GRIZZLY BEAR
POPULATION ABUNDANCE, DISTRIBUTION & CONNECTIVITY ACROSS BRITISH COLUMBIA'S SOUTHERN COAST RANGES

DRAFT Version 2.0

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Cover Photo (credit - Norm Dougan): Sow grizzly bear and two-year-old cub observed cavorting in the Blackwater Valley of British Columbia's southern Coast Ranges.

PREFACE

This report is the culmination of a long-term research program spanning 2004 - 2012. Much of this work is intended for academic publication, and some portions of data analyses, interpretation and conclusions are subject to change as a result of the review and editorial process. Also, additional field sampling within the region is still ongoing at the time of this report, and the analyses described herein may be updated as additional data come available. Readers are encouraged to inquire with the primary author about the availability of updated versions of this report or associated journal papers.

This report is intended for a diverse audience that includes resource managers, resource stakeholders, the general public, and other researchers. By necessity, some sections of this report are highly technical in nature in order to maximize scientific transparency in our research, inferences, and the development of decision-support products. However, to better facilitate the extension of this work to grizzly bear conservation, we have packaged the discussion of results from each analytical chapter into a final chapter (not included in this draft) that also presents conservation implications and applications of our outputs.

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ACRONYMS & ABBREVIATIONS USED

BEC	Biogeoclimatic Ecosystem Classification
BCRP	BC Hydro – Bridge Coastal Fish and Wildlife Restoration Program
BM	Boulder-McParlon
CSCR	Central South Chilcotin Ranges
CWH	Coastal Western Hemlock biogeoclimatic zone
ESSF	Englemann Spruce – Subalpine Fir biogeoclimatic zone
FIA	Forest Investment Account
GBPU	Grizzly Bear Population Unit
GP	Garibaldi-Pitt
GPS	Global Positioning System
GVI	Green Vegetation Index
HCTF	Habitat Conservation Trust Fund
IDF	Interior Douglas-fir biogeoclimatic zone
IER	Integrated Ecological Research
Interfor	International Forest Products Ltd.
JS	Jervis-Sims
Ledcor	Ledcor Power Inc.
LGBWG	Lillooet Grizzly Bear Working Group
LLRMP	Lillooet Land and Resource Management Plan
LRMP	Land and Resource Management Plan
MH	Mountain Hemlock biogeoclimatic zone
MME	Manatee-Meager-Elaho
MOE	Ministry of Environment
MOFR	Ministry of Forests and Range
MS	Montane Spruce biogeoclimatic zone
NCDE	Northern Continental Divide Ecosystem
SL	Squamish-Lillooet
SN	Stein-Nahatlatch
SSLRMP	Sea to Sky Land and Resource Management Plan
SSNR	Southern South Chilcotin Ranges
TB	Toba-Bute
TB-PD	Toba-Bute/Powell-Daniels
TC	Taseko-Chilko
TSA	Timber Supply Area
WGI	Wildlife Genetics International
WLAP	Ministry of Water, Land and Air Protection

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Many individuals played important roles in this study. Tony Hamilton encouraged Clayton Apps to seek funding to initiate this study more than a decade ago. Significant in-kind contributions were then provided by MOE and what is presently FLNRO. We are especially grateful for the time and dedication of Steve Rochetta. In various capacities, important contributions were also made by Matt Rochetta, Bruce McLellan, Bryce Bateman, and Tony Hamilton. Safe and proficient helicopter services were provided by Blackcomb Helicopters, and we appreciate the courtesy and commitment provided by their staff. Meticulous and timely genetic analyses were conducted by the staff of Wildlife Genetics International under the supervision of David Paetkau. Stable isotope laboratory analyses were conducted by Benjamin Harlow of the Laboratory for Biotechnology and Bioanalysis at Washington State University, as well as David Arkinstall under direction of Rob O'Brien at the UBC-Okanagan Regional Chemical Analysis Centre. We are grateful to the friendly staff of the MOE Alice Lake field office and compound for patiently accommodating us, and providing both a base for our field work and storage for our equipment and supplies. The Lillooet Grizzly Bear Working Group provided helpful encouragement and feedback to this study. Finally, we thank the many other individuals listed below who assisted and contributed in the field or in other capacities.

The technological and methodological advancements that have made this study possible are largely the result of efforts by several British Columbia researchers over the past 18 years. Clayton Apps wishes to acknowledge Michael Proctor and Garth Mowat for their particular contributions in the development of field sampling methods employed in this study, John Boulanger for providing an extensive foundation in population modeling from such data, and Bruce McLellan and John Woods for encouraging and contributing to the initial development of all aspects of related research approaches including the spatial analytical approach we apply in Chapter 4.

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ABSTRACT

British Columbia's southern Coast Mountains define a southwestern fringe of grizzly bear range. Until recently there has been no study and little known of grizzly bear population status and ecology here, a concern given the wide range of land resource demands and the potential for mounting cumulative human impacts. Between 2004 and 2011, we applied remote hair-snag and subsequent DNA techniques to systematically sample grizzly bear occurrence across 41,250 km^2 of potential range. In addition to establishing landscape occupancy, our objectives were to model population density, distribution, and connectivity, and to best explain associated patterns in terms of natural and human factors. Among geographically defined population units, grizzly bear density varied between 0 (likely extirpated) and at least 21.4 bears per 1,000 km^2. Tremendous spatial variation in abundance and complex distribution was explained by several surrogates of habitat quality, human influence, and associated dispersion. These landscape factors are highly predictive of grizzly bear occurrence and distribution across the region, and resulting models represent useful tools to support population-level conservation assessment and planning. Among 411 individuals detected to date, we identify 11 genetically discrete population clusters. We used spatial interpolation of the proportional assignment of individuals among clusters to infer generalized but spatially distinct ancestral landscapes most likely to have supported founding individuals of each group. The history of relative isolation and restricted gene flow across the region is related to human access (present and likely historic) and physiographic features that are likely to inhibit grizzly bear survival and movement. But overall mortality, population depression and localized genetic drift is likely to have also contributed to the clear spatial pattern of genetic structure. Most of the defined genetic groups are no longer panmictic, but gene flow continues to be restricted in some locales. One small group (n=~23) has remained entirely isolated with lower genetic variability than known for any other mainland grizzly bear population. Pedigree construction based on known parent-offspring relationships also indicates population expansion and reconnection particularly as a result of certain dominant breeders. Stable isotope signatures from hair samples of individuals across the greater region indicate clear dietary variation among regional locales, with major food influences obvious in some and unclear in others. The pattern of dietary variation is related to genetic structuring across the region, though cause and effect mechanisms are unclear. Our results and outputs will support assessment and planning for regional population recovery and conservation, for example, by focusing efforts to re-establish and maintain the functioning of population core, peripheral and linkage landscapes. In particular, the importance of secure source areas for population recovery and expansion to peripheral but connected landscapes is demonstrated.

Key Words: carnivore, connectivity, conservation, DNA, detection, diet, distribution, fragmentation, genetics, grizzly bear, population, spatial modeling, stable isotope*, Ursus arctos*

Chapter 1

BACKGROUND

INTRODUCTION

The grizzly bear (*Ursus arctos*) is an iconic species of high public profile. As a species of special concern in Canada (COSEWIC 2012), grizzly bear management garners attention at local, national and international levels. British Columbia's commitment to grizzly bear conservation is reflected in the provincial Grizzly Bear Conservation Strategy (MELP 1995) which seeks to maintain in perpetuity the diversity and abundance of grizzly bears and the ecosystems on which they depend. Like many other large carnivores, the primary challenge in grizzly bear conservation pertains to their incompatibility with human settlement and associated activity. Grizzly bear range in the conterminous United States is presently less than two percent of that prior to European settlement (Servheen 1990, Mattson and Merrill 2002), although there is no evidence that contraction has occurred in recent decades. Today, much of the southern fringe of grizzly bear range is defined by mountains and high plateaus associated with limited human presence (McLellan 1998). The foundation for population recovery and conservation along the southern fringe includes the provision of core population areas where human activities incompatible with grizzly bear conservation can be controlled, and opportunities for bears to move, survive and interbreed among such areas (MELP 1995).

British Columbia's Southern Coast Ranges comprise the southwestern-most lobe of grizzly bear distribution in North America. This range is generally defined by five grizzly bear population units (GBPUs; MOE 2012). These include four of the nine GBPUs within the province that are considered Threatened under the assumption that historic and current human influence has pushed present populations below 50% of their underlying potential. These Threatened populations are defined by the Squamish-Lillooet, Garibaldi-Pitt, Stein-Nahatlatch, and South Chilcotin Ranges GBPUs, while the Toba-Bute GBPU is considered Viable (Figure 1). The recovery of these Threatened populations to a healthy and viable state is Cabinet endorsed and also supported by the Squamish and Lil'wat First Nations through the Sea to Sky Land and Resource Management Plan (LRMP) and parallel native land use planning of the Squamish and St'at'imc First Nations. However, grizzly bear persistence is generally incompatible with high levels of human presence and development (McLellan 1998, Mattson & Merrill 2002) and there is evidence to justify growing concern about the recovery and future viability of South Coast grizzly bear populations. Mounting cumulative impacts are expected to result from the area’s growing recreational popularity, associated development trends, existing and proposed industrial activities, and accessibility from the nearby lower mainland.

Grizzly bear conservation and recovery requires proactive planning that begins at the regional level and includes provision for core population areas where human activities incompatible with grizzly bear conservation can be controlled, secure movement and genetic interchange among such areas and their peripheries, as well as habitat protection and enhancement measures necessary to achieve these. Such assessment and planning in turn depends on understanding of grizzly bear population abundance, distribution and connectivity and the factors that influence associated trends through space and time. Such information is particularly relevant across the southern Coast Ranges given the plethora and history of human activity and the diversity of ecological conditions. Methods to gain reliable knowledge about grizzly bear populations across regional areas are well established and mostly involve the application of systematic hair-snag detection sampling and subsequent DNA analyses.

This report describes a multi-year research program to sample and empirically model current and potential grizzly bear population abundance, distribution, and connectivity across British Columbia's southern Coast Ranges, with inferences regarding causal factors and probable trends - both current and historic. Results and outputs from this work are intended to provide a foundation for directing and monitoring grizzly bear recovery across this region at an appropriately broad, population scale. The report is arranged into chapters addressing different aspects of the study. In the remainder of this first chapter we present a detailed overview of the southern Coast Ranges study and modeling area, associated GBPUs, and broad variation in ecological and human conditions. In Chapter 2, we describe field-sampling strategy, methods, laboratory techniques, and we summarize sampling results across years. In Chapter 3, we present capture-recapture analyses to estimate population abundance according to defined spatial strata. In Chapter 4, we develop an empirical model of regional population distribution and connectivity, evaluating habitat and human factors that may influence associated spatial patterns. These outputs form the basis for defining current and potential population cores and associated landscape linkages among them. In Chapter 5, we characterize historic and current patterns of population fragmentation on the basis of genetic evidence, evaluating grizzly bear gene flow in terms of landscape and human factors. In Chapter 6 we evaluate parent-offspring relationships given our data, and we describe pedigrees and their relevance to understanding population connectivity, history and likely trend. In Chapter 7 we evaluate generalized variation in trophic-level diet among grizzly bears across the southern Coast Ranges. Finally, in Chapter 8, we discuss the conservation implications of our results and decision-support applications.

REGIONAL STUDY & MODELING AREA

Multi-Year Study Area

Our multi-year regional study area for this project encompassed roughly 50,000 km^2 of several major watersheds at the southwestern extent of current grizzly bear range (Figure 1-1). These drainages include the Southgate, Toba, Powell-Daniels, Jervis, Squamish, Lillooet, Seton, Cayoosh, Bridge, Stein, Nahatlatch, and Pitt systems. The regional study area was specifically defined by the following grizzly bear population units (GBPUs): Squamish-Lillooet, Garibaldi-Pitt, Stein-Nahatlatch, most of the South Chilcotin Ranges, and the southern half of the Toba-Bute. All of these GBPUs are currently assigned a conservation status of Threatened (current population = 1 – 50% of potential) with the exception of the Toba-Bute, which is considered Viable (Hamilton et al. 2004). The central to northern portion of the Toba-Bute and the southern portion of the Klinaklini-Homathko units have always been included in the regional study area. However, sampling in these areas had not been completed at the time of the previous iteration (ver. 1; 2009) of this report. This present report version includes sampling across all of the Toba-Bute but the Klinaklini-Homathko is still incomplete. There is currently no general open season or limited entry hunting for grizzly bears within the greater multi-year focal area.

The regional study area is ecologically diverse, including both the Coast and Mountains Ecoprovince and the Southern Interior Ecoprovince (Demarchi 1996) and with elevations ranging from sea-level to 3,000 m. The wetter, western portion falls within the Pacific Ranges Ecoregion, defining the southernmost ranges of British Columbia's Coast Mountains. Here, mountains are typically high and rugged, and biogeoclimatic ecosystems (Meidinger and Pojar 1991) transition from Coastal Western Hemlock at lower elevations, to Mountain Hemlock and then Alpine Tundra with increasing elevation. Moving toward the northeast in the study area, the climate transitions from a wetter coastal to a drier interior condition. Here, mountains become more subdued in the Chilcotin Ranges Ecoregion, beyond which is the Fraser River Plateau Ecoregion where terrain is gently rolling and climate more continental. Ecosystems in the northeast transition from Interior Douglas-Fir and Sub-Boreal Pine-Spruce at lowest elevations to Montane Spruce, Engelmann Spruce-Subalpine Fir and Alpine Tundra at highest elevations.

The regional study area lies directly north of the Greater Vancouver Regional District that encompasses 21 municipalities with a combined human population of 2.25 million. Several other regional districts are represented with human populations as follows: Powell River (20,000), Sunshine Coast (26,000), Squamish-Lillooet (35,000), Fraser Valley (257,000), and Cariboo (62,000). With the exception of the Squamish-Lillooet, the vast majority of people live around but not directly within the defined study area. Communities included within the study area include the towns of Squamish, Whistler, Lillooet, Pemberton, and several smaller communities. Central to the study area is the 11,000 km^2 Sea to Sky Regional Planning area with a resident human population of 31,000, a 20-year annual growth rate of 3.9%, and a large number of excursion visitors from the nearby greater Vancouver population and from around the world (Holman and Nicol 2001). Annual recreational visitation to Whistler exceeds two million and is expected to grow 38% in the 25 years from 2005, in step with population growth in the lower mainland (ILMB 2008).

