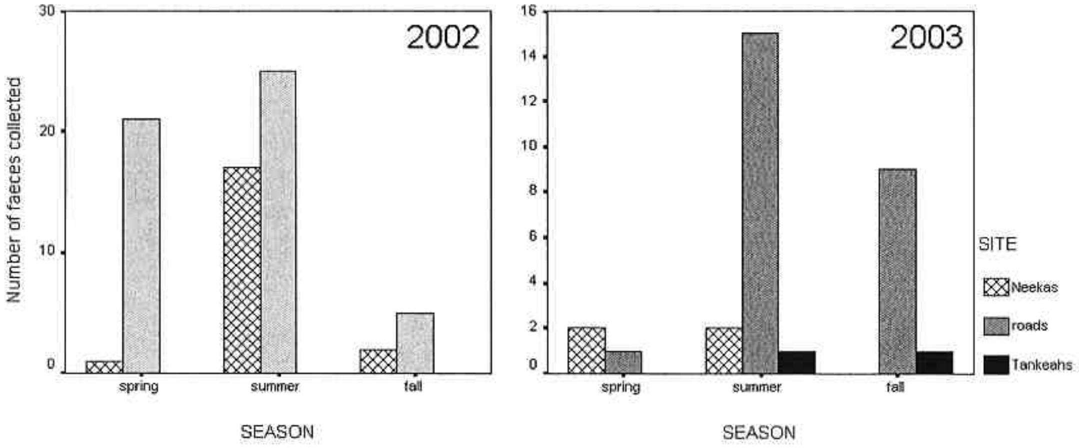
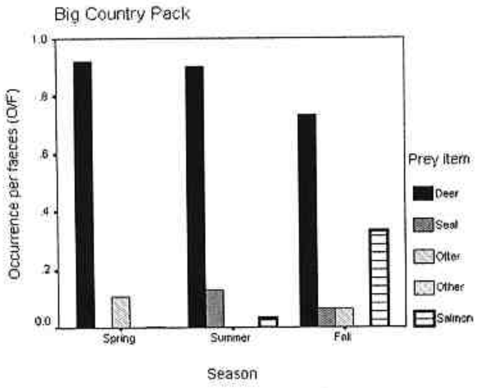
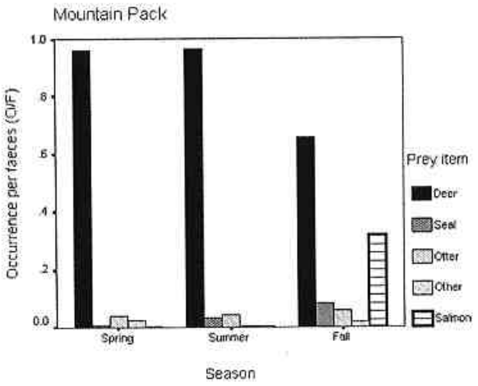
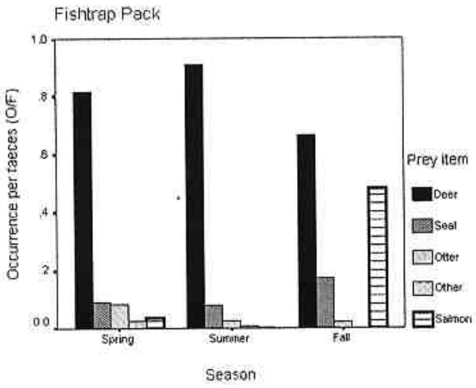
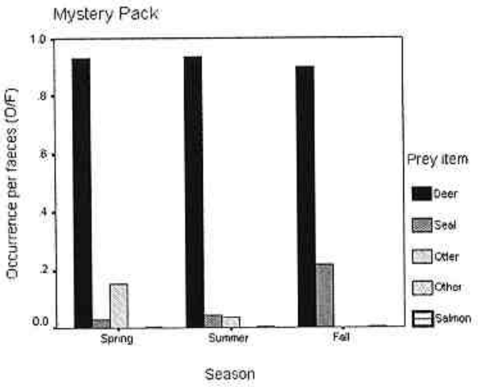


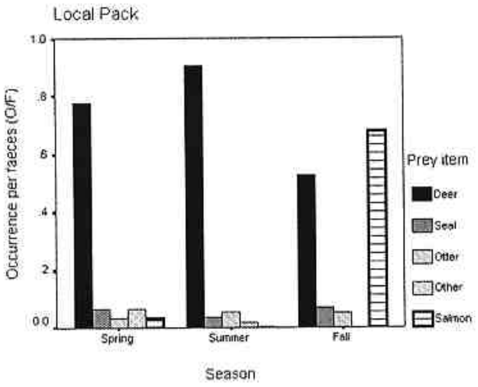
Figure 6.3. Inter-social group and seasonal variability in prey remains recovered in wolf (*Canis lupus*) faeces collected during spring, summer and fall, pooled across years spanning 2001 to 2003 in coastal British Columbia. Local, Ochre, Mosquito and Mystery Packs were sampled in 2002 and 2003 only. Remaining packs were sampled in all years.

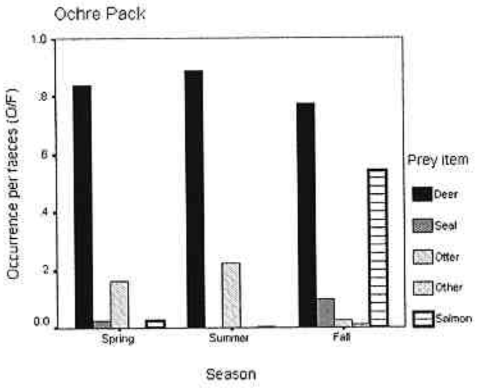

Big Country Pack
Occurrence per faeces (O/F)
1.0
.8
.6
.4
.2
0.0
Spring
Summer
Fall
Season
Prey item
Deer
Seal
Otter
Other
Salmon

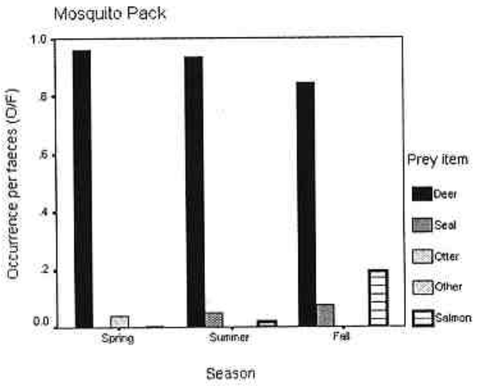

Mountain Pack
Occurrence per faeces (O/F)
1.0
.8
.6
.4
.2
0.0
Spring
Summer
Fall
Season
Prey item
Deer
Seal
Otter
Other
Salmon


Fishtrap Pack
Occurrence per faeces (O/F)
1.0
.8
.6
.4
.2
0.0
Spring
Summer
Fall
Season
Prey item
Deer
Seal
Otter
Other
Salmon


Mystery Pack
Occurrence per faeces (O/F)
1.0
.8
.6
.4
.2
0.0
Spring
Summer
Fall
Season
Prey item
Deer
Seal
Otter
Other
Salmon


Local Pack
Occurrence per faeces (O/F)
1.0
.8
.6
.4
.2
0.0
Spring
Summer
Fall
Season
Prey item
Deer
Seal
Otter
Other
Salmon


Ochre Pack
Occurrence per faeces (O/F)
1.0
.8
.6
.4
.2
0.0
Spring
Summer
Fall
Season
Prey item
Deer
Seal
Otter
Other
Salmon


Mosquito Pack
Occurrence per faeces (O/F)
1.0
.8
.6
.4
.2
0.0
Spring
Summer
Fall
Season
Prey item
Deer
Seal
Otter
Other
Salmon

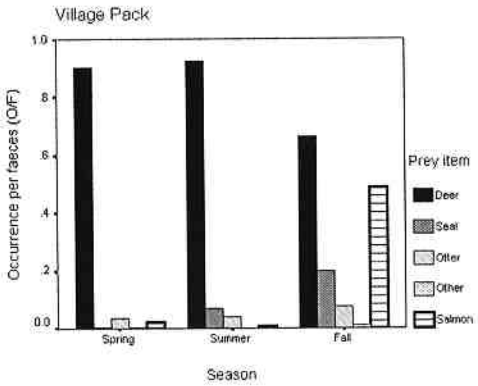

Village Pack
Occurrence per faeces (O/F)
1.0
.8
.6
.4
.2
0.0
Spring
Summer
Fall
Season
Prey item
Deer
Seal
Otter
Other
Salmon

Figure 6.4. Occurrence per item (O/I) of deer (*Odocoileus hemionus*) and salmon (*Oncorhyncus* spp.) remains in wolf (*Canis lupus*) faeces collected in autumns 2001 (n = 4 packs), 2002 (n = 8 packs), and 2003 (n = 8 packs) on the central coast of British Columbia. O/I measures the occurrence of an item among the total number of items identified in all faeces.