Resource use in the study area is varied and includes forestry, public and commercial tourism and recreation, hydro-electric development, range use, small-scale agriculture, settlement, and water supply. Several new recreation developments have been constructed, primarily associated with the resort community of Whistler/Blackcomb for the 2010 Winter Olympics. The cumulative effects of these projects are expected to result in additions to transportation infrastructure, urban development, population growth, and greater demand for outdoor recreation (Holman and Nicol 2001). Protected areas in the form of environmental reserves comprise 18% of the study area. Private lands and Indian reserves are primarily clustered along transportation corridors within the main valleys and in the lower mainland.

Sampling Areas

We conducted our field sampling over six years in different subsections of the above-described greater regional study area, with the multi-year sampling area encompassing 41,250 km^2. Each annual sampling area was defined according to grizzly bear population unit boundaries and to maximize expected opportunities for geographic closure to grizzly bear movements given geographic and human features. They were also constrained by budgetary and logistical considerations within the context of what we determined to be a minimum sampling intensity and duration (see Chapter 2). We expected several of our sampling areas to extend into and encompass landscapes currently unoccupied by grizzly bears. We made this choice in light of our objective to better understand and model population distribution, and considering the highly generalized and anecdotal nature of what is assumed to be the assumed “occupied line”. Thus, the Year 1 (2004) sampling area was 9,600 km^2 and encompassed all of the Squamish-Lillooet and part of the Toba-Bute GBPUs. The Year 2 (2005) sampling area comprised 8,200 km^2 and corresponded to the Stein-Nahatlatch GBPU. The Year 3 (2006) sampling area comprised 11,000 km^2 and included all of the Garibaldi-Pitt GBPU and the southern portion (south of Carpenter Lake) of the South Chilcotin Ranges GBPU. And the Year 4 (2007) sampling area comprised 8,000 km^2, extending ~60 km north of Carpenter Lake and the Bridge River and bounded by Chilko Lake in the West and the Fraser River in the east. For analysis purposes, we split our 2004 and 2006 sampling areas each into two smaller units using appropriate geographic boundaries that we expect to minimize or constrain grizzly bear movements. During 2008 and 2010, we conducted more intensive sampling within the Toba, Orford and Southgate drainages that represent most if not all of landscapes occupied by grizzly bears within the Toba-Bute GBPU. Henceforth, we refer to annual sampling areas/analysis units by acronym (Table 1-1).

Table 1-1. Stratification for sampling and analysis of grizzly bear population abundance across the southern Coast Ranges of British Columbia, 2004 – 2010. For several strata, geographically distinct sub-areas within were also considered for abundance estimation (Chapter 3).

Stratum Acronym	Area Description	GBPU	Year Sampled
TPD-04	Toba / Powell Daniels	Toba/Bute	2004
SL-04	Squamish-Lillooet	Squamish-Lillooet	2004
SN-05	Stein-Nahatlatch	Stein-Nahatlatch	2005
GP-06	Garibaldi-Pitt	Garibaldi-Pitt	2006
SSCR-06	South South Chilcotin Ranges	South Chilcotin Ranges	2006
CSCR-07	Central South Chilcotin Ranges	South Chilcotin Ranges	2007
TO-08	Toba and Orford drainages	Toba-Bute	2008
SGC-10	Southgate drainage & Southwest Chilko Lake	Toba-Bute (primarily)	2010

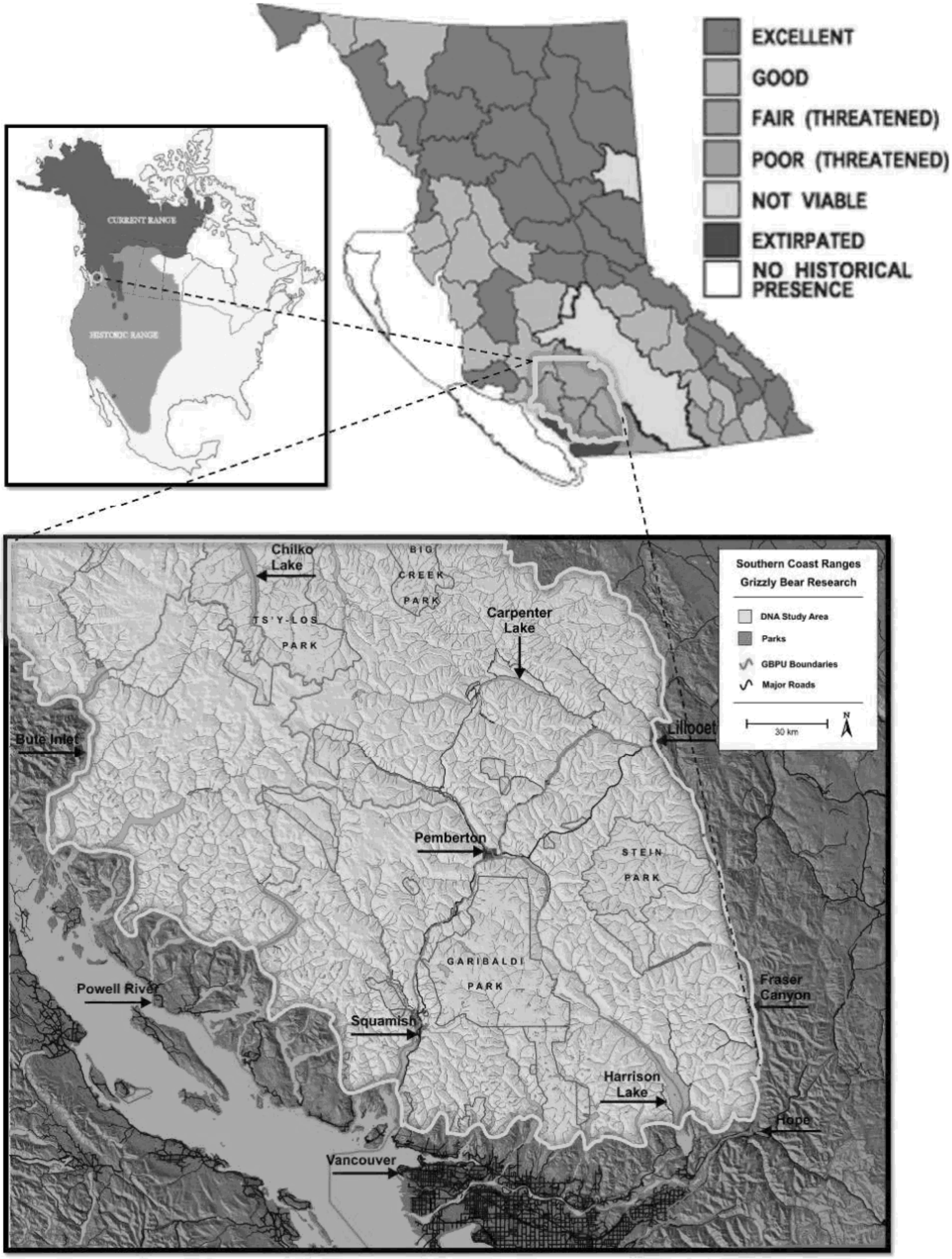

Figure 1-1. Southern Coast Ranges regional study area and location relative to North American grizzly bear range, and British Columbia grizzly bear population units and associated status.

Chapter 2

GRIZZLY BEAR DETECTION & GENETIC PROFILING

INTRODUCTION

Over the past decade, there have been important advancements in the extraction, amplification, and analysis of trace amounts of mitochondrial and nuclear DNA from minute tissue samples derived from sources such as hair and scat. As a result, the use of DNA-based detection methods for various species has swelled (Waits 2004, Waits and Paetkau 2005). For carnivores, the main advantage of DNA sampling over other detection methods (e.g., Zielinski and Kucera 1995) has been the ability to identify individual animals, facilitating the application of capture-recapture analyses to estimate population size and monitor trends. The most common approach to remote DNA sampling has been through hair-snagging, a method that has become routine for bears (Woods et al. 1999, Mowat and Strobeck 2000, Boulanger et al. 2002). In this chapter, we describe our design and field methods for systematic, wide-spread sampling of grizzly bear abundance and distribution using remote hair-snagging and subsequent DNA profiling. We then summarize sampling results among years of this study.

METHODS

Field Sampling

We conducted field sampling from 2004 - 2012[1], with the multi-year study area split into annual sampling areas of 8,000 to 11,000 km^2 (2004 - 2007) and 6,650 km^2 (2008 & 2010). To sample grizzly bear occurrence, we deployed stations to snag grizzly bear hair remotely and noninvasively, generally consistent with Woods et al. (1999). Stations were systematic-randomly distributed according to a grid with grid cell sizes of 10 x 10 (2004 - 2007) and 5 x 5 (2008 & 2010) km. We sampled 90 cells during year 1, 82 cells during year 2, 110 cells during year 3, 80 cells during year 4, 99 cells during year 5 and 48 cells during year 6 for a total coverage of 41,250 km^2 to date with some spatial overlap (resampling) among certain years. Using consistent criteria based on office evaluation and aircraft reconnaissance, we selected sites within each cell to maximize the likelihood of grizzly bear detection, in addition to helicopter landing-ability, with some also placed strategically within what we expected to be movement “pinch-points”. At each site, a single strand (~25 m) of standard four-pronged barbed-wire was placed around a group of trees at a height of 40-50 cm to form a closed polygon, within

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[1] systematic sampling for population survey was carried out 2004 - 2010

which a small brush pile was built and baited with a liquid lure consisting of 3.8 litres rotted cow blood and 1.9 litres fish oil (e.g., Figure 2-1). Sites were installed by teams of two or three.

We accessed all sampling sites by helicopter (Astar™ 350) for both installation and subsequent checks. Among most years, our effort consisted of four sampling sessions of approximately ten days each, from early June to late July. However, specific session dates varied somewhat among years, and we conducted a fifth session during 2005[2]. Session dates and duration varied slightly, primarily due to weather (Table 2-1). Between sessions, we collected hair samples, sterilized wire-barbs, and re-lured but did not move stations. Samples collected during each year (including probable black bears) were stored were and we built an associated database by site (cell) and session.

As previously outlined (Chapter 1), this study was intended to address the primary objectives related to the estimation of population distribution and connectivity (current and historic), as well as absolute population abundance for relevant management units. Our field sampling approach was designed to optimally address all objectives within a realistic budget. In subsequent chapters, we discuss the implications of our sampling design to analysis objectives, specifically as related to the spatial intensity of sampling (i.e., cell size), representation of natural and human conditions across the regional study area, and spatial scale of distribution modeling.

Table 2-1. Number, timing and duration (median among stations) of grizzly bear hair-snag/DNA sampling sessions across the southern Coast Ranges, British Columbia, 2004 – 2010.

	Start Date (Days)				
Stratum-Year	Session I	Session II	Session III	Session IV	Session V
TPD-04	10 June (13)	23 June (10)	3 July (10)	13 July (10)	
SL-04	10 June (13)	23 June (10)	3 July (10)	13 July (10)	
SN-05	5 June (11)	16 June (11)	27 June (11)	8 July (11)	19 July (11)
GP-06	7 June (13)	20 June (12)	2 July (13)	15 July (16)	
SSCR-06	7 June (13)	20 June (12)	2 July (13)	15 July (16)	
CSCR-07	7 June (12)	19 June (10)	29 June (11)	10 July (10)	
TO-08	14 June (12)	26 June (15)	11 July (11)	23 July (13)	
SGC-10	26 June (12)	8 July (12)	20 July (10)	30 July (11)	

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[2] This decision was made in response to unusually inclement weather during the previous sessions and the expectation of relatively low detection rates.

Figure 2-1. An example of bear bait-station hair-snag setup involving a closed polygon barbed-wire strand enclosing a brush pile baited with a non-reward liquid lure (top), and the process by which hair samples are snagged from visiting bears (bottom).

Genotyping

All hair-snag samples were sent to Wildlife Genetics International (WGI) of Nelson, BC, for DNA analysis under the supervision of Dr. David Paetkau.

<u>Sample Subselection & Species Assignment</u> – Although visual inspection in the laboratory can be used to exclude many if not most black bear samples with guard hairs (Woods et al. 1999), many of our samples were of underfur and could not be visually screened in this way. Considering the total number of samples collected (year 1 = 2,017; year 2 = 1,519, year 3 = 1,637, year 4 = 1,028, year 5 = 2,099, year 6 = 1,081), we applied subsampling rules to avoid costly redundancy in DNA extraction

and analysis among samples. Specifically, samples collected on adjacent barbs were considered eligible for analysis if they were at either end of the contiguous sample string and were separated from the other "eligible" sample by at least one barb. Samples within an adjacency string were to be selected if the outer sample was of poor quality. Using these criteria, all eligible samples with guard-hairs were evaluated to species for a given site (cell) and session. Species determination involved visual inspection of guard-hair shafts to exclude obvious black bears, and a single-locus (G10J) test to confirm the species of remaining samples (associated alleles are odd-numbered in grizzly bears and even-numbered in black bears). These results and the colour of all other (underfur) samples not analyzed were recorded in the database. Species was to be initially determined for at least half (to a maximum of 4) of all eligible samples for each site and session. If necessary to meet this criterion, species was genetically determined from other eligible samples (underfur) with priority given to those with lighter-coloured hairs. If the above criteria resulted in a grizzly bear detection for a given site/session, then it was ensured that the species test was conducted for half of all eligible samples, with no maximum, and according to an alternating selection of samples from their sequential order. Genotyping of grizzly bear DNA samples was then conducted to at least seven nuclear microsatellite loci for identification of individual bears (see Selection and Variability of Genetic Markers, below).

Selection and Variability of Genetic Markers – The use of a minimum number of genetic markers is required to discriminate among individual grizzly bears with acceptably low error rates (Paetkau 2004). In selecting makers at the analysis outset, WGI initially looked to the Owikeno and Kingcome studies (S. Himmer, *unpubl. data*) for guidance. In comparison to these datasets, WGI found lower genetic variability in the 59 of our Year-1 samples initially evaluated (see Results). This was especially apparent for one particular marker, which was excluded from consideration for individual genotyping. The genetic variability among our Year-2 samples was considerably lower still. Rather than the five or six markers typically required for other grizzly bear populations, WGI used seven markers for individual genotyping of Year-1 samples[3]. These same markers were used for Year-2 samples, but an additional eight were also used (15 total) due to the very low genetic variability among individuals in this sampling area[4]. In Year-3, individuals were initially identified based on a seven-locus analysis, after which all individuals were profiled to 15 (and eventually to 22) loci. For those individuals genetically similar to the relatively homogenous Year-2 (Stein-Nahatlatch) population, all samples were then re-analyzed to ten loci to ensure that all individuals had in fact been identified. After routine error-checking, it is highly improbable that the number of individuals identified has been overestimated due to inconsistent genotyping of different samples from the same individual (*ibid.*). Preliminary genetic results from the first two years indicated that there is considerable genetic structuring among grizzly bears, conforming to spatially defined groups across our greater study area. As of Years 3 and 4, we therefore obtained 15-locus genotypes for all individuals identified to date.

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[3] G10J (species), amelogenin (sex), G1A, G10B, G10C, G1D, G10L, G10X MU50,
[4] CXX110, CXX20, G10H, G10M, MU59, G10P, G10U

As of study completion, additional markers[5] were used to obtain 22 loci genotypes for evaluation of parent-offspring relationships.

Confirmation of Species Identity – WGI has found the standard species test (using the G10J marker) to be completely reliable for differentiating black from grizzly bears. However, for independent confirmation, they considered allele frequency data for other makers and performed a six-locus assignment test against a sample of known black bears captured during a radiotelemetry study. Results provided an unambiguous confirmation that all samples successfully genotyped to individual were in fact from grizzly bears (*ibid.*).

Microsatellite Analysis and Error Checking for Individual Identification – Each grizzly bear sample was genotyped for individual identity. This involved a step-down process of exclusion and subsequent error-checking to ensure that the identification of unique genotypes was appropriately conservative but that individuals could be unequivocally distinguished from even their close relatives (Taberlet et al. 1996, Mills et al. 2000, Paetkau 2003). Samples that did not produce acceptable results for at least four of the seven loci were excluded from further consideration. An enhanced second stage of analysis was conducted for samples that produced results at four to six loci resulting in a final set that produced results for all seven loci. In the third (error-checking) stage, a computer search was conducted on all successfully genotyped samples to identify pairs with suspiciously similar genotypes (i.e., mismatch at only one or two loci), and these were re-analyzed to identify or rule-out genotyping errors. An automated search for identical genotypes was then conducted and multiple samples from the same individual were identified.

Gender Analysis – For each individual grizzly bear identified, WGI analyzed for gender based on a size polymorphism in the amelogenin gene (Ennis and Gallagher 1994).

RESULTS

Samples

We collected 9,381 hair-snag samples across all six years (2004 – 2010). For various reasons, most samples were excluded by WGI in the process of identifying individual grizzly bears (Table 2-2). Some samples (5%) were not suitable for DNA extraction due to insufficient material. Many samples (47%) were excluded from extraction either because they had the obvious visual appearance of black bears or due to subselection rules. Of those samples from which DNA was extracted, some (4%) produced insufficient data to derive identity during either the species test or the multi-loci analysis. A small proportion of samples (<1%) were mixed from >1 bear (>2 alleles per marker). Many samples (28%) were genetically determined to be black bears. Whereas 16% of samples collected and extracted were of grizzly bears that could be assigned individual identity.

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[5] MU23, 145P07, MSUT2, CPH9, 144A06, MU51

Table 2-2. Hair-snag samples collected across among annual sampling strata in the southern Coast Ranges, British Columbia, 2004 – 2010, and associated DNA analysis classification, success, and outcome.

		Proportion					
Stratum-Year	Total Samples	Unsuitable	Excluded[a]	Insufficient Data	Mixed Samples	Black Bear[b]	Grizzly Bear
SL-TPD-04	2,017	0.09	0.46	0.02	0.00	0.34	0.09
SN-05	1,519	0.02	0.37	0.03	<0.01	0.51	0.08
GP-SSCR-06	1,637	0.03	0.54	0.03	<0.01	0.27	0.12
CSCR-07	1,028	0.06	0.32	0.04	0.01	0.24	0.32
TO-08	2,099	0.06	0.56	0.05	<0.01	0.18	0.16
SGC-10	1,081	0.06	0.45	0.08	0.01	0.07	0.35
Combined	9,381	0.05	0.47	0.04	<0.01	0.28	0.16

[a] Excluded on the basis of being obvious black bear or due to subselection rules.

[b] Genetically determined in addition to obvious samples excluded (see above note).

Detections and Individuals

Across all six years (2004 – 2010), we conducted 2,118 sampling site/session combinations. We obtained samples from 80% of site-sessions, but grizzly and black bear detections varied among sampling strata (Table 2-3). Overall, we detected black bears at 62%, grizzly bears at 30% and both species at 15% of site/session combinations.

Across all six years (2004 – 2010), we detected at least 340 (166 male, 174 female) individual grizzly bears 832 times. Detection results varied among sampling areas, as did the rate of individual re-detection among sampling sessions (Table 2-4). The rate of grizzly bear detection varied considerably across our regional multi-annual study area. We present details of species and individuals detected among cells and sessions, and their spatial distribution, in Appendix 1.

For all individuals identified to date from sampling conducted through this study as well as from other sources, we have characterized genetic variability among individuals at 22 (21 + sex) loci, beyond the seven typically required for individual identity. Using these results, we address questions related to genetic variability (Chapter 5) and establish parentage to build pedigrees (Chapter 6). However, we note here that the populations we have sampled are clearly associated with very low genetic variability, likely a function of their history as small and relatively isolated pockets of animals. The relatively high genetic similarity among individuals presented challenges to their error-free discrimination. Across the six years of field sampling, WGI went through an iterative process of selection, refinement and addition of genetic markers in order to correctly discriminate among all individuals and to prevent the erroneous identification of new individuals from mixed samples. By the end of year-4, all identified individuals had been profiled to 15 loci and potential for the above errors had been thoroughly explored and removed. As a result of this process, WGI has identified a new minimum 7-locus system of genetic markers for optimal discrimination of new individuals within the southern Coast Ranges into the future.

Table 2-3. Hair-snag site/session combinations and proportions of which yielded samples and detections of black and grizzly bears among annual sampling strata in the southern Coast Ranges, British Columbia, 2004 – 2010.

		Proportion of Site-Sessions			
Stratum-Year	Site-Session Combos	Samples	Black Bear	Grizzly Bear	Both Species
SL-TPD-04	360	0.85	0.70	0.25	0.13
SN-05	410	0.75	0.66	0.13	0.07
GP-06	272	0.79	0.76	0.00	0.00
SSCR-06	168	0.79	0.48	0.48	0.15
CSCR-07	320	0.75	0.48	0.45	0.20
TO-08	396	0.86	0.68	0.38	0.23
SGC-10	192	0.81	0.45	0.57	0.28
Combined	2,118	0.80	0.62	0.30	0.15

Table 2-4. Grizzly bears identified, known independent detections, and among-session re-detection rates across annual sampling strata in the southern Coast Ranges, British Columbia, 2004 – 2010.

	Individuals			Independent Detections			Re-Detection Rate Among Sessions
Stratum-Year	M	F	Total	Identity Known	Identity Unknown	Total	
SL-TPD-04	33	25	58	98	13	111	0.19
SN-05	9	12	21	68	7	75	0.44
GP-06	0	0	0	0	0	0	n/a
SSCR-06	23	24	47	107	4	111	0.33
CSCR-07	46	48	94	188	5	193	0.22
TO-08	33	36	69	198	7	205	0.39
SGC-10	22	29	51	132	5	137	0.47
Combined [a]	166	174	340	791	41	832	

[a] Does not equal sum among years due to individuals detected in common among strata.

Chapter 3

ESTIMATING GRIZZLY BEAR POPULATION ABUNDANCE

INTRODUCTION

As previously outlined (Chapter 1), this study was intended to address primary objectives related to the estimation of population distribution and connectivity, both current and historic. However, deriving estimates of population abundance for relevant management units was also a key goal. Thus, our field sampling approach was designed to optimally address all objectives within a realistic budget. In this chapter, we discuss analytical issues that derive from our multi-objective regional sampling design, and we consider options to obtain unbiased grizzly bear population estimates for defined spatial strata across the southern Coast Ranges.

DESIGN CONSIDERATIONS

Of primary concern in our design was achieving an appropriate representation of grizzly bear distribution across a regional study area of ~50,000 km^2, including associated variation in ecological and human conditions. Where we expected relatively high grizzly bear densities we sampled with high spatial intensity. Such intensive sampling (one site per 5 x 5 km grid-cell) was specifically conducted within the Toba-Bute GBPU during years 5-6 (2008 & 2010). Where low densities were expected and landscape occupancy was uncertain, we sampled with lower spatial intensity (grid-cell size = 10 x 10 km) but with sampling sites selected to maximize the expected potential for grizzly bear detection. This lower-intensity sampling involved much of the rest of the regional study area during years 1 - 4 (2004 - 2007). Here, our primary objectives were to model grizzly bear occurrence, distribution, and population connectivity over an extensive area, requiring representative sampling of roughly 10,000 km^2 each year within realistic funding targets. Across all years, our sampling design involved re-visiting hair-snag stations established within each cell, resulting in 4 - 5 sampling sessions of ~10-12 days each (Chapter 2).

While population estimation was not a primary goal based on data collected during years 1 - 4, understanding absolute grizzly bear abundance within defined areas is relevant to conservation. Thus, we were interested in deriving unbiased estimates from our data recognizing potential limitations of our sampling design. For population estimation from detection data of individuals, a K-samples capture-recapture design is typically employed (Williams et al. 2002). A limitation of our design for population estimation may pertain to the relatively large grid cells employed in sampling distribution (years 1 - 4) and the fact that stations were not rotated within cells among sampling sessions. Larger cells facilitate more extensive and geographically representative sampling (with given funding) resulting in a greater area of inference, and such an approach can be particularly appropriate in surveys near range peripheries where landscape occupancy is uncertain. However, notwithstanding issues of site-selection and placement, fewer and more widely spread sampling sites across a sampling area can be expected to reduce detection probabilities and thus the precision of estimates. Detection probabilities that are low or variable cannot be said to bias estimates. For bears, detection rates are expected to vary among age/sex cohorts reflecting differing life-history strategies and related movement rates and patterns. Such unequal detection probabilities among animals (termed capture heterogeneity) are common for this and other reasons such as waning interest in sites after initial detection, weather and other factors that influence station attractiveness over time (Boulanger et al. 2002). Commonly applied estimator models for closed populations account for and are robust to such heterogeneity variation (Otis et al. 1978).

Beyond lower detection rates and increased heterogeneity, the consideration of greatest importance in moving to a larger cell size is the potential for violating the underlying assumption in closed-population capture-recapture modeling that all animals in the sampled population have >0 probability of detection. As the spacing among stations widen beyond a certain point, there is increasing potential that some bears will have no opportunity to encounter or be attracted by a hair-snag sampling station. If a portion of the population is hence undetectable, derived population estimates are likely to be biased low. The point at which bias is introduced by station spacing is unclear and undoubtedly depends on many factors. Larger cell sizes may be accommodated where grizzly bears move extensively during the sampling period. Since sites are most likely to be placed within landscapes of highest habitat suitability, large cells may also be feasible where there is great variability in landscape conditions, as is the case across much of our southern Coast Ranges regional study area. Here, a design employing 10 x 10 km cells is roughly equivalent to a design of 7 x 7 or 8 x 8 km cells since many such cells would be excluded due to rock, ice or other inherently unsuitable habitat (C. Apps, unpubl. data). The potential for station encounter may also be at least subjectively evaluated by considering the movements of GPS-collared grizzly bears during the sampling period where such data exist. Among such study animals primarily occurring within the Squamish-Lillooet GBPU, space-use patterns of all adult females and males indicate that multiple DNA hair-snag stations could have easily been encountered given station distribution across the 10 x 10 km grid (C. Apps, unpubl. data). That said, these movement data are limited with respect to females with cubs of the year, the cohort likely to move least. Moreover, it is possible that movements by grizzly bears elsewhere across the southern Coast Ranges are more concentrated than those of the Squamish-Lillooet GBPU. While the assumption of >0 probability of detection is not required for models that assume "open" populations, such models are either inflexible to heterogeneity in capture probabilities (Jolly-Seber) or do not estimate abundance (e.g., Pradel).

ALTERNATIVE APPROACHES

Initially, we applied traditional closed-population capture-recapture analyses to estimate grizzly bear populations across the southern Coast Ranges. We see several ways to explore the potential for aforementioned bias in estimates derived through sampling based on 10 x 10 km grid cells. First, we could compare spatially-apportioned estimates (Chapter 4) derived from 5 x 5 km sampling to those from 10 x 10 km sampling within the Toba drainage where these different sampling grids overlapped (primarily the Toba drainage). Second, we could re-derive 10 x 10 km grid estimates, deleting re-detections of bears that were constrained to only a single station. If some bears did in fact have no potential for detection then these re-detections of bears at only a single station will artificially inflate detection probabilities leading to estimates that are biased low as described. Aside from evaluating bias that would result from non-spatial capture-recapture analyses, we have explored three alternative approaches for population estimation as described below.

CAPWIRE Estimator - Traditional population estimation based on capture-recapture data employs models designed for datasets where an individual may be captured only once per session. The type of data obtained through hair-snag DNA sampling as employed in our study obviously allows for individuals to be detected ("captured") multiple times per session - that is, at different sampling sites. The closed population models available through programs MARK and CAPTURE (e.g., M_h Chao & M_h jacknife) do not make use of this additional information. As a result, we believe that such estimators are more susceptible to low biased estimates as the spacing of sampling sites increase, and detection heterogeneity increase with some animals becoming detectable only at single sites. However, a relatively new method for estimating population size from such DNA-based detection data is available that takes into account recaptures at different sites within a given session (Miller et al. 2005). This method, employed through program CAPWIRE, apparently is particularly well suited to small populations ($n \leq 100$) with substantial detection heterogeneity as is particularly true within our study. Moreover, this analytical approach may prove especially valuable in future surveys whereby higher spatial intensity with fewer (possibly even single) sessions may be more economical and thus preferred over larger sampling grids but more sessions.