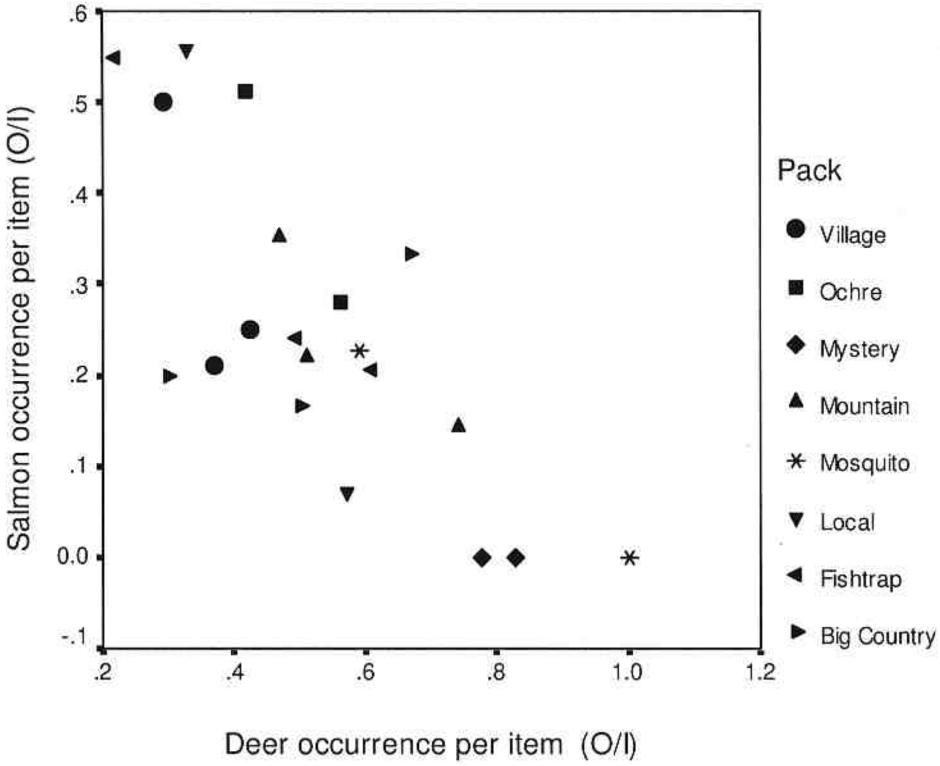


Figure 6.5. $\delta^{13}C$ and $\delta^{15}N$ values in wolf (*Canis lupus*) hair collected from eight packs in coastal BC, 2001 to 2004. Shown also are mean isotopic values (and SD) for major prey items (note: prey values adjusted for fractionation, or diet to consumer hair enrichment; see chapter 5). *Marine mammals are river otter (*Lontra canadensis*), harbour seal (*Phoca vitulina*), and mink (*Mustela vison*), which were pooled because they are similar marine prey and had similar isotopic values.

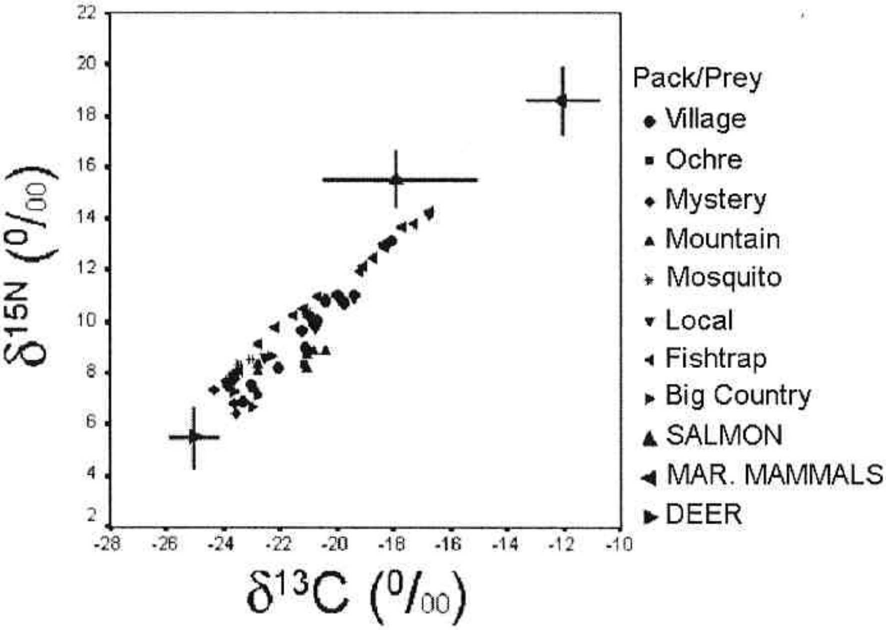


Figure 6.6. Seasonal $\delta^{13}C$ and $\delta^{15}N$ isotopic shifts (fall minus summer) in wolf (*Canis lupus*) hair grown from summer to fall, 2001 to 2004. Samples collected from eight packs in coastal British Columbia. n = 60.

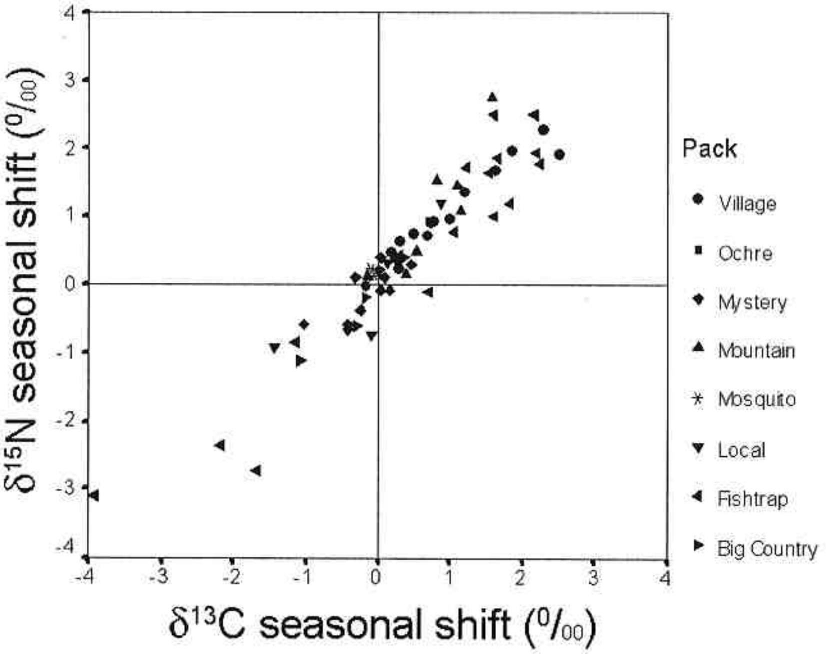


Figure 6.7. Salmon (*Oncorhynchus* spp.) remains in wolf (*Canis lupus*) faeces expressed as their occurrence per item in each social group (O/I salmon) during autumns 2001 to 2003 and the mean fall seasonal enrichment in δ^{13}C in wolf hair among individuals of the same social group grown during the same year.

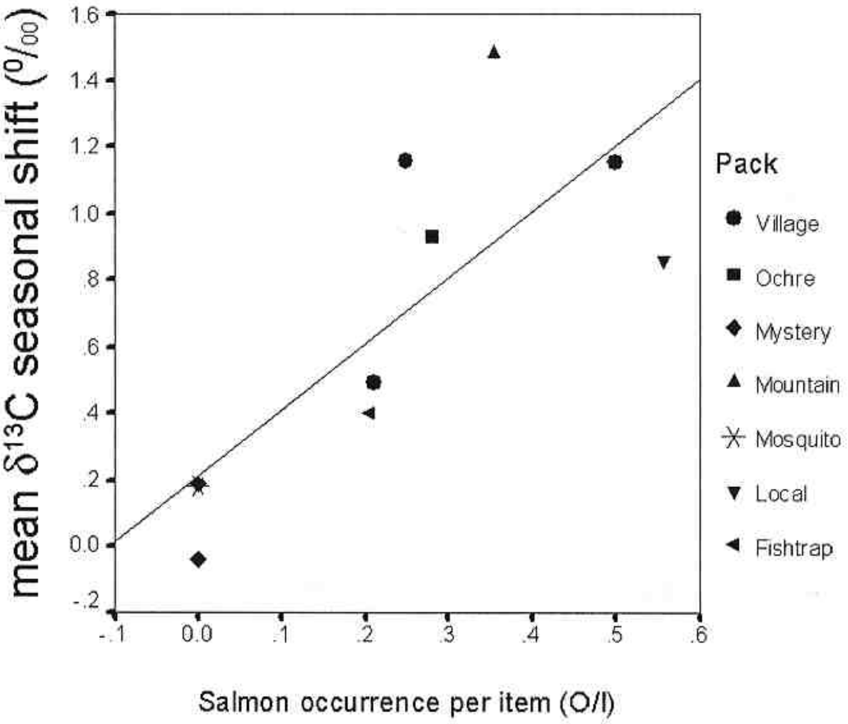


Figure 6.9a,b. Seasonal $\delta^{13}C$ isotopic enrichment in wolf (*Canis lupus*) hair as a function of a) salmon (*Oncorhyncus* spp.; SALMON) and b) deer (*Odocoileus hemionus*; DEER) availability to each pack in coastal British Columbia, 2000 to 2003. *Mosquito pack SALMON biomass estimate excludes the Neekas River, the largest in the study area, but one where wolves were rarely observed. Bivariate correlations showed a strong and positive correlation between seasonal $\delta^{13}C$ enrichment and salmon abundance($r = 0.67$, $n = 15$, $P = 0.006$) but no relationship with deer abundance.