Spatially-Based Population Estimation - Most recently, spatially explicit capture-recapture (SECR) modeling (Efford & Fewster 2012) has been proposed as a preferred alternative to conventional capture-recapture analyses (Williams et al. 2002) in studies such as ours where sampling stations are set up in a specific spatial array and there is a spatial element to animal detections that is related to home range use. This approach takes into account spatial as well as temporal detection histories but considers the geographic orientation of those detections to estimate home range centres. The primary assumptions are that animals are distributed independently and move within home ranges. Capture probability is modeled as a function of the distribution of animals and their distance to a sampling (detection) site (trap). The method fits a spatial model of detection, and derives population density unbiased by edge effects and incomplete detection. Population size is derived secondarily. Simulations have indicated that SECR estimates are robust in scenarios such as ours where stations are not evenly distributed, animals are not necessarily all detectable, and landscape occupancy is patchy. However, the spatial trend models on which this method relies can produce misleading results in extrapolation beyond a sampling area. Hence, SECR is recommended for sampling that is spatially representative of the area of interest with one continuous grid or widely dispersed clusters of sampling sites, as is consistent with our sampling design.

Interpolation of Population Density - In this alternative approach, grizzly bear population density could be predicted on the basis of its relationship with several measures of per-cell detections of individuals among DNA-based capture-recapture grizzly bear population surveys across western North America to date. Variations of this approach have been previously employed (Romain-Bondi et al. 2004). Specifically, linear modeling could be applied to characterize the relationship between grizzly bear detection rates and population (size/density) given the results of DNA-based grizzly bear mark-recapture surveys that have been conducted elsewhere. Potential predictors include (1) the number of individuals detected per cell during session 1, (2) the average number of individuals detected across sessions, (3) the total number of individuals detected across four sessions, and (4) the number of individuals detected per 100 days, measuring catch per unit effort (CPUE). To evaluate these relationships, least-squares linear regression could be applied with sampled predictors from each study weighted by the inverse of standard error. The strength and validity of regressions could be considered in determining which equation to apply to infer grizzly bear population density across the southern Coast Ranges.

In applying the above regression model to predict South Coast grizzly bear population density beyond sampling areas where unbiased estimates are possible (i.e., Toba-Bute, sampled using 5 x 5 km grid), there are two options. In option 1, the average of the selected predictor could be calculated among sampling sites across each annual sampling area and used to infer a single estimate for that area. Each area-specific estimate could then be applied to infer spatial variation in density on the basis of spatial modeling of grizzly bear occurrence and distribution (occupancy; Chapter 4). This option assumes that hair-snag sampling stations are perfectly representative of landscape conditions across the sampling area. Option 2 essentially involves the reverse. Occupancy probabilities derived through landscape modeling (Chapter 4) themselves predict the relevant measure from which density is inferred (e.g., CPUE), which is in turn transformed to density. This option is preferable if spatial modeling of landscape occupancy does not require significant extrapolation beyond the range of conditions of which hair-snag sampling is representative. Moreover, detection data can be pooled among annual sampling areas. For any given area (e.g., GBPU or WMU), density and abundance can then be calculated from the spatial model and confidence limits applied.

Comparative Assessment - Our southern Coast Ranges study may provide a worthwhile dataset for comparative application of the above analytical approaches. However, for the present iteration of this chapter, we have limited our analyses to two approaches in deriving population estimates specific to defined spatial units. We compare traditional non-spatial capture-recapture analyses to the newer approach employing spatially-explicit capture-recapture modeling, the latter being the most valid approach for our dataset in our opinion. These results are subsequently applied for modeling the spatial variation of population abundance/density (Chapter 4).

METHODS

Non-Spatial Capture-recapture Analyses

Stratification & Model Selection – Our primary approach to population estimation involved the application of a K-sample capture-recapture design (Williams et al. 2002) with individuals identified through genetic profiling (Chapter 2). Each annual sampling area was defined to maximize geographic and demographic closure. However, both 2004 and 2006 sampling straddled established GBPU boundaries that we expected to correspond with spatial (though possibly semi-permeable) population breaks. With this in mind, our analyses were primarily stratified as follows (see Table 1-1, pg 4): Squamish-Lillooet GBPU (2004), Toba and Powell-Daniels drainages (2004), Stein-Nahatlatch GBPU (2005), Garibaldi-Pitt GBPU (2006), southern portion of South Chilcotin Ranges GBPU (2006), central portion of South Chilcotin Ranges (2007), Toba and Orford drainages (2008), and Southgate to Chilko Lake (2010). For several of these strata, we secondarily considered geographically distinct sub-areas within. To estimate population size among these strata, we employed capture-recapture models available within program CAPTURE (Rextad and Burnham 1991). The models differed in their consideration for the effects of differential rates of detection success among sessions (i.e., denoted by subscript t), potential behavioural conditioning (subscript b) and the influence of heterogeneity in detection-probability (subscript h). We based model selection upon qualitative assessment of our data coupled with knowledge of bear behaviour, as well as earlier simulations (Otis et al. 1978, Mowat and Strobeck 2000, Boulanger et al. 2007).

Accounting for Closure Bias – Our initial derived population estimates were naïve to potential bias caused by incomplete geographic closure of sampling areas to grizzly bear movement (*sensu* Boulanger and McLellan 2001). To account for resulting population overestimation, we first defined borders along each sampling area that we expected to be permeable to movement by resident adults of each sex. In addition to subjective knowledge of geographic features potentially hindering grizzly bear movements, we made use of evidence from (1) differences in detection rates and naïve estimates between sex, (2) bears detected in common between adjacent sampling areas, (3) movements of radiocollared bears, and (4) genetic structuring of populations across the southern

Coast Ranges (Chapter 5). Assuming a home range size (during our ~2 month sampling period) of 400 km^2 for males and 200 km^2 for females, we then extended a home range radius beyond the permeable border(s) and defined an additional area to be included within the sex-specific "superpopulation". We then determined the area of the sampling grid and, for each sex, the additional area of the superpopulation we expected to have actually sampled. At this point we applied our regional model of grizzly bear detection probability (Chapter 4) as a basis for estimating the proportion of time bears that do range beyond the sampling area are likely to spend there. To account for closure violation bias, we calculated an adjustment factor ($\mathcal{H}$) specific to each sampling area as:

$$\mathcal{H} = \frac{\Sigma_S \left\{ {}^{p(A_O - A_G)}\!\big/_{p(A_G)} \right\}}{2} \qquad \text{(3-1)}$$

where S is sex cohort, p is detection probability, A is area, O is the superpopulation, and G is the sampling grid. That is, we determined the additional area beyond the grid area that is attributed to the superpopulation, we multiplied this figure by that area's mean detection probability, and we divided this by the area of the grid also multiplied by its mean detection probability. We made the calculation independently for each sex, then summed and divided by 2 under the assumption of an equal sex ratio.

Spatially Explicit Capture-recapture Analyses

We carried out SECR analyses using DENSITY 5.0 software (Efford 2012). We estimated closed population density by fitting spatial detection models independently for each sampling area using full maximum likelihood (Borchers & Efford 2008). We expected that our sampling areas targeted subsets of animals from larger "superpopulations" and thus assumed that the distribution of home range centres follows a Poisson distribution in 2-D space (Efford & Fewster 2012). In SECR, capture probability is treated as a decreasing function of the distance between a sampling site and the assumed centre of each animal's home range. We assumed this relationship to follow a halfnormal function (Efford 2012), expressed as follows:

$$g(d) = g_0.\exp(-d^2/(2\sigma^2))$$

where d is the distance between an animal's home range centre and a sampling site, g_0 is an intercept, and σ is a spatial scale parameter. We used an automatic algorithm to determine the initial values for D, g_0 and σ (Efford 2012). In light of results from non-spatial model comparisons and our knowledge of grizzly bear behaviour, we accounted for the influence of individual heterogeneity on both g_0 and σ using a 2-class mixture model (Efford 2012). We applied the model (null or heterogeneity) best supported by the data as described above. Since male and female home range sizes can differ substantially, we stratified SECR analyses by sex to estimate male/female ratios.

In modeling population density and inferring abundance, we defined each annual sampling grid as the "region of integration" rather than using a buffer around sampling sites. We also constrained the spatial distribution of estimated home range centres by masking out habitat conditions that preclude resident grizzly bears and within which we assume population density to be 0. These conditions included waterbodies, icefields, and slopes exceeding 150%.

RESULTS

Non-spatial Capture-Recapture Estimates – A comparison among sampling areas/years, and sex-cohorts within, indicated minor differences in support among competing estimators (Table 3-1). Given our sampling design, we expected that heterogeneity would be a relevant factor, and this was apparent among most analysis strata, with the exception of males during 2006 (SSCR). There was support for a behavioural response and/or a combined behaviour/heterogeneity effect for females among all sampling years. Variation in capture success among sessions appeared to be of little consequence during any year as is also reflected by detection statistics among sessions (Figure 3-1). We selected Mh-Jacknife as the most appropriate population estimator among all strata that pooled males and females (Table 3-2).

Closure Bias (2004 - 2007) - We expected that the influence of closure bias would differ among annual sampling areas. However, with the exception of the population sampled within CSCR-07 which we knew to be particularly open to the north, we expected each sampling area to envelope grizzly bear populations that were largely closed and to include some if not many unoccupied landscapes. For SL-TPD-04, we expected that the sampled population was partially open in the extreme west-northwest corner leading into the Orford drainage of Bute Inlet, and from the upper Elaho to the upper Lillooet valleys. For SN-05, we knew the sampled population to be completely isolated demographically from any adjacent population as suggested by its genetic isolation (Chapter 5), and as supported by the distribution of grizzly bear detections and lack of individuals common to adjacent sampling areas, as well as the movements of radiocollared individuals. For GP-06, no individual grizzly bears were detected. For SSCR-06, a potential connection exists from the upper Lillooet to the Elaho Valley (as noted for SL-TPD-04) but no movements are expected to occur southward or eastward of this sampling area. There is, however, expected to be some permeability between the SSCR and the CSCR via the upper Bridge drainage that separates the western portion of both areas. This connection is evidenced by the fact that six males and two females were detected in common in this portion of the two areas, and two radicollared males are known to have made a forays northward from SSCR to CSCR. Chilko Lake represents what we expect to be an impermeable western border to

CSCR, though westward movements off the grid undoubtedly occur south of Chilko. While the eastern portion of CSCR-07 was largely unoccupied and the Fraser River represents an obvious geographic boundary, we expect that any resident bears could still move eastward. The northern boundary of the CSCR-07 sampling area did not conform to any geographic boundary and we expect that resident grizzly bears could freely range north of the grid. We considered the above in our calculation of population adjustment factors to account for closure bias (Table 3-3; Figure 3-2).

Closure Bias (2008 & 2010) - Both Toba/Orford 2008 and Southgate/Chilko 2010 sampling areas were delineated to maximize geographic closure of the sampled grizzly bear population. Given the topography and physiographic features (including rock, ice and ocean) associated with the sampling boundaries, we expect that closure was near to complete in both areas, especially for females. However, there is evidence that normal seasonal movements (aside from fall movements to salmon) of some bears do range beyond the sampling areas, particularly for males. This evidence, described below for each sampling area, was considered in our calculation of population adjustment factors to account for closure bias (Table 3-3).

There is little known about the movements of grizzly bears within the Toba/Orford 2008 sampling area, but several males were detected during previous years in landscapes beyond the Toba 2008 area. In particular, six males had been previously detected in the Clendenning and Sims drainages to the southeast, and two had been previously detected in the South Chilcotin Ranges, north of Carpenter Lake. We also expected some limited permeability for males between the Orford drainage and the Southgate to the northwest of the sampling area.

We consider the Southgate drainage to be largely closed to most non-breeding seasonal movements by resident grizzly bears. The exceptions are two passes that lead to landscapes southwest of Chilko Lake, a minor high-elevation pass that leads to the Orford drainage, and the option for bears to move along or near tidal flats that connect to the lower Homathko Valley. We expected the two passes that lead to Chilko Lake to facilitate a some degree of movement which is why the sampling area extended over these passes and was partly bounded by Chilko Lake, a certain barrier to movement. In fact, of the 13 (6M, 7F) individuals on the Chilko side, four (2M, 2F) were also detected on the Southgate side (more extensively for the males). We believe there is considerably less potential for grizzly bear movement between the Southgate and the Orford drainage to the south,. The one pass is notably lower in suitability than those that lead to Chilko, and no detected individuals were common to both the Southgate (2010) and Orford (2008) drainages. Regarding movement between the lower Southgate and the lower Homathko, our data suggest this is quite likely for males. Site #30 was located at the head of Bute Inlet and in fact fell slightly outside the sampling grid. This site was located on the Homathko side of the most restrictive point of the topographic pinch. Of the six (4M, 2F) individuals detected at this site, neither of the two females were detected elsewhere in the sampling area, whereas three of the four males were.

For the purpose of this study, a population estimate was required for the Southgate drainage proper, which defines the northern end of the Toba-Bute GBPU. One option was to derive an estimate for the entire sampling area, including landscapes sampled southwest of Chilko Lake, and then use the spatial distribution model (Chapter 4) to estimate that portion of the population specific to the Southgate drainage. However, in light of the above evidence for closure, we felt it was more appropriate to rely on the estimate derived directly from sampling conducted only within the Southgate (Table 3-3). That is, we excluded the five Chilko sampling sites, and we also excluded site 30 at the head of Bute Inlet since this site did fall slightly outside the Southgate drainage and there is no evidence that the two females detected here move into the Southgate.

Table 3-1. Criteria for selecting among models for estimating grizzly bear populations among distinct sampling areas within the southern Coast Ranges of British Columbia, 2004 – 2010. Selection criteria are based on goodness of fit tests (Otis et al. 1978) among estimators that, in addition to the null model (o), account for the influence of differential capture success among sessions (t), heterogeneity in detection probability among individuals (h), behavioural conditioning to sampling efforts (b), and combinations thereof. Larger values indicate higher support.

		Model							
Stratum [a]	Cohort	M_o	M_h	M_b	M_{bh}	M_t	M_{th}	M_{tb}	M_{tbh}
SL-TPD-04	M&F	0.95	1.00	0.41	0.52	0.00	0.50	0.38	0.55
SL-TPD-04	M	1.00	0.88	0.47	0.76	0.00	0.49	0.38	0.80
SL-TPD-04	F	0.74	0.60	0.92	0.95	0.00	0.75	0.80	1.00
TPD-04	M&F	1.00	0.82	0.32	0.60	0.00	0.42	0.29	0.67
SL-04	M&F	1.00	0.91	0.36	0.61	0.00	0.37	0.35	0.69
SN-05	M&F	0.90	1.00	0.78	0.98	0.00	0.42	0.60	0.84
SN-05	M	1.00	0.83	0.35	0.64	0.00	0.38	0.32	0.71
SN-05	F	0.88	0.78	0.59	0.91	0.00	0.65	0.47	1.00
GP-06 [b]	--	--	--	--	--	--	--	--	--
SSCR-06	M&F	0.86	1.00	0.50	0.58	0.00	0.39	0.42	0.60
SSCR-06	M	0.51	0.28	0.96	1.00	0.00	0.25	0.56	0.76
SSCR-06	F	1.00	0.87	0.41	0.73	0.00	0.46	0.38	0.81
CSCR-07	M&F	1.00	0.97	0.45	0.56	0.00	0.30	0.44	0.63
CSCR-07	M	1.00	0.84	0.32	0.61	0.00	0.41	0.31	0.69
CSCR-07	F	1.00	0.73	0.26	0.68	0.00	0.41	0.31	0.94
TO-08	M&F	0.83	1.00	0.27	0.43	0.00	0.39	0.30	0.51
TO-08	M	0.90	1.00	0.29	0.49	0.00	0.40	0.32	0.60
TO-08	F	0.92	1.00	0.47	0.60	0.00	0.54	0.41	0.64
SGC-10	M&F	0.75	1.00	0.32	0.47	0.00	0.40	0.31	0.53
SGC-10	M	0.98	1.00	0.33	0.52	0.00	0.43	0.33	0.64
SGC-10	F	1.00	0.94	0.41	0.67	0.00	0.43	0.37	0.74
SG-10	M&F	1.00	0.92	0.41	0.62	0.00	0.47	0.37	0.67
SG-10	M	0.47	0.58	0.24	0.47	0.00	1.00	0.21	0.50
SG-10	F	1.00	0.81	0.26	0.56	0.00	0.38	0.28	0.65

[a] See Table 1-1, pg 4

[b] No detections of either cohort.

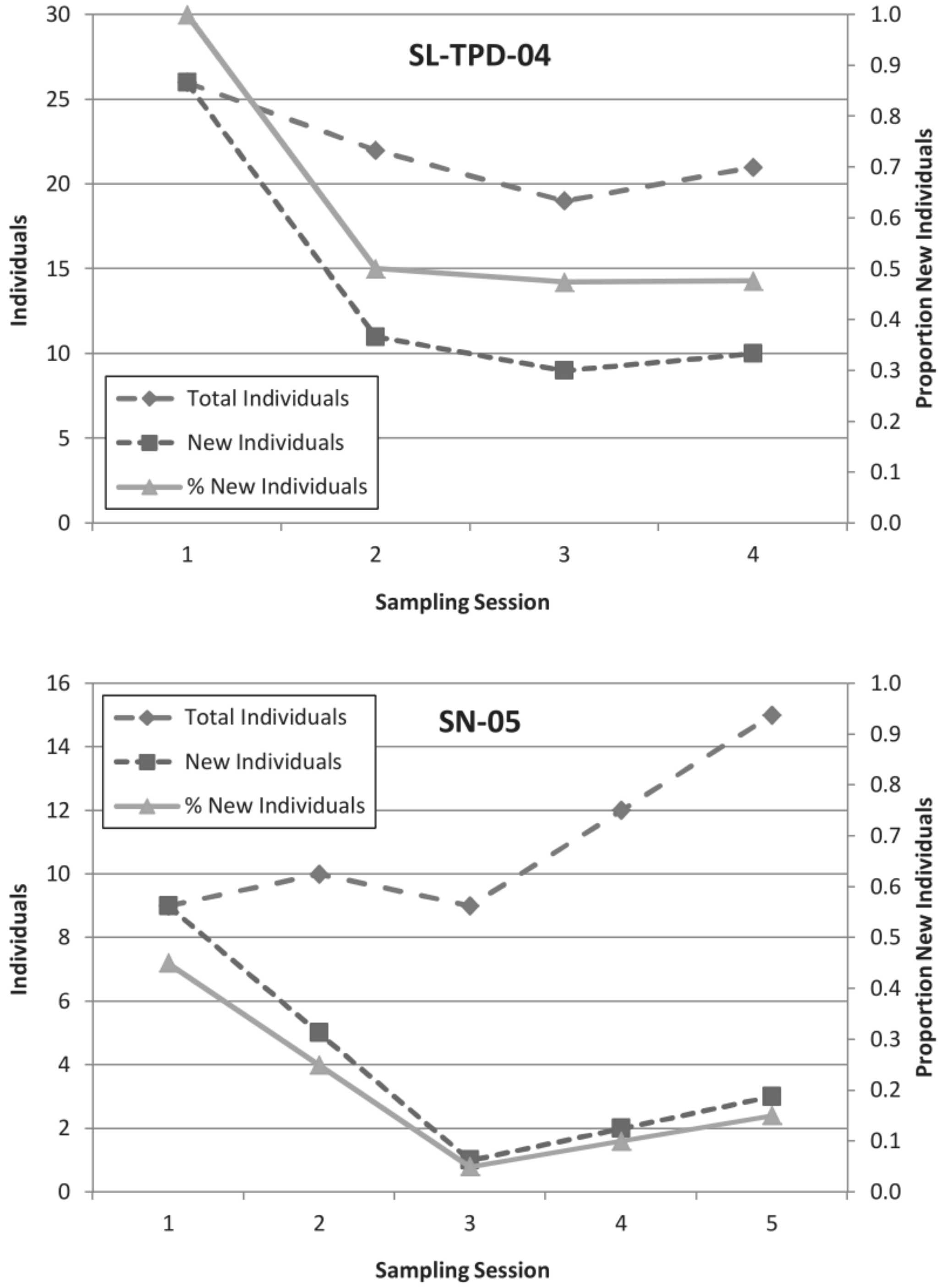
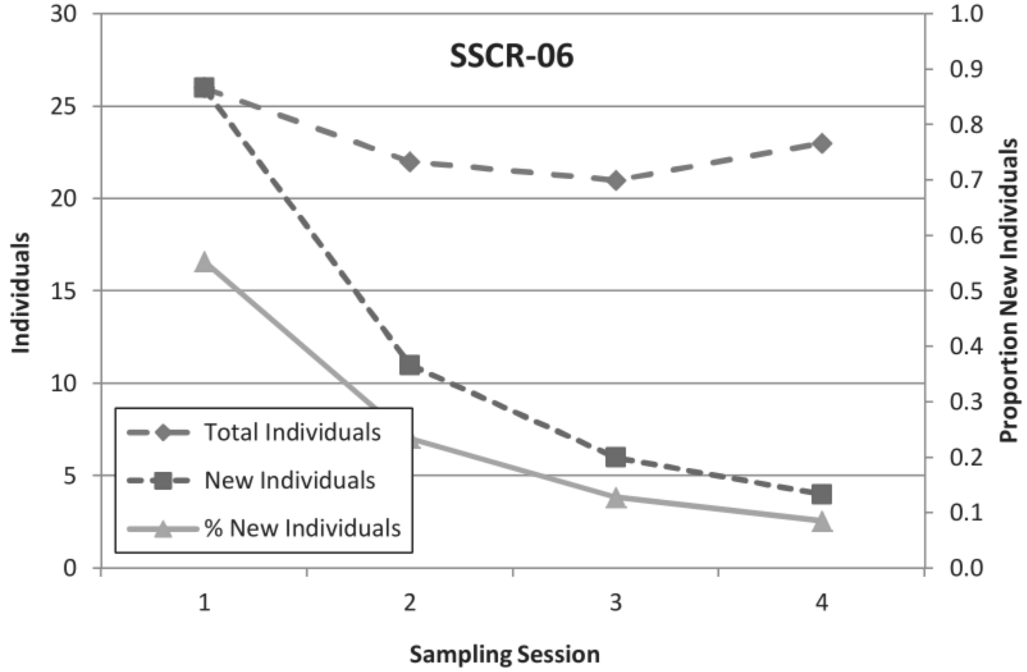


Figure 3-1. Total individuals, new individuals, and proportional representation of new individuals among sampling sessions, for annual sampling areas within the southern Coast Ranges of British Columbia, 2004 – 2010. Annual sampling areas are referred to as Squamish-Lillooet/Toba-Powell-Daniels 2004 (SL-TPD-04) and Stein-Nahatlatch 2005 (SN-05). (*Figure continues on next page*)



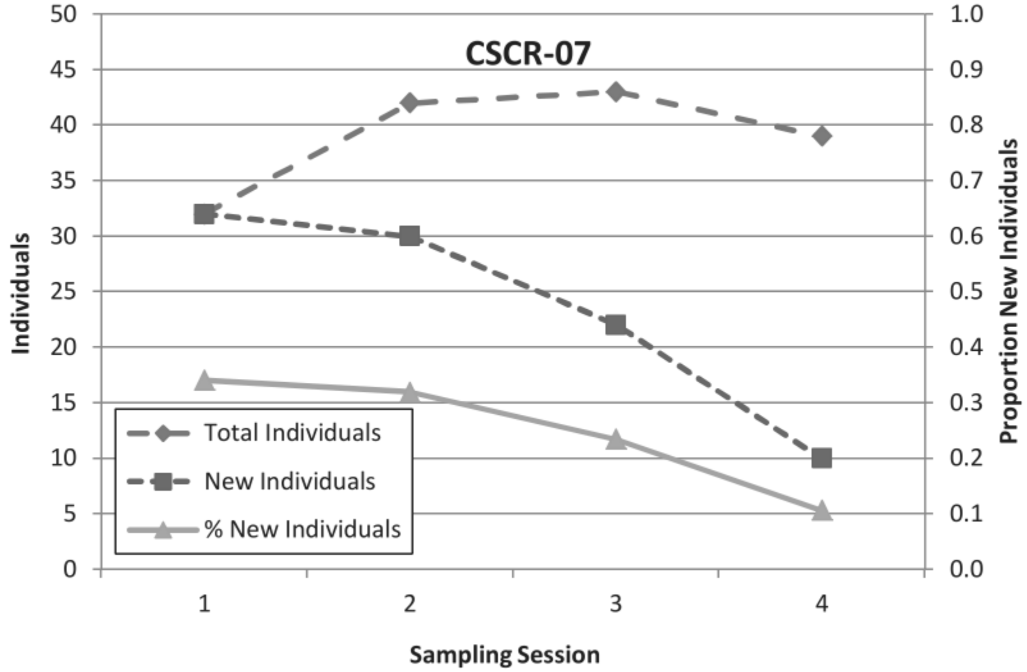
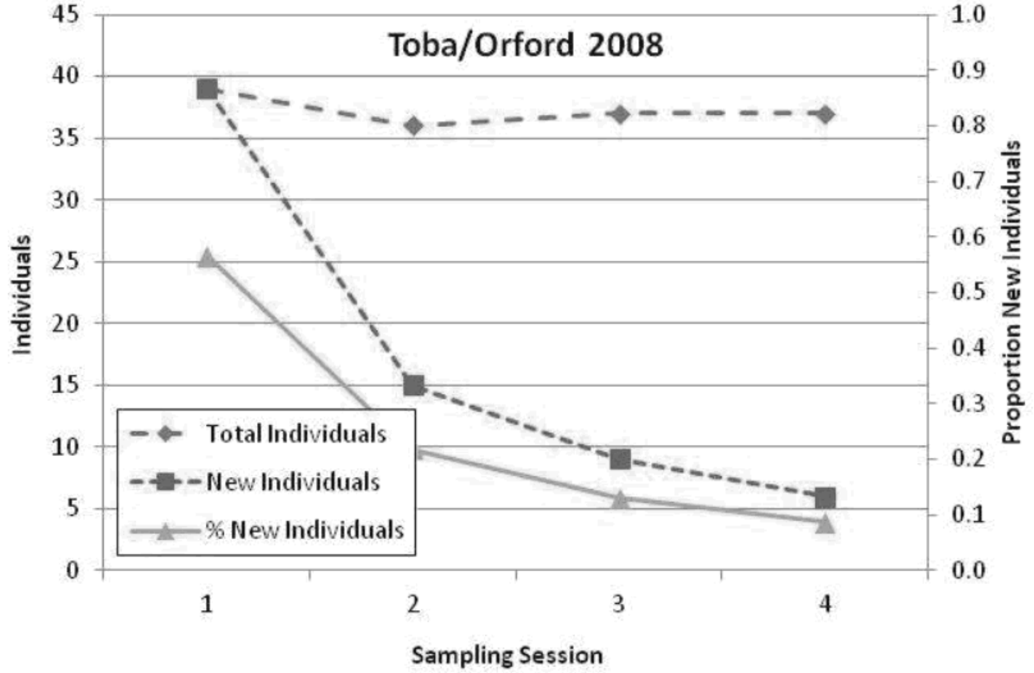


Figure 3-1. ***Continued from previous page*****. Annual sampling areas are referred to as southern South Chilcotin Ranges (SSCR-06) and central South Chilcotin Ranges (CSCR-07). The Garibaldi-Pitt (GP-06) sampling area is not included due to lack of grizzly bear detections. (*****Figure continues on next page*****)**



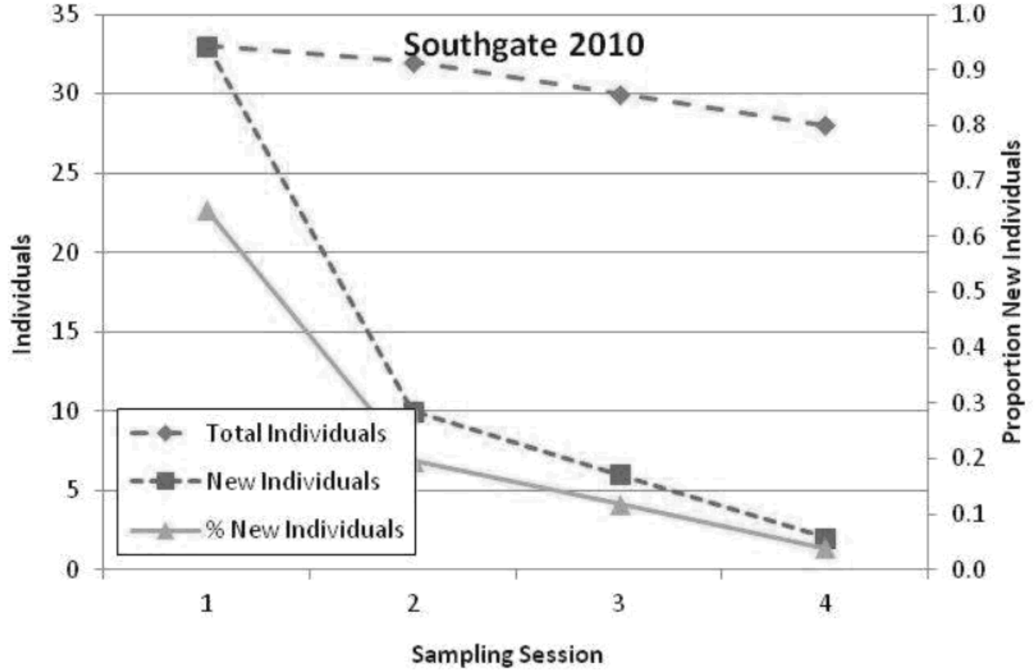


Figure 3-1. ***Continued from previous page*****. Annual sampling areas are referred to as the Toba/Orford 2008 (TO-08) and the Southgate/Chilko 2010 (SGC-10).**

Table 3-2. Naïve estimates of grizzly bear populations among distinct sampling areas (see Table 1-1) within the southern Coast Ranges of British Columbia, 2004 – 2010. The model from which each estimate is derived is that with the greatest empirical support (Table 3-1).