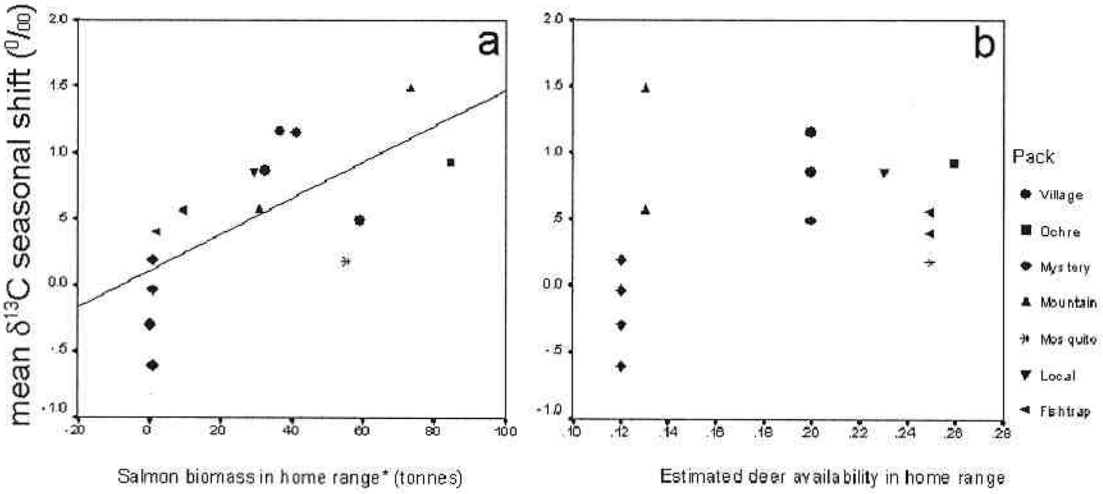


Figure 6.10. Seasonal δ^{13}C isotopic enrichment in wolf (*Canis lupus*) hair as a function of salmon (*Oncorhyncus* spp.) biomass, expressed in quadratic form (r = 0.74, n = 15; P = 0.009). *Mosquito pack SALMON biomass estimate excludes the Neekas River, the largest in the study area, but one where wolves were rarely observed.

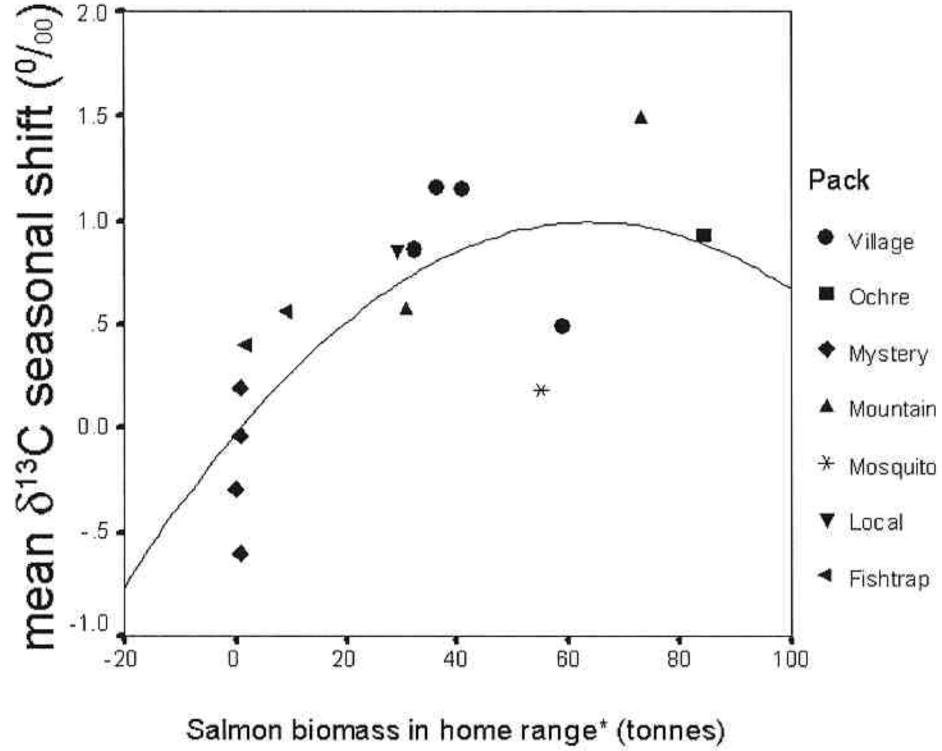


Table 6.1. Estimated mean masses of salmon (*Oncorhyncus* spp.) used for biomass calculations. Data for sockeye, chinook, and coho from Groot and Margolis (1991), for sexes combined and from populations nearest to study area (n not reported). Pink and chum data from Hocking (2006), who sampled the Clatse and Neekas watersheds in this study area; sexes measured separately (n range: 30 to 73).

Species	**Mass (kg)**		
	Males	**Females**	**Sexes combined**
Sockeye (*Oncorhynchus nerka*)			2.7
Pink (*O. gorbuscha*)	1.4	1.1	1.3
Chum (*O. keta*)	4.1	3.0	3.6
Chinook (*O. tshawytscha*)			13.6
Coho (*O. kisutch*)			3.2

Table 6.2a. Top model set to predict the use of salmon (*Oncorhyncus* spp.) by wolves (*Canis lupus*) in eight packs from 2000 to 2003 in coastal British Columbia. Shown are model structure, ΔAIC_c, and Akaike weight (ω_i). SALMON is salmon biomass estimate in metric tonnes, and DEER is relative abundance of deer available to each pack, estimated from a model derived from deer pellet group data in study area (see Methods). YEAR is random factor. Shown also are parameter coefficients (for SALMON and DEER), their standard errors, and model R^2. $^{**}p < 0.01$, $^{*}p < 0.05$. Shown are results from using all data, n = 15 ‘pack years’.

Model Form	**ΔAIC_c**	**ω_i**	**β_0**	**S.E.**	**SALMON**	**S.E.**	**DEER**	**S.E.**	**SALMON x DEER**	**S.E**	**R^2**
β_0 + (SALMON)	0.000	0.406	0.452**	0.177	0.002	0.003					0.43
β_0 + (YEAR)	0.129	0.382	0.494	0.435							0.40
β_0 + (SALMON) + (DEER) + (SALMON x DEER)	2.101	0.142	-0.787	0.428	0.048**	0.011	5.574*	2.141	-0.197**	0.047	0.64
β_0 + (SALMON) + (YEAR)	3.808	0.060	0.429	0.473	0.001	0.003					0.57

Table 6.2b. Excluding Mosquito Pack 2002 datum; n = 14.

Model Form	**ΔAIC_c**	**ω_i**	**β_0**	**S.E.**	**SALMON**	**S.E.**	**DEER**	**S.E.**	**R^2**
β_0 + (SALMON)	0.000	0.609	0.113	0.159	0.016**	0.004			0.52
β_0 + (SALMON) + (YEAR)	2.864	0.145	-0.366	0.376	0.019**	0.005			0.56
β_0 + (DEER) + (SALMON)	3.705	0.095	-0.188	0.412	0.015**	0.004	1.683	2.119	0.55

Table 6.2c. Excluding Neekas salmon biomass from Mosquito Pack 2002 datum; n = 15.

Model Form	**ΔAIC_c**	**ω_i**	**β_0**	**S.E.**	**SALMON**	**S.E.**	**DEER**	**S.E.**	**R^2**
β_0 + (SALMON)	0.000	0.568	0.121	0.168	0.014**	0.004			0.43
β_0 + (SALMON) + (YEAR)	2.824	0.138	-0.270	0.399	0.017**	0.005			0.54
β_0 + (YEAR)	3.622	0.093	0.494	0.435					0.14
β_0 + (DEER) + (SALMON)	3.742	0.087	-0.028	0.434	0.014*	0.005	0.835	2.226	0.44

Table 6.3. Protein, fat, and energy content in 100 grams of raw black-tailed deer (*Odocoileus hemionus*) and pink salmon (*Oncorhynchus gorbuscha*) muscle tissue. Data from United States Department of Agriculture Nutrient Database (http://www.nal.usda.gov/fnic/foodcomp/search//).

Content	**Deer**	**Salmon**
Protein (g)	19.94	21.5
Fat (g)	2.66	3.45
Energy (kj)	111	485

Chapter 7:

Behavioural and ecological context of wolf-salmon associations in coastal British Columbia

Below follows a brief summary of:

Darimont, C. T., T. E. Reimchen and P. C. Paquet. 2003. Foraging behaviour by gray wolves on salmon streams in coastal British Columbia. Canadian Journal of Zoology **81**:349–353.

A reprint in PDF appears as Appendix 1.4

7.1. Chapter Summary

Sampling faeces or isotopic signatures in the tissues of consumers provide no insight into the behavioural and ecological context of the consumption activities that defines their niche. Herein, I report observations of direct and indirect evidence of salmon predation by wolves in several watersheds of coastal British Columbia and in detail report on the foraging behaviour of 4 wolves at 1 river during September and October 2001. Wolves oriented themselves upstream during detection and pursuit of salmon. The pooled mean capture rate was 21.5 salmon/h and mean efficiency (successes/attempt) was 39.4 %. In most cases, wolves consumed only heads of salmon, perhaps for nutritional reasons or parasite avoidance. Preying on salmon may be adaptive as this nutritious and spatially constrained resource imposes lower risks of injury compared with hunting large mammals. I infer from capture rates, efficiencies, as well as stereotyped hunting and feeding behaviour, a history of salmon predation by wolves and, as a corollary, a broad distribution of this foraging ecology where wolves and salmon still coexist.