Stratum [a]	Cohort	$\hat{p}$	$\widehat{N}$	SE	95% CI	CV
SL-TPD-04	M&F	0.33	95	11.0	79 - 122	0.116
SL-TPD-04	M	0.36	37	3.7	33 - 49	0.100
SL-TPD-04	F	0.19	29	8.1	26 - 73	0.279
TPD-04	M&F	0.24	56	8.7	45 - 79	0.155
SL-04	M&F	0.31	39	5.8	32 - 56	0.149
SN-05	M&F	0.48	23	3.1	21 - 36	0.135
SN-05	M	0.34	11	1.8	10 - 18	0.164
SN-05	F	0.55	12	2.4	12 - 25	0.200
GP-06	--	n/a	0	0.0	0 - 0	n/a
SSCR-06	M&F	0.40	58	4.9	52 - 72	0.084
SSCR-06	M	0.42	23	0.4	23 - 23	0.017
SSCR-06	F	0.41	29	3.5	26 - 41	0.121
CSCR-07	M&F	0.29	135	11.5	118 - 164	0.085
CSCR-07	M	0.31	62	6.5	54 - 80	0.105
CSCR-07	F	0.29	68	7.6	58 - 88	0.112
TO-08	M&F	0.42	89	7.7	79 - 110	0.087
TO-08	M	0.35	49	6.8	41 - 68	0.139
TO-08	F	0.49	41	3.7	38 - 54	0.091
SGC-10	M&F	0.52	59	4.3	54 - 72	0.072
SGC-10	M	0.60	23	2.6	23 - 37	0.114
SGC-10	F	0.52	33	3.3	30 - 45	0.101
SG-10	M&F	0.59	39	2.9	38 - 52	0.074
SG-10	M	0.61	16	1.1	16 - 16	0.070
SG-10	F	0.60	22	2.3	22 - 37	0.107

Table 3-3. Adjusted (accounting for population closure bias) estimates of grizzly bear population abundance and density among annual sampling areas within the southern Coast Ranges of British Columbia, 2004 – 2010.

Stratum[a]	Adjust Factor	$\widehat{N}$	SE	95% CI	Density /1000 km^2	SE	95% CI
SL-TPD-04	0.049	90	10.5	75 - 116	9.4	1.1	7.8 - 12.1
SN-05	0.000	23	3.1	21 - 36	2.8	0.4	2.6 - 4.4
GP-06	0.000	0	0.0	0 - 0	0.0	0.0	0.0 - 0.0
SSCR-06	0.083	53	4.5	48 - 66	12.7	1.1	11.4 - 15.7
CSCR-07	0.306	94	7.9	82 - 114	11.7	1.0	10.2 - 14.2
TO-08	0.169	74	6.4	66 - 91	20.1	1.7	17.9 - 24.9
SG-10	0.141	36	2.6	35 - 48	14.5	1.1	14.2 - 19.4

[a] SL=Squamish-Lillooet; TPD=Toba/Powell-Daniels; SN=Stein-Nahatlatch; GP=Garibaldi-Pitt; SSCR=southern South Chilcotin Ranges; CSCR=central South Chilcotin Ranges; TO=Toba/Orford; SGC=Southgate/Chilko; SG=Southgate drainage only.

<u>Spatially-Explicit Capture-Recapture Estimates</u> – The population estimates derived from SECR analyses differed somewhat from those derived from traditional capture-recapture analyses above (Table 3-4). However, there was little consistency in the nature of these differences. Among other factors, differences could relate to incomplete detectability and our ability to account for closure bias, issues to which SECR is apparently robust (Efford & Fewster 2012). The SECR estimate derived for the Squamish-Lillooet and Toba/Powell-Daniels in 2004 (SL-TPD-04) is 19% higher than previously estimated using non-spatial modeling. For the Stein-Nahatlatch 2005 (SN-05), the new estimate is lower by just 1 bear, or 4%. For the southern South Chilcotin Ranges 2006 (SSCR-06), the new estimate is higher by 2 bears, or 4%. Whereas, for the central South Chilcotin Ranges 2007 (CSCR-07), the new estimate is higher by 24%. For the Toba and Orford drainages in 2008 (TO-08), the new SECR estimate is 4% higher. Finally, for the Southgate/Chilko (SGC-10) sampling grid, the new estimate is 3% higher than the previously unadjusted estimate for the entire grid, while the SECR estimate is 10% lower for the Southgate drainage proper (SG-10).

Table 3-4. Estimates of grizzly bear population size and density, derived using spatially explicit capture-recapture analyses among sampling strata across the southern Coast Ranges of British Columbia, 2004 - 2010.

					Within Grid		Useable Habitat	
Stratum[a]	$\widehat{N}$	SE	95% CI	M/F	Area	Density[b]	Area	Density[a]
SL-TPD-04	107	35	58 - 200	0.84	9,600	11.2	8,141	13.2
SL-04	45	19	20 - 99	0.76	5,100	8.8	3,766	11.9
SN-05	22	2	20 - 25	0.80	8,200	2.6	7,864	2.8
GP-06	0	-	- - -	-	-	0	-	0
SSCR-06	55	8	41 - 74	0.77	4,100	13.4	3,637	15.1
CSCR-07	117	13	95 - 145	0.76	8,000	14.7	7,478	15.7
TO-08	79	10	62 - 100	0.93	3,675	21.4	2,898	27.1
SGC-10	58	9	43 - 77	0.71	3,075	18.7	1,951	29.5
SG-10	34	6	24 - 49	0.68	2,450	14.0	1,476	23.2

[a] SL=Squamish-Lillooet; TPD=Toba/Powell-Daniels; SN=Stein-Nahatlatch; GP=Garibaldi-Pitt; SSCR=southern South Chilcotin Ranges; CSCR=central South Chilcotin Ranges; TO=Toba/Orford; SGC=Southgate/Chilko; SG=Southgate drainage only.

[b] Bears per 1,000 km^2.

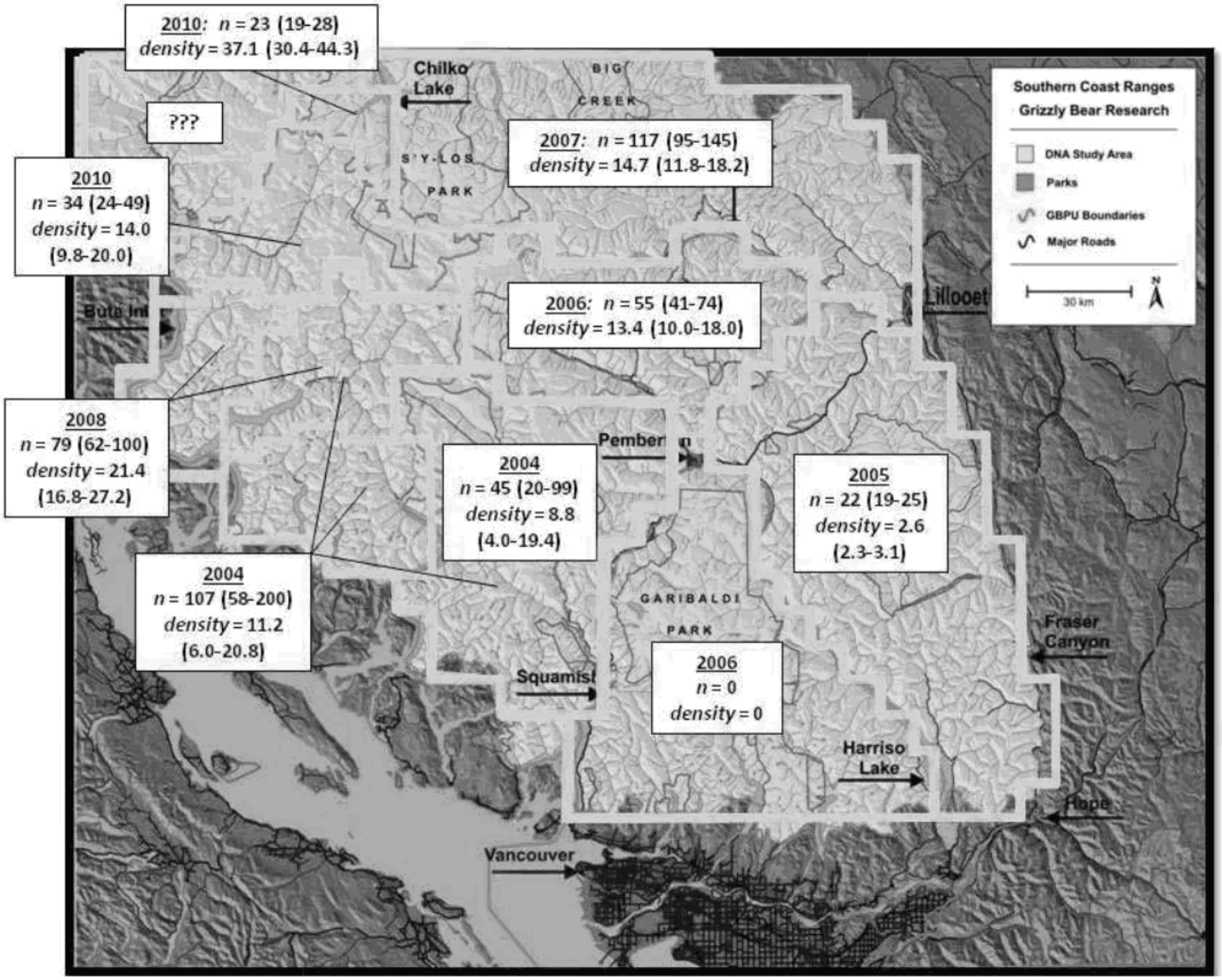


Figure 3-2. Grizzly bear population and density (bears/1000 km^2) estimates for annual sampling strata across the southern Coast Ranges of British Columbia, 2004 – 2010, based on spatially-explicit capture-recapture analyses. Confidence intervales (95%) are shown in parentheses. Sampling of the lower portion of the Klinaklini-Homathko GBPU has not been completed at the time of this report.

Chapter 4

MODELING LANDSCAPE POTENTIAL & REGIONAL DISTRIBUTION TO INFER GRIZZLY BEAR POPULATION CORES & CONNECTIVITY

INTRODUCTION

The spatial structure of a population has direct bearing on its dynamics, resiliency, and thus viability (Kareiva and Wennergren 1995, Ritchie 1997, Wiegand et al. 2002). Adaptive conservation planning for any species requires an understanding of population abundance, distribution and connectivity, along with the factors that influence this pattern and associated spatial and temporal trends. Such knowledge can facilitate resource planning and mitigation to maintain or enhance core habitat areas that anchor regional populations as well as the peripheral and linkage landscapes that allow demographic and genetic flow (Wiens 1996). The result is a regional metapopulation that is resilient in the face of localized perturbation, natural or human-caused. Further, spatially-explicit predictions of population abundance can assist in the optimal management of populations in association with other resource values to achieve conservation objectives (Turner et al. 1995, McCullough 1996). Hence, the primary goal of this study has been to estimate current and historic grizzly bear population distribution and connectivity across the southern Coast Ranges, and to characterize influential and related factors.

Despite the Threatened status assigned to most grizzly bear population units of southwestern British Columbia, there has been, prior to this study, limited understanding of landscape occupancy and spatial variation in abundance and distribution. Without this understanding effective planning for the recovery and conservation of Viable populations is virtually impossible, particularly in light of human population and resource development demands within the region. In this chapter, we attempt to explain and predict spatial patterns of grizzly bear abundance and distribution across our 41,250 km^2 regional study area encompassing the southern Coast Ranges of southwestern British Columbia. Improving on a previously described analytical approach (Apps et al. 2004), we evaluate landscape composition relative to grizzly bear detection frequency sampled at a scale relevant to understanding and modeling population distribution across the southern Coast Ranges. We then use generalized linear modeling as the basis for probability-based spatial allocation of population estimates derived in Chapter 3. Results and predictive output provide a foundation for regional conservation planning to minimize and mitigate population-level impacts to grizzly bears. For example, spatial output can allow specific population estimates to be derived for any given area, and population core, peripheral, and linkage landscapes can be defined and assigned conservation priorities and strategies.

METHODS

Grizzly Bear Detection Data

Methods of field sampling and molecular analyses for grizzly bear detection were as previously described (Chapter 2). The spatial distribution of sampling with the goal of modeling population distribution was controlled using a grid with cells of 10 x 10 km (100 km^2; 2004 - 2007) or 5 x 5 km (25 km^2; 2008 & 2010). Independent site/session combinations across all six years of regional sampling totaled 2,118. For this analysis, we also included localized sampling in defined landscapes where grizzly bear occupancy was demonstrated through regional sampling, and for which refined knowledge of resident animals was needed for conservation and monitoring (Apps & Rochetta 2008). This more localized sampling was conducted at a spatial distribution controlled by a 5 x 5 km (25 km^2) cells, and sampling effort corresponded to 461 site/session combinations. Methods at both sampling scales were otherwise identical and involved site selection within cells to maximize detection probability and facilitate helicopter landing. We did not sample some cells that were composed of >90% rock, ice, or water.