Chapter 8:

Intrapopulation variability in niche III: niche variation among individuals within social groups and across an archipelago

8.1. Introduction

Ecologists often view populations as ecologically and functionally homogenous assemblages of individuals. Such an assumption critically simplifies empirical and theoretical insights in ecology that relate to competition and other processes. Likewise, such an oversight ignores the evolutionary implications of variation among individuals. This simplification pervades historical and contemporary ecological research, both theoretical and applied, regarding resource use in populations. Even within literature that popularized the ecological concept of the niche or measured population niche breadth, most papers omitted discussion of the possibility that individuals within a species or population can use markedly different resources (*e.g.* Hutchinson 1957, Colwell and Futyma 1971, Abrams 1980 *but see* Lomnicki 1988, DeAngelis and Gross 1992). Moreover, some believe that niche variation among individuals is uncommon and/or small in magnitude (*e.g.* Case 1981, Schoener 1986). Likewise, even current research overwhelmingly examines diet at the population level, with little or no attention to intra-population variation (*review in* Bolnick et al. 2003).

Such oversights continue despite a growing literature on niche width variation, which originated with Van Valen's (1965) niche variation hypothesis. Examining mainland and island birds, Van Valen proposed that population niche expansion can occur via increased among-individual variation in foraging. In his study, Van Valen (1965) observed niche expansion among island compared with mainland populations, where inter-specific competition was stronger. This novel insight ignited numerous examinations of niche variation and the concept of the 'individual niche'; before interest waned in the 1980's, there was considerable evidence for and against the hypothesis (*review in* Bolnick et al. 2003).

Within and beyond the scope of the niche variation hypothesis, there since has been ample evidence to demonstrate that individuals with access to similar food resources can vary widely in their food niche. Recently, Bolnick et al. (2003) amassed support for the individual niche, detecting evidence in 97 species from a broad range of taxa. In some cases, among-individual foraging niche accounted for most of the total population niche breadth.

As a consequence, some current elaborations on foraging theory now focus on variation among individuals, rather than treating it as statistical interference in describing or testing population level trends and hypotheses (Mangel and Clark 2000). What remain rarely examined, however, are the conditions that promote or restrict variation among individuals.

The influence of sociality on niche variation, in particular, is relatively unknown, and theory leads to two opposite predictions. First, if individuals in a social group forage together and presumably encounter an analogous suite of resources, a prediction may be to expect little inter-individual variation in niche. If this is the case, one may expect much smaller variation within compared with among social groups. Second, and in contrast, such proximity while foraging may lead to intense interference competition (Goss-Custard et al. 1984, Giraldeau and Caraco 2000). And if dominance hierarchies exist, one may expect that dominant individuals would out-compete subordinates if quality differences exist among food niches (Radford and du Plessis 2003).

Also relatively unknown are the ecological conditions that can influence niche variation. In theory, ecological conditions such as food availability (*i.e.* diversity, quantity) and presence of competitors, which could vary among areas, would affect how individuals feed. Examinations in this context have been few (*but see* Van Valen [1965]). Providing additional insight was Morse (1974), who reviewed cases of interactions between dominant and subordinate competing species. He concluded that the latter typically maintain narrower niches. Additional tests, however, are needed to examine niche variation among areas that differ in interspecific competition.

Until recently, our ability to examine foraging niche variation among individuals was constrained by methodological limitations. Traditional analyses (*i.e.* faecal and gut contents) are often limited by theoretical and logistical issues (*review in* Bearhop et al. 2004). For example, fecal data alone cannot assign variability to individuals, whereas examinations of gut contents provide only a temporal snapshot of resource use by individuals. To demonstrate niche variation one must document persistent differences among individuals, while controlling for environmental variation.

Appropriately, stable isotope analysis can offer discrete information about individuals that share common ecological conditions over long time periods (*reviews in* Peterson and Fry 1987, Rundel et al. 1989, Kelly 2000). Operating like a modified 'you are what you eat' process, stable carbon and nitrogen signatures provide a cross-referenced proxy for diet. Specifically, as carbon signatures change little among trophic levels, these data reflect dietary sources (DeNiro and Epstein 1978, Tieszen et al. 1983, Peterson and Fry 1987), which themselves may differ. For example, marine food sources have higher, or more enriched, signatures than terrestrial foods (Chisholm et al. 1982). Nitrogen signatures are also enriched in marine foods but also follow a stepwise enrichment at each trophic level (DeNiro and Epstein 1981, Tiezen et al. 1983). Metabolically inert tissue such as hair is especially valuable in isotopic analyses because it reflects diet only during growth and therefore provides an estimate of integrated niche over the growth period (chapter 3).

Stable isotopic analysis is a reliable method with which to identify and estimate intra-population variability in diet, but has only recently been exploited to examine its causes or consequences (Bolnick et al. 2002). In cases in which this technique was tested, it has shown good correlation with other measures of variation in resource use. For example, isotopic variation was related to cross-sectional variation in gut contents of fishes (Gu et al. 1997, Beaudoin et al. 1999). Moreover, I demonstrate in chapter 6 that variation in marine isotopic enrichment in terrestrial carnivores was strongly related to the variation of salmon remains detected in their faeces.

Wolves (*Canis lupus*) of coastal British Columbia provide an ideal model system with which to examine niche variation in the context of sociality and landscape ecology. First, and generally, canids are behaviourally plastic, which is consistent with predictions from their large brain to body mass ratio (Gittleman 1986). Second, like elsewhere, wolves here are social carnivores, and are generally thought to hunt communally and potentially cooperatively (Peterson and Ciucci 2003). Third, a number of social groups occupy one of three ecologically divergent landscape regions among which the suite of prey and competitors differ: the mainland, inner islands, and outer islands. Moreover, in this archipelago and adjacent mainland, data from wolf faeces suggest that total population niche breadth is broad and includes a diverse suite of terrestrial and marine prey (chapters 4, 6, Bryan et al. in press [appendix 2.1]). Without associated information about individuals, however, faecal data cannot provide insight into individual variation. Two predictions emerge. One may predict that such variation is 'washed-out' over time; individuals converge on similar diets averaged over time. Alternatively, such variation in faeces is representative of persistent variation among individuals over long time periods. Accordingly, I use here stable isotopic analysis to assess these hypotheses by examining variability in foraging within and among these social groups. Moreover, I also examine the potential role of landscape conditions (under which competition differs) in influencing niche variation.

8.2. Materials and Methods

8.2.1. Study area

This is the same study area described in detail in chapter 5. Ecological conditions vary considerably throughout the study area. Habitat heterogeneity corresponds to landscape variability, which includes the following general regions: mountainous mainland, topographically complex inner islands, and flatter outer islands. These habitat differences coupled with the effects of isolation likely influence the distribution and abundance of prey and competitors of wolves. Several general patterns can be described (Table 8.1).

8.2.2. Sample collection and preparation

This is the same dataset I examine in chapter 5.

8.2.3. Statistical methods

I assessed how pack membership, year, their interaction, and 'error' contributed to overall variance in isotopic signatures, assuming the latter represented variation among individuals within social groups as well as any measurement error. I used a General Linear Model (GLM) Variance Components procedure (ANOVA design), weighted by the square root of sample size in each 'pack year'. Pack and year were random factors. I used only packs for which I had more than two individuals in each pack year (n = 14 packs, 74 wolves, over 4 years). Number of individuals in each pack ranged from two to 11 in each year, with an average of 3.4.

To assess how variation among individual wolves may be influenced by ecological conditions in different landscape areas, I used a Levene's test. I tested whether variances were equivalent between mainland and island locations, as well as among mainland, inner, and outer islands. I defined inner islands as those adjacent to the mainland, and outer islands as those not adjacent to the mainland (chapter 4). Because yearly variation was limited (see Results), I pooled individuals among all four years. The data set included all samples from the above Variance Components procedure, plus four individuals that were the only ones sampled from four additional different packs (n = 78). Finally, in addition to examining $\delta^{13}C$ and $\delta^{15}N$ signatures separately, I calculated an 'Euclidean distance' metric, which calculates for 2 or more traits (*i.e.* $\delta^{13}C$ and $\delta^{15}N$ signatures) the deviation of a sample from central tendency (the population means in this case, which would be mainland and island populations in the first comparison, and mainland, inner, and outer islands in the second comparison). Measured in Z scores, this metric allows both traits to contribute equally to this distance. All tests and calculations in these analyses were weighted by the square root of the sample size for each area.

I considered the potential contribution of measurement error to contribute to observed niche variability within the population. I used the same values for precision as in chapter 5. Likewise, I approached potential sampling biases in the same way, randomly removing 4 samples because they had similar isotopic signatures (+/- mean measurement error plus SD) as others from the same 'pack year' (see also chapter 9). This resulted in the removal of only 4 of the original 82 samples. If these were removed unnecessarily (*i.e.* they were indeed different individuals), then this would increase the apparent niche breadth within the population. Notably, these four removed individuals occurred in all three landscape regions, and their inclusion in analyses showed similar results (data not shown).

8.3. Results

8.3.1. Intra-social group variability in niche

There was considerable variability in isotopic niche not only among but also within packs. Across the entire poplation, carbon and nitrogen signatures ranged 9.3 and 9.5 $^0/_{00}$, respectively. The distribution of these signatures was primarily oriented in one vector, from relatively low $\delta^{13}C$ and $\delta^{15}N$ signatures up to coupled enrichments of both isotopes. Across all years, pack membership explained only about 50% to 60% of variation in carbon and nitrogen signatures, respectively.

There was also substantial variation within groups; many individuals departed considerably from mean pack signatures (Figure 8.1a-d). 'Error variation', which represents intra-pack variation (and measurement error), accounted for roughly 40% of variation in both isotopes. Year and 'pack x year' effects were small (Table 8.2).

8.3.2. Intra-landscape variability in niche

The magnitude of variation among individuals differed according to the region wolves were sampled. Inter-individual variation was greater among island wolves compared with mainland wolves (Levene's Test; $F_{1,76} = 17.66$, $P < 0.001$ and $F_{1,76} = 35.57$, $P < 0.001$ for $\delta^{13}C$ and $\delta^{15}N$ respectively). Variances were likewise heterogeneous among mainland, inner and outer island wolves (Levene's Test; $F_{2,75} = 8.01$, $P = 0.001$ and $F_{2,75} = 18.06$, $P < 0.001$ for $\delta^{13}C$ and $\delta^{15}N$ respectively), with inner island wolves showing the largest variation.

Tests with Euclidean distance metrics were consistent with Levene's tests. Collectively, wolves from all islands combined had higher variability (greater Euclidean distance from mean sub-population signatures) than individuals from the mainland (T-test; $t = -7.24$, $P < 0.001$, Figure 8.2.). Separating inner and outer islands revealed that inner islands had significantly greater mean Euclidean distance than outer islands and the mainland (ANOVA; $F_{2,75} = 18.31$, $P < 0.001$; Bonferroni Post-hoc comparisons; $P < 0.001$ and $P = 0.003$; Figure 8.3). Plotting packs separately showed repeatability among packs in these trends (Figures 8.4 and 8.5).

A more detailed relationship between isolation and inter-individual niche variation can be described. With all islands combined, the more isolated the island, the greater the variability among individuals. Specifically, there was a significant positive correlation between the average Euclidean distance for each pack and the distance to the mainland for the island on which the pack lived ($r = 0.94$, $n = 11$ islands, $P < 0.001$, Figure 8.6). After removal of the Dundas Island pack, the relationship was not evident ($r = 0.40$, $n = 11$ islands, $P = 0.255$). Repeating this analysis among the subset of packs on the inner islands only, the relationship between isolation and mean Eucliden distance (relative to inner island median signatures) was also positive and significant ($r = 0.85$, $n = 8$ packs, $P = 0.046$, Figure 8.7).

8.4. Discussion

8.4.1. General discussion

Bearhop et al. (2004) remarked that isotopic variance within a population is often of more ecological interest and relevance than the mean. Such a statement is intuitive for the following reasons. Individuals should use resources to maximize benefits such as net energetic gain or ultimately reproductive success. Solutions to optimize these currencies would depend on multiple ecological conditions including the rate at which alternative resources are encountered and competition for these resources (Stephens and Krebs 1987, chapter 1). Such conditions may differ across a landscape. Whereas these ecological factors are resource-specific, the niches of individuals also would be influenced by traits unique to the individual. Accordingly, an individual's realized niche is a function of an intricate interaction among traits of both the ecological landscape and the individual.

Consistent with this theory, there is accumulating evidence across animal taxa showing that individuals can vary markedly in their niche or resource use (*review in* Bolnick et al. 2003). There is, however, uncertainty regarding the contexts and processes that can promote or restrict inter-individual niche variation. Herein I examined the influences of sociality and landscape (which influences the competitive milieu). I present evidence that individuals within a social carnivore population with access to a similar suite of foods can deviate considerably in resource use, both within the social group and as a function of occupying different locations within the landscape.

Variation among prey in isotopic signatures created an isotopic landscape in which niche variation in consumers could be easily interpreted. As Matthews and

Mazumder (2004) highlighted, data on the isotopic composition of potential prey is important in assessing individual niche variation because observed isotopic variation in consumers depends not only on divergence in feeding behaviour but also on variability among food sources. Notably, I demonstrate two important qualities of isotopic data of prey in chapters 5, 6. One, the commonest prey items – deer, marine mammals (seals,otters), and salmon - are isotopically distinct. Second, each of these items does not vary considerably in signature across the landscape. Consequently, niche variation I observe here can be treated as real variation in foraging among individuals.

Specifically, I interpret much of the variation the isotopic signatures as differential marine resource use among individuals. For example, wolves that showed low carbon and nitrogen signals likely were consuming common terrestrial prey such as deer, whereas others with coupled enrichments in both isotopes would have frequently consumed oceanic foods such as salmon and marine mammals (chapter 5). Those with intermediate signatures would have regularly consumed both terrestrial and marine prey. And collectively, wolves of a social or landscape (*i.e.* mainland, island) group had an average signature, from which individuals departed, and considerably.

Isotopic niche variation represented here an integrative and unique dimension of niche, and may not be analogous to others, such as diversity of prey. For example, a social group that consumed a wide variety of terrestrial animals (with similarly 'terrestrial' signatures) would appear less isotopically diverse as a group that consumed only deer and salmon, which differ widely in their isotopic signatures (chapter 5).

My estimated measurement error was small, and accordingly I assume the 'error' variation I detected represented real differences in foraging among individuals. Moreover, the isotopic range among wolves I measured was also far greater (and my measurement error less) than the variation Roth and Hobson (2000) observed among individual foxes (*Vulpes vulpes*) fed an isotopically homogenous diet (0.1 and 0.3 $^{0}/_{00}$ for $\delta^{13}C$ and $\delta^{15}N$ respectively). Urton and Hobson (2005) made similar conclusions when interpreting isotopic variation in wolves of the Boreal Forest.

Urton and Hobson (2005) were one of two previous investigations that have examined intrapopulation isotopic variation in wolves, and compared to both, I present here additional insight. Urton and Hobson (2005) compared variation among wolves of three different regions of the Boreal forest, within and beyond a protected area. Signatures among wolves inside the protected area were significantly less variable than outside, where wolves were exploited by trapping and hunting. They attributed the higher variation to more solitary hunting of individuals from exploited packs, which often have fractured structures and high turnover. Urton and Hobson (2005) did not, however, examine variation at the intra-pack level. Also using isotopic tools, Szepanski et al. (1999) investigated the use of salmon by wolves of coastal and interior Alaska. In contrast to this dataset, these authors found significantly less variability on islands compared with the mainland (see chapter 5 for discussion). Similarly, however, they also did not examine intra-pack variability.

8.4.2. Intra-social group variability in niche

Within social groups I studied, individuals made distinctively different livings. Remarkably, roughly 40% of the isotopic variation occurred *within* social groups, which was only marginally less than the variation *among* groups. This is in contrast to the prediction that individuals that hunt together have similar diets, and aligns with hypotheses relating to intra-specific competition, which may manifest in multiple ways.

Such mechanisms related to the individual that would influence inter-individual variation in niche are numerous and ostensibly conflated. Proximally, they can relate to differences in physiology and behaviour. In turn, these can be governed by age (Polis 1984), sex (Shine et al. 1989), and morphology (Price 1987). For example, different sexes may be able to exploit different niches more efficiently (behaviour), or require different resources to meet sex-specific life histories needs (physiology).

In addition to age and sex effects, differences may arise due to other inter-individual effects, which may be more difficult to detect in study. Recently, Börger et al. (2006) examined what factors influenced the home range sizes of Roe Deer (*Capreolus capreolus*) in Italy. Differences among individuals explained a considerable proportion of variance, but of that, sex and age explained very little. In these cases, other differences among individuals may be invoked. For example, an individual's experience can influence resource use (Werner et al. 1981). Moreover, although individuals within a social group may be related, there are likely underlying heritable components to resource preference (*review in* Jaenike and Holt 1991).

Without data relating to the age, sex, and other individual traits, I am limited to only listing these possible explanations. Szepanaski et al. (1999), however, detected no significant differences in isotopic niche between sexes or ages in wolves of adjacent Alaska. The tissue type analyzed, however, was bone collagen. Due to its low turnover rate, signatures in collagen reflect the isotopic foraging niche averaged since birth, which may be too coarse-grained to detect any age or sex effects. In contrast, Bryan et al. (in press [appendix 2.1]) found ontogenetic niche partitioning among wolves of coastal BC; adults provisioned pups disproportionately more juvenile deer than they consumed themselves during the summer months. In this current study, however, I used hair collected in the spring and early summer. Only adults and yearlings – not pups – could have shed hair for samples.

Another potential, and parsimonious, explanation relates to variability in spatial behaviour among pack members during the breeding season, which the period of hair growth closely mimics. During this time, mature pack members sometimes leave the group for periods ranging from several days to several weeks. Occasionally, large contingents hunt nomadically, leaving only the breeding female and/or maturing offspring to feed and care for the pups (Mech et al. 1998, Mech and Boitani 2003). Recently, Hebblewhite (2006) used global positioning telemetry collars to track wolves of five packs across a southwestern Albertan landscape for 2.5 years. A resource selection function analysis indicated that among-wolf variance in habitat use was actually *greater* than among-pack variance during summer (April to October), a similar time period as this study. If habitat and foraging dimensions of niche are related, one would predict similar feeding niche variation among these wolves. Ultimately, any departure from the group when there are additional members with which prey is shared – in this case, pups - would reduce intra-group competition.

Especially when mediated by a dominance hierarchy, one would expect competition within the social group to lead to inter-individual niche variation. In another social carnivore, but one in which hierarchies are absent, female pride mates in lion (*Panthera leo*) groups show no significant inter-individual variation in food intake

(Packer et al. 1990). In contrast, wolf social groups have what is best described as an 'age-graded model' of dominance in which older members are typically able to effectively intimidate and out-compete younger individuals. Access to carcasses large enough to share is often unequal, and context dependent. Interactions among prey availability, maturation rates, and social conditions best predict food-sharing (Packard 2003).