The detection of grizzly bears at hair-snag stations was confirmed by molecular analyses (mtDNA) of hair samples obtained at each site (Chapter 2). In most cases, individual identification was possible through allele distribution at ≥7 microsatellite loci. Although we could not always identify individuals from each known grizzly bear sample because alleles could not be resolved for some loci, we did compare allele frequencies among samples to determine the minimum number of different bears occurring at each station during each sampling session in a given year. Samples collected at a station during different sessions but from the same bear were assumed to represent independent visits. We assumed that our attractants provided no reward and that a bear's visit to a station did not influence the probability of subsequent visits during different sampling sessions. This expectation is supported by the apparent lack of a behavioural response in detection frequency (Chapter 3). We identified probable family groups as individuals occurring together during >1 station visit and that shared half of their alleles at the loci considered. Different bears within a family group were not considered to be moving independently and their station visits were treated as a single bear for analysis. Some concurrently detected individuals may have been mated pairs not travelling independently, but the likelihood of this is low enough to have negligible effect on our analysis (Apps et al. 2004). The aforementioned data-sources/sampling-scales totaled 2,579 site/session combinations.

Habitat and Human Use Variables

We assembled a GIS database for the study area, from which habitat and human use variables were derived as raster layers with a 1 ha pixel size, smaller than the minimum mapping unit of our finest-scale (1:20,000) source data (Table 4-1). Our broadest-scale (1:250,000) source data have a minimum mapping-unit radius that is 31 times smaller than the 8.8 km mean distance between adjacent sampling stations and are thus appropriate for analysis.

We considered ecosystem variation across the regional study area using 1:250,000 mapping of biogeoclimatic subzones and variants (BEC; Meidinger and Pojar 1991). We considered variation among ecological subzones common within the study area (BEC_xxxx). To account for macro-climatic variation, we assigned BEC subzones one of four ordinal classes pertaining to the frequency of expected stand-initiating or stand-maintaining fire-disturbance under natural conditions (natural disturbance type; NDT). Within alpine tundra and subalpine parkland subzones, we interpolated NDT class based on adjacent ecosystems.

We derived terrain variables from a 1:20,000 digital elevation model (DEM; Geographic Data BC 1996). Candidate predictors included elevation (m; ELEV) and slope (%; SLOPE). A terrain curvature index (CURVA) reflected the maximum rate of change of a curve fit through each pixel in the context of its neighbors (profile curvature; Pellegrini 1995). Using known sun azimuths and a digital elevation model, mean daily maximum solar insolation (kJ; SOL_EN) and duration (h; SOL_DU) was calculated for each pixel in the study area based on 1-hour increments between 1 May and 30 October (Kumar et al. 1997, Meszaros et al. 2002). We also derived a terrain complexity index (COMPLEX) that is independent of slope by measuring the standard deviation of terrain curvature values within a defined landscape radius.

We derived general land-cover classes from 1:250,000 baseline thematic mapping (BTM) data that is based on a remotely sensed classification (Geographic Data BC 2001). Classes included alpine (ALPINE), avalanche chutes (AVAL), old forests (>100 yrs; FOR_OLD), young forests (<100 yrs; FOR_YNG), disturbance due to logging (FOR_LOG), disturbance due to wildfire (FOR_BURN), “barren” surfaces (BARREN), glaciers (ICE), open range (RANGE), and wetlands (WETLAND).

We built variables pertaining to human access and influence from several data sources. We obtained a comprehensive inventory of roads and linear human features from 1:20,000 planimetric and forest roads databases (Surveys and Resource Mapping Branch 1992). We derived a road-density variable (ROADS) by classifying these data following a standard weighting system reflecting expected traffic type and volume (Apps 1997), and then removing road networks to which we knew public motorized access was closed or restricted during the study period. We also derived a variable (ROADDIST) reflecting the distance from the nearest road of any type. From BTM and a provincial municipality database, we defined urban and settled areas (URBAN) and agricultural lands (AGRI). Using 1:50,000 recreational opportunity spectrum data (Forest Practices Branch, 1998a), we derived a 7-class ordinal index of human accessibility (ACCESS), ranging from primitive to urban. From these data, we also defined only primitive or semi-primitive, non-motorized recreation (PRIMITIV).

Soil conditions may influence ecological communities and the availability of grizzly bear foods. From 1:250,000 data of soil landscapes of Canada (SLC; CLBRR 1996), we derived soil variables pertaining to the kind of surface material (KIND_xx), parent material deposition mode (PARENT_x), coarse fragment content (CFRAG), and rooting depth (ROOTDP).

The seasonal availability of concentrated salmon in stream reaches during spawning is well-known to be a key factor influencing grizzly bear populations. We obtained data of spawning salmon occurrence and distribution by stream reach from the provincial fisheries information summary system (FISS; 2006 update; Desrochers 1997, BC Fisheries 2001, Ministry of Fisheries et al. 2001). Based on the 1:50,000 provincial watershed atlas we derived a salmon availability variable (FISH) by tallying the number of different salmon species accessing stream reaches.

We derived indices of vegetation characteristics and a land-cover classification from orthorectified Landsat 7 Enhanced Thematic Mapper Plus (ETM+) satellite imagery (30 m native resolution of multispectral bands)[6]. Coverage for our study area required a mosaic of 11 cloud-free scenes all with dates between 26 July and 13 August, 2005. We expected that reflectance values in these mid-summer scenes would most accurately depict spatial variation in vegetation conditions across the regional study area with minimal influence of snow-cover. We further expected that phenological variation among scenes was negligible since the mean difference among dates was six days. Each scene was initially corrected for atmospheric and geometric distortions. However, to correct for variation among scenes due to atmospheric conditions and time of day (sun angle), we adjusted reflectance values for each spectral band using an averaging algorithm that compares values at shared pixels between overlapping scenes (Schowengerdt 2007). Using a DEM at 25 m resolution, we modeled the spatial distribution of solar energy for the minute each image was taken (Kumar et al. 1997, Meszaros et al. 2002), and we used this to apply a correction for topographic redistribution of solar radiation for all spectral bands (Civco 1989).

From the Landsat data, we derived a land-cover classification as well as vegetation-attribute indices (Franklin 2001). From spectral bands 1-5 and 7, we extracted three principal component images and we conducted an unsupervised classification to cluster radiance values within a composite of these images (Eastman 1999). This process distinguished 13 discrete habitat classes that we could recognize and describe based on available forest inventory data and our knowledge of the study area (HAB_xx). In addition to the land-cover classification, we derived ratio-scale indices of vegetation characteristics. We calculated the normalized difference vegetation index (NDVI) using the standard formula (Band4 – Band3) / (Band4 + Band3). We also applied a Tassled-Cap transformation to the component spectral bands (Crist and Cicone 1984, Mather 1989) to obtain the green (GVI), wet (WVI) and bright (BVI) vegetation indices. The GVI is known to respond to net primary vegetation productivity within pixels (Schwartz and Reed 1999) and appears to relate to the nutritional quality and

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[6] Due to an irreversible failure of the "scan line corrector" on the Landsat-7 satellite on 31 May 2003, all imagery acquired beyond that date has systematic data gaps affecting 22% of each image. However, the pattern of distribution of these gaps, which are maximum ~200 m distance between pixels among merged scenes (<400 m for individual scenes) is of no consequence to this analysis at the landscape scales being considered.

abundance of many grizzly bear plant foods (Mace et al. 1999, Stevens 2001). For each VI, we constrained extreme values within a range that reflects variation in habitat conditions we expect to be relevant to grizzly bears (e.g., variation in values within rock/ice or water was considered irrelevant).

We expected that the above VIs would correlate similarly with functionally-different habitat conditions. However, we know that some discrete habitat conditions with similar site-specific VIs differ according to the patterns of spectral variability within the surrounding landscape, a factor that may relate to grizzly bear habitat selection (Apps & McLellan 2008). Thus, for each of the aforementioned VIs, we derived variables reflecting both its standard deviation (*VI_SD) in the landscape at a specific scale (see Scale-Dependent Design) and the interaction between the mean and standard deviation of index values (*VI_X) at that scale.

Table 4-1. Independent landscape variables explored to explain and predict grizzly bear occurrence and distribution in the southern Coast Ranges of British Columbia, 2004 – 2012.

Ecosystems & Macro-climate		Human Influence	
BEC_*	Biogeoclimatic ecosystem subzone	AGRI	Agriculture (%)
NDT_1	Ecosystems with rare stand-initiating events	URBAN	Urban development (%)
NDT_2	Ecosystems with infrequent stand-initiating events	MUNI	Municipalities
NDT_3	Ecosystems with frequent stand-initiating events	ROADS	Density of weighted road classes
NDT_4	Ecosystems with frequent stand-maintaining fires	ROADDST	Distance (m) from nearest road
Terrain Conditions		PRIMITIV	primitive & semi-primitive, (non-motorized) recreation
ELEV	elevation (m)	ACCESS	ordinal index (7 class) from primitive recreation to urban
SLOPE	slope (%)	Soil Conditions	
CURVA	Terrain curvature index	CFRAG	Coarse fragment content ordinal class (%)
COMPLEX	Terrain complexity index	ROOTDP	rooting depth ordinal class (cm)
ASPECT_S	North → south aspect (0 to→ 1)	KIND_IC	surface material - ice and snow
ASPECT_W	East → west aspect (0 to→ 1)	KIND_OR	surface material - organic soil
SOL_DU	Mean daily max solar duration (hrs), May - Oct	PARENT_C	parent material - colluvial deposition
SOL_EN	Mean daily max solar insolation (KJ), May - Oct	PARENT_U	parent material - undifferentiated deposition
Land Cover		KIND_R2	surface material - granite
ALPINE	Non-forested alpine tundra (%)	KIND_R4	surface material - undifferentiated
AVAL	Subalpine avalanche chutes (%)	KIND_SO	surface material - mineral soil
BARREN	Barren surfaces (%)	Fish	
ICE	Glaciers and snow (%)	FISH	Tally of salmon species by stream reach
FOR_LOG	Recently logged (%)	Landsat [a]	
FOR_OLD	Old (>100 yr) forest (%)	HAB_*	spectral cluster class 1 - 13 (%)
RANGE	Rangelands	*VI	Mean of the specified vegetation index
WETLAND	Wetlands (%)	*VI_SD	Standard deviation of the VI at specified scale
FOR_YNG	Young (<100 yr) forest	*VI_X	interaction b/w the mean & SD of the VI at scale

[a] Landsat vegetation indices are specified as either bright (B), green (G), normalized difference (ND) or wet (W).

Scale-dependent Design

Our analysis compared landscape attributes associated with independent grizzly bear detections to those at all sites sampled, leading to the development of a detection probability function. Our design corresponded to Johnson's (1980) second-order resource selection and Thomas and Taylor's (1990) study design 1 whereby inferences are relevant at the population level. We analyzed associations of grizzly bear detection with factors of habitat and human influence across three spatial scales (*sensu* Apps et al. 2004), aggregating data for each variable at each scale using a moving window routine (Bian 1997) and excluding water bodies from the landscape. Pixels thus reflected each variable's mean attribute value or proportional composition within a circular landscape surrounding each sampling station. At level 1, the broadest analysis scale, a 200-km^2 circular landscape was defined by an 8.1 km-radius, approximating an assumed annual 90% home range size of an adult female grizzly bear within our study area. At level 3, the finest analysis scale, a 13-km^2 landscape was defined by a 2.0-km radius, which approximates the average net daily movement of female grizzly bears in our region according to available data from GPS-collared bears (Apps, Rochetta, McLellan & Hamilton unpubl. data). Level 2 defined a scale intermediate between levels 1 and 3 corresponding to a landscape of 79 km^2 area and 5.0 km radius.

Analyses

We carried out analyses independently for sampling conducted at a scale of 100 km^2 (2004 - 2007) and 25 km^2 (2008 & 2010). For each variable and scale, we extracted attributes associated with sample sites to a database. We analyzed differences in landscape composition at stations where grizzly bears were detected relative to all sites sampled. We constructed a weighting factor for each site that reflected the number of independent sampling sessions conducted and the number of independent detections per site-session combination. We also recognized that detection rates are likely to have varied among years depending on weather and other factors that may have influenced sampling efficiency, for example, as potentially due to our inability to perfectly standardize bait preparations. We therefore calculated a third weighting factor that accounts variation in detection probability among years after accounting for the influence of population closure (see Chapter 3 for calculation of these parameters).

We explored univariate differences between sites where grizzly bears were detected and all sites sampled using *t*-tests without assuming equal variances. In describing grizzly bear associations with landscape composition, we compared the size and direction of *t* statistics among variables within each spatial scale. We were not testing hypotheses, but we note that a Dunn-Sidak adjustment (Sokal and Rohlf 1981) would normally be applied according to the number of variables considered within each scale if interpreting univariate results in this sense.

Recognizing that grizzly bear persistence, density and distribution are undoubtedly determined by contributions and interactions among several if not many spatial factors, we entered a multivariate analysis to derive a resource selection function (Manly et al. 2002). With slight modification, we followed methods of Apps et al. (2004) with the goal of predicting grizzly bear distribution based on meaningful variation among variables, while excluding spurious associations (Rextad et al. 1988).

At each scale, we considered only variables with at least a marginal ($P < 0.1$) univariate association. We then applied a principal components analysis to reduce variables to a minimum number of orthogonal factors that explain maximum variation among original variables. Factors with eigenvalues >1 were extracted, and we applied a varimax rotation to the component matrix to facilitate improved interpretation (McGarigal et al. 2000). We interpreted the principal component structure to describe factors that may be relevant to grizzly bears. For all possible factor subsets, we then evaluated the weighted-deviation of grizzly bear detections from the conditions sampled using multiple logistic regression (Hosmer and Lemeshow 2000). We applied information-theoretic methods (Burnham and Anderson 2002) using Akaike's Information Criterion (AIC; Akaike 1973) to rank models in terms of parsimony and prediction. We further evaluated goodness of fit and predictive power using an adjusted coefficient of determination (Nagelkerke 1991), and the area under the relative operating characteristic curve (Pearce and Ferrier 2000) or c statistic (Norusis 1999). The latter is the proportion of paired cases between the two groups in which a higher probability is assigned to cases where the event (i.e., grizzly bear detection) has occurred. To account for model uncertainty, we used Akaike weights to average parameter coefficients among all competing models according to the $\tilde{\bar{\beta}}$ (shrinkage) estimator (Burnham and Anderson 2002), such that model contribution was proportional to the evidence that each is best fit to the data. Model averaging in this way can result in greater precision and reduced bias relative to the single best model, and this approach is therefore appropriate where prediction is the primary objective (Anderson et al. 2000, Anderson and Burnham 2002).