Evidence for niche variation within social groups, with and without dominance hierarchies, also can be found in non-mammalian taxa. Holbrook and Schmitt (1992), for example, showed that competitively superior surfperch (*Embiotoca lateralis*) fishes specialized on caprellid amphipods. By default, subordinates were either gammarid specialists or generalists. In birds, Schneider (1984) showed that dominant white throated sparrows (*Zonotrichia albicollis*) out-competed subordinates for a feeding niche that was closer to cover. Similarly, dominants excluded subordinates from preferred microhabitat in willow tits (*Parus montanus*; Ekman and Askenmo 1984). Finally, there is considerable evidence for intra-group niche variation in eusocial insects (*i.e.* Heinrich 1976, Johnson 1986, Wells and Wells 1986, Muller 1996). For example, Muller (1996) showed that individual bees captured in mixed flower fields consistently carried proportions of species' pollen that diverged from those collected by others.

Radford and duPleiss (2003) offered a particularly relevant example because, similar to most wolf packs, the social groups they studied were also comprised of related individuals. These authors demonstrated interference competition among social ranks in green woodhoopoe birds (*Phoeniculus purpureus*), which led to niche differentiation in this cooperatively-breeding species. They suggested that dominant individuals probably monopolized preferred foods, resulting in a relatively narrower niche compared with subordinates of the same sex.

8.4.3. Intra-landscape variability in niche

In addition to variation within social groups, I also observed that niche variation differed across the landscape. Specifically, among all islands combined, niche variation increased as a function of isolation from the mainland. Moreover, a finer scale examination demonstrated that individuals that occupied inner islands had more divergent diets within the sub-population compared with those of the mainland and outer islands, which foraged less variably (relative to their sub-population mean signatures). I suspect that ecological differences, namely presence and abundance of prey and competitors, influenced this niche variation.

The distribution and abundance of prey differs among mainland, inner, and outer islands (Table 8.1), and likely affects inter-individual isotopic variation in diet. On the mainland, wolves can forage on the entire suite of terrestrial prey present in the biome. Owing to isolation effects, moose and goat – common prey items on the mainland – become nearly absent on islands and in island diet (chapter 4, Darimont et al. 2005 [appendix 2.4], Price et al. 2005 [appendix 2.3]). Smaller animals like porcupine (*Erethizon dorsatum*) and fisher (*Martes pennanti*), though infrequent dietary items, also have not been detected on islands (Price et al. 2005 [appendix 2.3], *unpublished data*). Isotopic variation among these terrestrial prey, however, is relatively minimal (chapter 5), and therefore would contribute minimally to observed variation in wolf signatures.

In contrast, isotopic variation among all prey, both terrestrial and marine, is large (chapter 5) and could generate the differences in observed niche variation. This is possible because mainland and island systems likely differ in the presence and abundance of terrestrial and marine prey (Table 8.1). Specifically, owing to their larger coastline to area ratio compared with the mainland, islands likely offer more prey (species and biomass) that inhabit the coastal fringe. This ratio is a major and universal determinant of nutrient subsidies across a range of habitats (Polis and Strong 1996). Consistent with this pattern, river otter (*Lontra canadensis*), mink (*Mustela vison*), birds, and intertidal animals, for example, have been more commonly detected in wolf faeces on islands compared with the mainland (Chapter 4). Moreover, on outer islands, wolves receive stochastic marine subsidies, such as beached whales and washed-up squid (chapter 5), which are not common on the inner coast. In chapter 5, however, I find no relationship between the coastline to interior ratio of island and average isotopic signatures of wolves that occupy those islands. Rather, isotopic signatures become more marine enriched with greater isolation of islands, and I postulate that marine prey – while likely being more available on islands – are consumed not as a function of their presumed greater availability but because deer become less available with greater isolation.

That deer may be less abundant with greater isolation, either to wolves or in general, would contribute to greater foraging variability on the islands. In chapter 4, I demonstrate that the probability of detecting deer in wolf faeces declines as a function of island isolation. Likewise, isotopic data, collected over multiple years, show a similar pattern of decreased deer consumption with greater isolation. With reduced foraging on deer, more individual wolves would feed on alternative marine-based prey. Generally being smaller, spatially scattered, and isotopically distinct from terrestrial prey, inclusion of marine prey would increase variation among individuals in isotopic niche.

Wolves are not the only terrestrial carnivores to include marine resources in their niche, and any competition among species also would promote niche variation. Relevant here is that bears (*Ursus* spp.) and salmon have tightly coupled ecological and evolutionary relationships (Reimchen 2000). Isotopic analyses have shown that grizzly bears acquire as much as 90% of their yearly protein from salmon (Hilderbrand et al. 1996). Moreover, there is accumulating evidence that bears and wolves compete for salmon. Smith et al. (2003a) provided detailed behavioural accounts of interference competition with grizzly bears on spawning grounds in Alaska, and I have observed similar interactions in coastal BC (*personal observation*). Moreover, in chapter 6, I hypothesize that the decrease in salmon use by wolves at the highest salmon density could be the result of competition with bears, which also presumably maintain highest densities where salmon are plentiful.

This competition argument is clarified when one considers the distribution and density of grizzly bears and salmon across the landscape. On the mainland, bears are at highest density, whereas they are rare on inner islands, and absent from outer islands (Table 8.1). One then needs to overlay the spatial availability of salmon, which occur throughout the mainland and inner islands in relatively high numbers, whereas they occur at less streams per given area and/or at relatively low numbers per stream on outer islands. Coupled, these patterns would lead to wolves facing the greatest competition for salmon on the mainland, less so on the inner islands, and none on the outer islands. In summary, if the presence and density of bears influence wolf foraging, the consequences of this competitive environment are largely consistent with isotopic patterns among wolves; relatively invariable and mostly terrestrial on the mainland whereas they are more variable on the islands.

This pattern is also consistent with a review relating to interspecific competition and niche. Morse (1974) concluded that species that are typically subordinate in interspecific competition are restricted to narrower niches, often to a subset that are not of primary interest to the dominant one. In the absence or reduction of competing species, however, individuals that can use otherwise claimed resources will experience reduced intra-specific competition and have higher fitness (Roughgarden 1972). This pattern is consistent with wolves being out-competed for salmon on the mainland, and limiting their foraging to deer and other terrestrial prey, while minimally preying on salmon. Such a context would lead to the minimal inter-individual niche variation observed on the mainland.

8.4.4. Conclusions

Individual wolves that comprised social groups across the heterogeneous landscape encountered ecological conditions that would promote niche variation. Specifically, this system had two ecological prerequisites, which varied in magnitude across the landscape: weak interspecific competition coupled with strong intraspecific competition (Roughgarden 1972, Grant and Price 1981, Estes et al. 2003). First, on islands in particular, decreased bear densities (or their absence) would reduce interspecific competition. This is consistent with many documented cases of inter-individual variation, including specializations, in so-called ‘empty niches’ (Simpson 1953, Skúlason and Smith 1995) on other islands (*e.g.* behavioural polymorphism in finches) or isolated water bodies that mimic islands (*e.g.* trophic polymorphisms in fishes of post-glacial lakes). Second, owing to their social structures, strong intraspecific competition would exist among individuals within any pack, regardless of which area they inhabit.

Inter-individual variation in niche - and its acknowledgement - has myriad ecological implications. Niche variation has implications in disease dynamics, for example, because prey are often vectors of disease. In stickleback fishes (*Gasterosteus aculeatus*), for example, owing to different habitats and dietary niches, males have different parasite exposure and infections compared with females (Reimchen and Nosil 2001).

The variability among individuals I observed also has evolutionary implications. For example, individuals that become specialists by exploiting underutilized resources can exhibit higher fitness (Slatkin 1980, Wilson and Turelli 1986, Doebeli 1996, Bolnick 2001). Populations comprised of such individual specialists may be more likely to show evolutionary diversification (Wilson and Turelli 1986, Doebeli 1996, Dieckman and Doebelli 1999). Moreover, 'ecological opportunity' in underutilized niches can lead to increased phenotypic variation, or 'character release' among individuals that use those novel resources (Van Valen 1965, Grant 1972, Roughgarden 1972, Doebeli, 1996, Nosil and Reimchen 2005). Accordingly, one may predict morphological or physiological adaptations among island wolves of coastal BC distinct from mainland conspecifics that occupy narrower niches. Perhaps this would manifest in body size, colouration, and digestive physiology (see also chapter 5).

On a planet facing a loss of diversity, however, such ecological variability among individuals should be recognized as an important component of biodiversity (Bolnick et al. 2003). Populations are typically evaluated on morphological and genetic variation, often without functional context. The value of ecological variation within populations is now being recognized by conservation biologists, with the aim of preserving the underlying genetic diversity and 'evolvability' (Moritz 1994, Crandall et al. 2000). Immediate implications of these data challenge management policies for not only coastal wolves but also for other organisms that prescribe some 'average population niche', which disregards or discounts variability among individuals and the processes underlying them.

Figure 8.1a-d. Intra-pack variability in $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures in wolves (*Canis lupus*) of coastal British Columbia, 2000 to 2003. Large symbols are pack means; small symbols represent individuals within packs. n = 78 wolves.

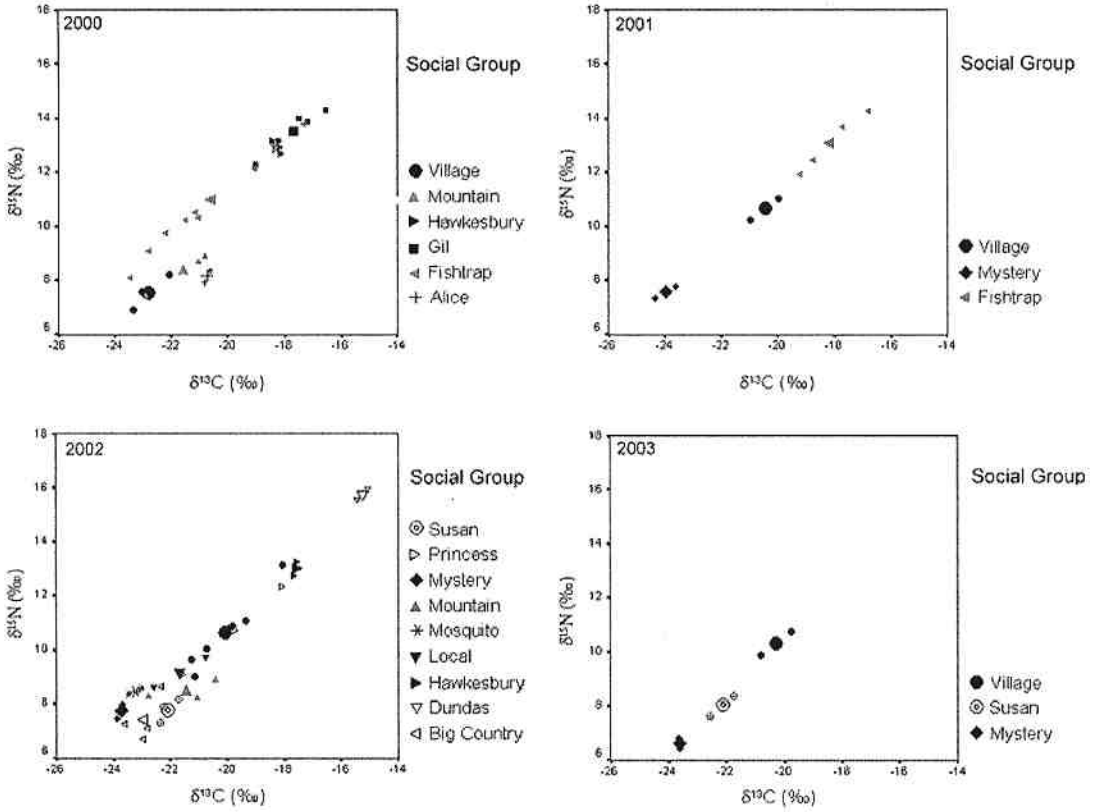


Figure 8.2. Mean Euclidean distances in isotopic signatures from sub-population mean for wolves (*Canis lupus*) of 18 packs from mainland and islands of coastal British Columbia. Hair samples collected 2000 to 2003. Higher values represent greater sub-population divergence from sub-population mean isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$).

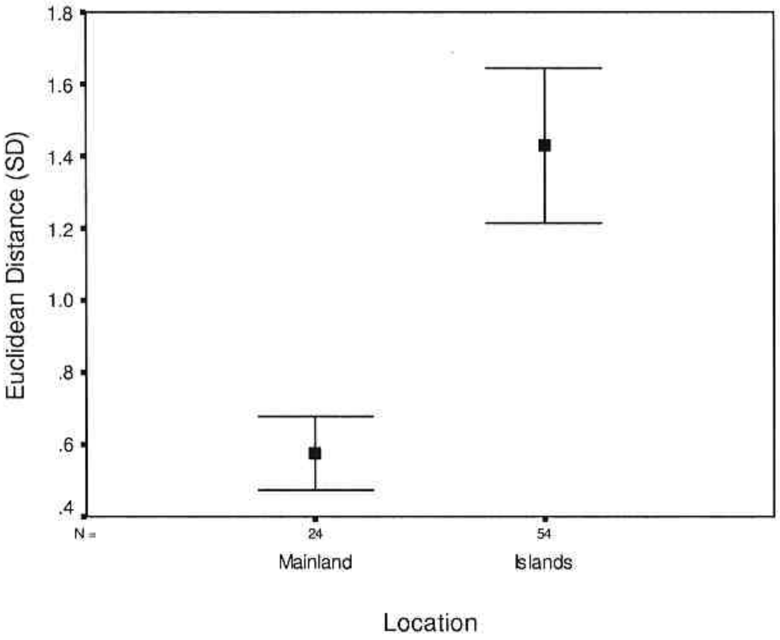


Figure 8.3. Mean Euclidean distances in isotopic signatures from sub-population mean for wolves (*Canis lupus*) of 18 packs from mainland, inner, and outer islands of coastal British Columbia. Hair samples collected 2001 to 2003. Higher values represent greater sub-population divergence from sub-population mean isotopic signatures (δ^{13}C and δ^{15}N).

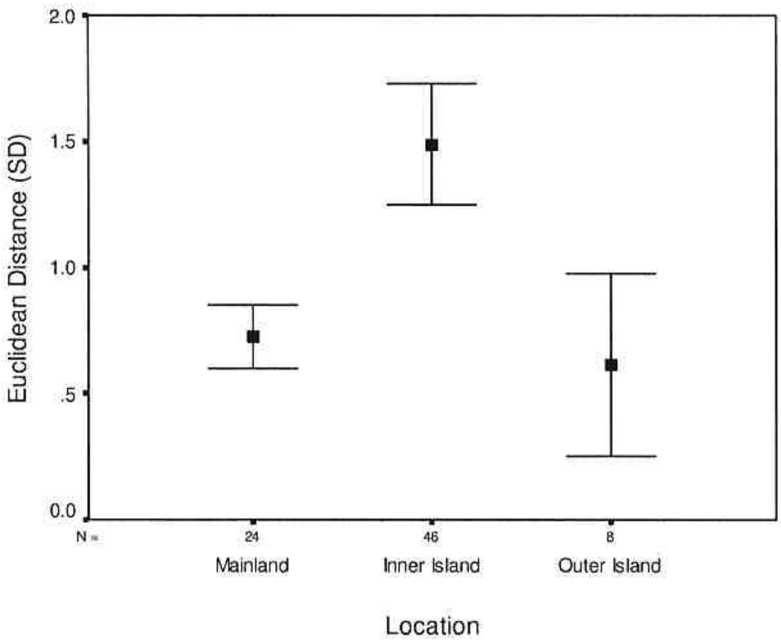


Figure 8.4. Euclidean distances for each social group of wolves (*Canis lupus*) from 18 packs from the mainland and islands of coastal British Columbia. Higher values represent greater sub-population divergence from mean isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$). Hair samples collected from 18 packs (78 individuals) during summers 2001 to 2004. Islands ordered by increasing isolation to mainland.

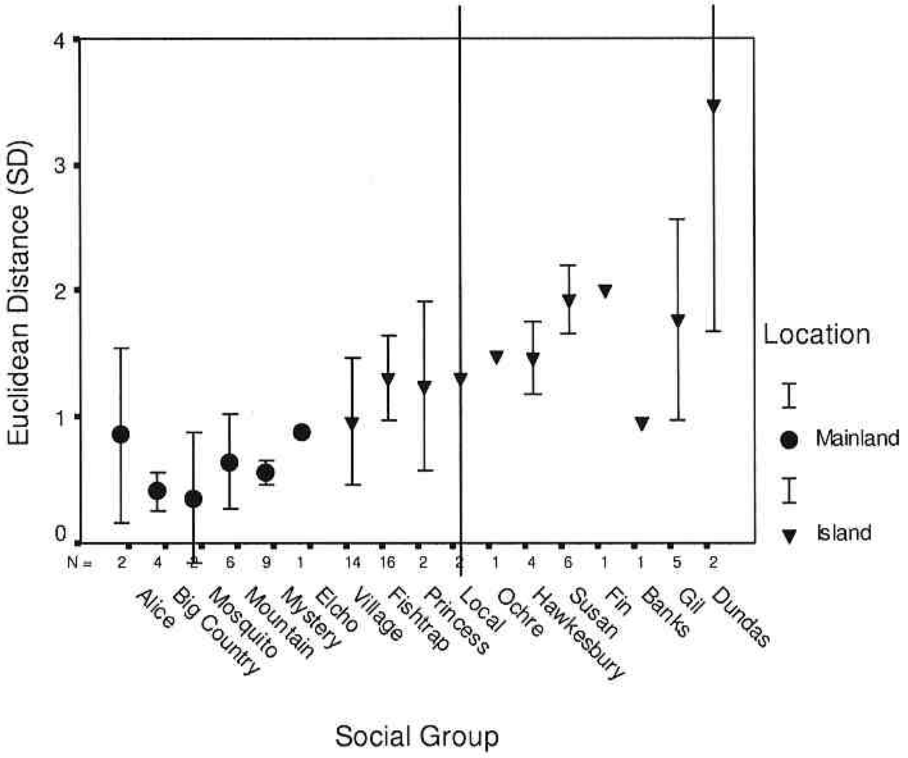


Figure 8.5. Euclidean distances of each social group of wolves (*Canis lupus*) from 18 packs of the mainland, inner, and outer islands of coastal British Columbia. Higher values represent greater sub-population divergence from mean isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$). Hair samples collected from 18 packs (78 individuals) during summers 2001 to 2004. Islands ordered by increasing isolation to mainland.

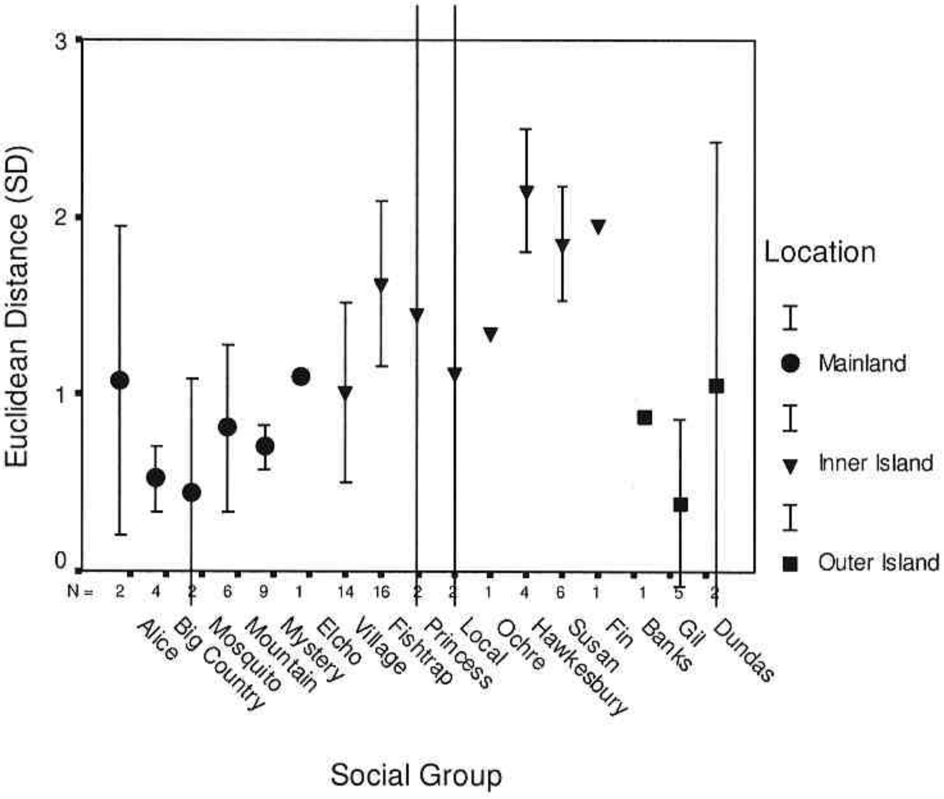


Figure 8.6. Euclidean distances for each wolf (*Canis lupus*) social group as a function of the isolation of the island where each group resides. Hair samples collected from 11 packs (78 individuals) during summers 2001 to 2004. With greater isolation, individual wolves are more different from one another in their isotopic niche (r = 0.94, n = 11 islands, P < 0.001, Figure 8.6). After removal of the Dundas Island pack, the relationship was not evident (r = 0.40, n = 11 islands, P = 0.255).

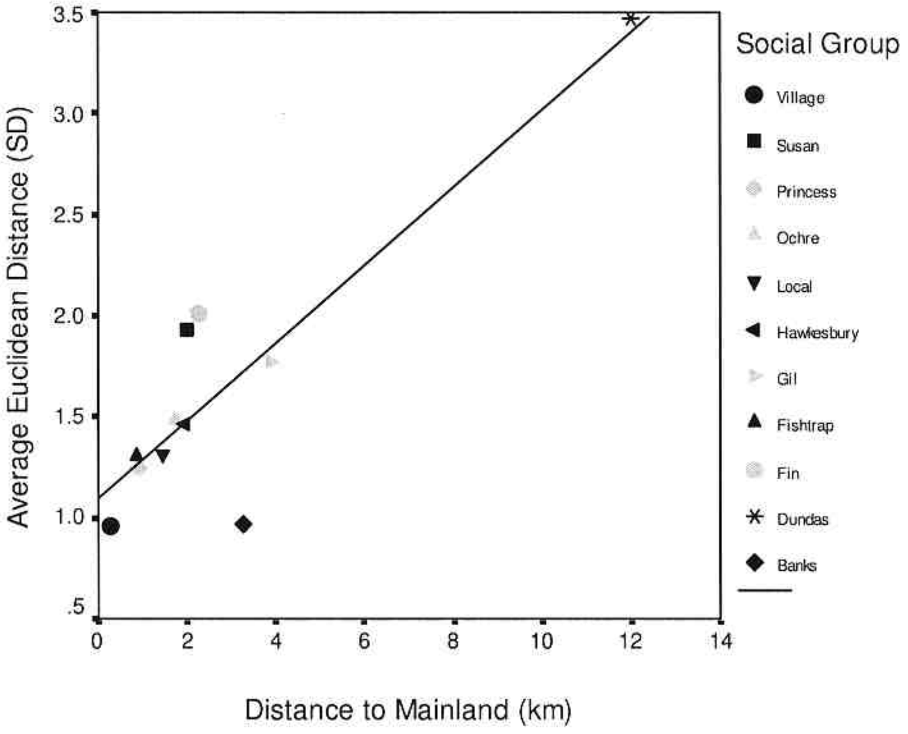


Figure 8.7. Average Euclidean distance for each wolf (*Canis lupus*) social group from 'mean inner island' isotopic signature as a function of the isolation of the island where each group resides. With greater isolation, individual wolves are more different from one another in their isotopic niche. Hair samples collected from 8 packs (54 individuals) during summers 2001 to 2004.

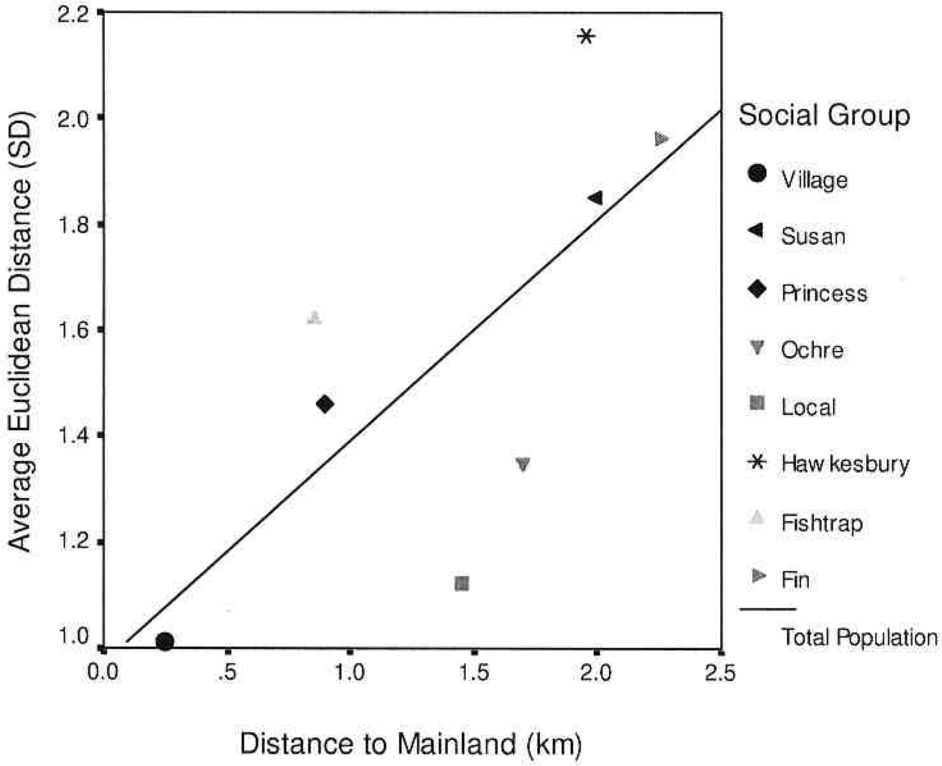


Table 8.1. Ecological conditions relating to wolf (*Canis lupus*) prey and competitors in different landscape regions of coastal British Columbia. [a]Price et al. 2005 (appendix 2.3); *unpublished data*. [b]*personal observation*. [c]W. McCrory *personal communication*.; I. McAllister *personal communication*; *personal observation*.

Location	**Terrestrial prey species richness**[a]	**Marine prey species richness**[b]	**Grizzly bear abundance**[c]
Mainland	high	moderate	common
Inner Islands	moderate	moderate	rare
Outer islands	low	high	absent

Table 8.2. Variance components (ANOVA Design) accounting for variation in isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) among wolves of coastal British Columbia. Hair samples collected from 14 packs between 2001 and 2004. Number of individuals in each pack ranged from two to 11 in each year, with an average of 3.4 (n = 74). 'Error' variance represents intra-pack variation among wolves and any measurement error.

Variance component	**Percent explained ($\delta^{13}C$)**	**Percent explained ($\delta^{15}N$)**
Pack	48.8	57.6
Year	5.7	6.1
Pack x Year	2.5	0.1
'Error'	43.0	36.1

Chapter 9:

Evolutionary consequences of intrapopulation variability in niche: stable isotopic niche predicts fitness of prey in a wolf-deer system

Below follows a brief summary of:

Darimont, C. T., P. C. Paquet, and T. E. Reimchen. 2007. Stable isotopic niche predicts fitness of prey in a wolf-deer system. Biological Journal of the Linnean Society **90**:125–137.

A reprint in PDF appears as Appendix 1.5

9.1. Chapter summary

Inter-individual variation in niche presents a potentially central object on which natural selection can act, and may have important evolutionary implications because habitat use governs a suite of selective forces foragers encounter. In a free-living native deer population from coastal British Columbia, I used stable isotope analysis to identify individual variation in foraging niche and investigated its relationship to fitness. Using an intra-generational comparison of surviving and non-surviving deer over two years of predation by wolves, I detected resource-specific fitness. Individuals with isotopic signatures that suggested they foraged primarily in cedar-dominated and low-elevation hemlock-dominated forest stands were more likely to be killed by wolves. High quality forage in cedar stands, as indexed by protein content, may be involved in maintaining this foraging phenotype. Moreover, non-survivors diverged more than survivors from median isotopic signatures, suggesting selection against foraging specialization. Stable isotope analysis provides novel opportunity to integrate the ecological and selective landscapes to identify underlying ecological mechanisms of selection and provide insight into the maintenance of variability.

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