Within the GIS, we standardized original variables $\left([\chi - \hat{\mu}]/\hat{\sigma}\right)$ according to values at sampling stations. Each component factor was calculated by summing the products of standardized variables and factor score coefficients (McGarigal et al. 2000). We then applied the model-averaged parameter coefficients within a resource selection probability equation (Manly et al. 2002; section 5.4) resulting in scale-dependent grizzly bear detection probability surfaces across the study area. Finally, we compared efficiencies among scale-specific models, and averaged predictions among scales according to AIC weights. Spatial modeling was carried out independently for each geographically distinct modeling area (regional: 2004-2007 & Toba-Bute:2008-2010), and we combined spatial outputs into one coverage by weighted averaging based on both sampling representation and differences in overall grizzly bear detection rates between regional and Toba-Bute sampling.

For each modeling area, we evaluated the fit of the final output by tabulating the proportion of actual grizzly bear detections within 16 equal-interval classes of predicted detection probability (class width = 0.063). For each class, we divided the number of detections by the number of station-session combinations in the class to account for variation in sampling effort among classes (*sensu* Boyce et al. 2002). We then evaluated the relationship between area-adjusted frequency values and the ordinal classification of habitat-selection probability using a Spearman rank correlation coefficient.

Spatial Inference of Grizzly Bear Density

We transformed the probabilistic model of grizzly bear detection to reflect population density (*sensu* Boyce and McDonald 1999, Apps et al. 2004). Across the greater regional (2004 - 2010) study area, we applied population estimates derived for specific geographic strata (mostly annual sampling areas) including upper and lower confidence limits (Chapter 3). For each pixel (i), estimated population density $(\hat{D}_i)$ was calculated as

$$\hat{D}_i = \hat{D}_{SA}\left(\hat{P}_i \Big/ \left[\sum_{i=1}^{n} \hat{P}_i \Big/ n\right]\right) \tag{4-1}$$

where $\hat{D}_{SA}$ is the population density estimate for the study area, n is the total number of pixels in that area, and $\hat{P}_i$ is each pixel's detection probability. That is, for each pixel, we multiplied $\hat{D}_{SA}$ by a factor that is the pixel's detection probability value divided by mean detection probability for the study area. We used this approach to transform the detection probability model across the entire study area using a single combined population estimate among sampling areas, and we also transformed the model independently for, and only within, each annual sampling area. Resulting outputs reflected estimated density and distribution of grizzly bears rather than detection probability.

We then combined the area-specific spatial models of population density using weighted averaging on the basis of proximity, such that 10 km transition zones along borders between sampling areas received an average density estimate weighted based on proximity to either area. Areas that were sampled but within which no grizzly bears were detected and are likely to be unoccupied (e.g., Garibaldi-Pitt GBPU) were assigned a maximum number of resident grizzly bears consistent with the current Ministry of Environment assumption. This allowed some variation in potential density among landscapes to be reflected in the final output.

RESULTS

Among the 2,579 site/session combinations sampled during 2004 to 2010, we independently detected 362 grizzly bears at least 1,169 times. We detected at least one grizzly bear at 513 sampling site-sessions, and we did not detect grizzly bears at 2,066 site-sessions (Table 4-2). Landscape conditions associated with sites where grizzly bears were detected clearly differed from those of the collective sampling effort, and these differences varied somewhat by spatial scale (Figures 4-2a,b).

After initial variable screening, principal components analysis extracted a much smaller set of orthogonal factors explaining most of the environmental variation at each scale. At level 1, the top 13 factors explained 83% of the variance among 64 variables considered. At level 2, the top 13 factors explained 80% of the variance among 62 variables considered. At level 3, 12 factors explained 78% of variance among 58 variables considered. For each scale, the rotated component matrix showing the factor loadings for each variable on each factor are presented in Appendix 2.

Table 4-2. Grizzly bear detections among sampling stations and sessions and by annual sampling strata, in the southern Coast Ranges, British Columbia, 2004 – 2010.

		Detections per site-session combination		
Stratum (Year)	*n*[a]	Total[b]	≥1	0
SL-TPD (2004)	360	111	48	312
SN (2005)	410	75	20	390
SSCR & GP (2006)	440	111	31	409
CSCR (2007)	320	188	63	257
Monitoring (2005)	114	58	20	94
Monitoring (2006)	91	36	17	74
Monitoring (2007)	256	201	50	206
Toba-Orford (2008)	396	198	140	256
Southgate-Chilko (2010)	192	178	108	84
Total	2,579	1,156	497	2,082

[a] Number of site and session combinations sampled.

[b] Known visits by independently traveling bears.

For each analysis area, a composite of all model subsets derived through weighted averaging indicated that factors varied in their predictive influence (Table 4-3). For the 2004 - 2007 (primarily 10 x 10 km intensity), the level-1 model carried the most power in predicting grizzly bear detections, while the level-3 model carried the least predictive weight. For the 2008 and 2010 sampling (5 x 5 km intensity), the level-3 model carried the most power in predicting grizzly bear detections, while the level-2 model carried the least predictive weight (Table 4-4). For both sampling intensities, the composite multi-scale model performed better than any of its constituents, and its probabilistic predictions were highly correlated with the grizzly bear detection data from which it was derived (Figure 4-3). Both models fit the data very well (2004 - 2007: r_s=0.991, df=16, P<0.001, 2008 & 2010: r_s=0.87, df=16, P<0.001).

The spatial output from the final models reflects variation in grizzly bear detection probability across the multi-annual study area (Figure 4-4). Based on area-specific density estimates (Table 3-3), a transformation of the regional detection probability model to reflect our best understanding of population density during the multi-annual sampling period demonstrates our best understanding in the spatial variation of grizzly bear abundance across the southern Coast Ranges (Figure 4-5). Conservation implications and applications of this model output are discussed in Chapter 8.

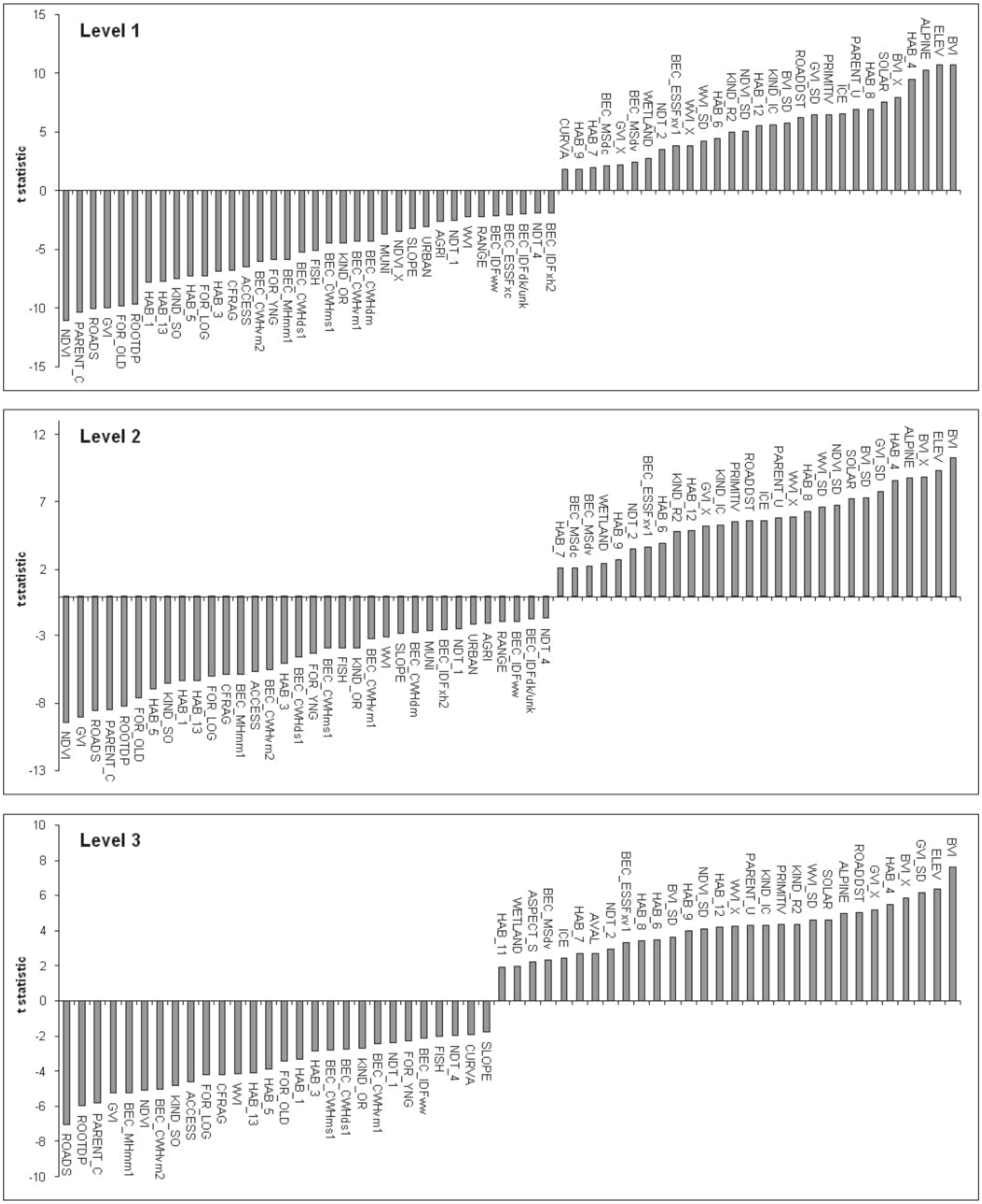


Figure 4-2a. Relationships between individual variables and grizzly bear detections at broader (level 1) to finer (level 3) scales in the southern Coast Ranges of British Columbia, 2004 – 2007. The strength and direction of correlation is defined by the univariate t-statistic, and only relationships of *P* < 0.1 are shown.

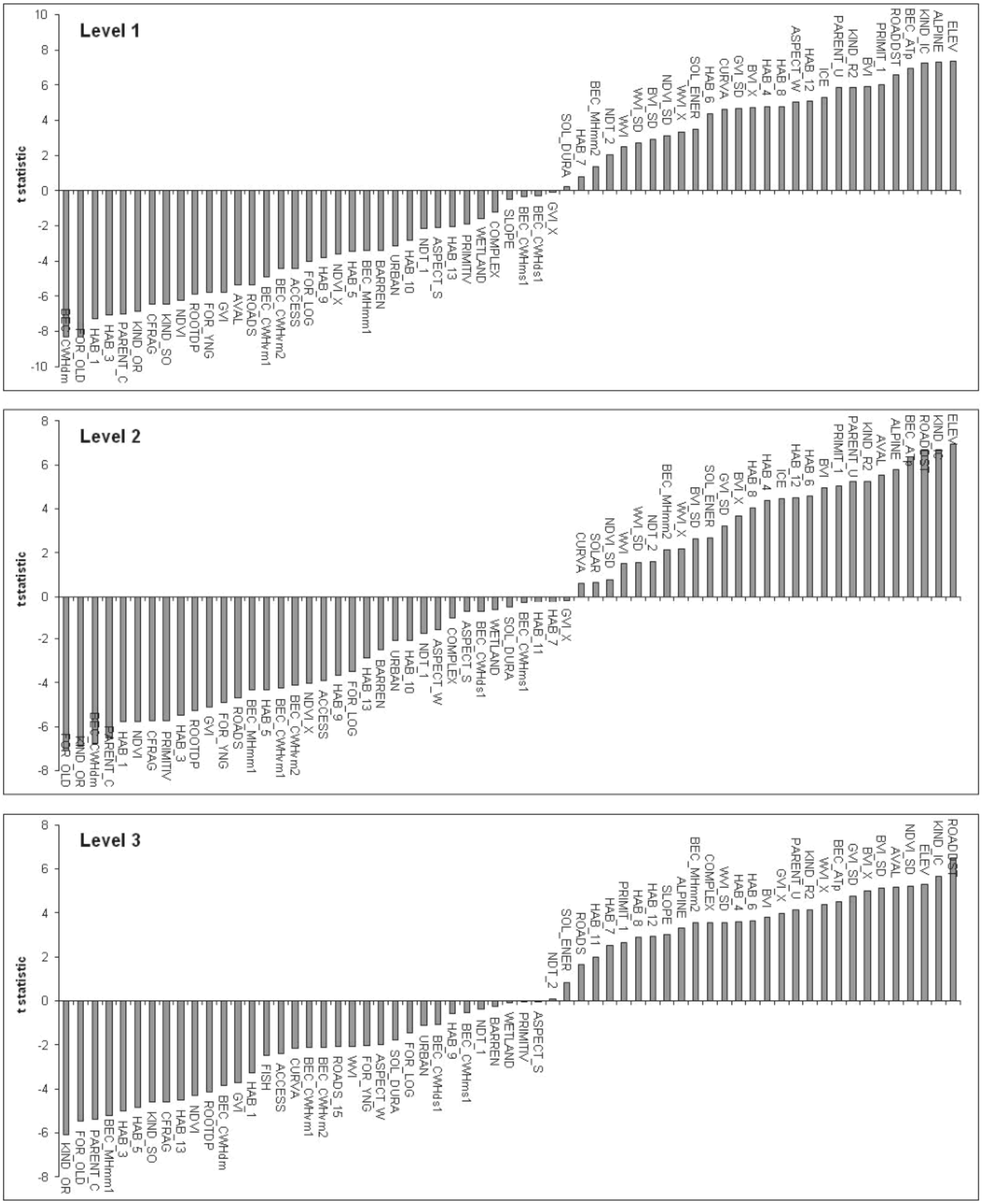


Figure 4-2b. Relationships between individual variables and grizzly bear detections at broader (level 1) to finer (level 3) scales across the Toba/Bute 2008/2010 combined survey area. The strength and direction of correlation is defined by the univariate t-statistic, and only relationships of *P* < 0.1 are shown.

Table 4-3a. Coefficients (directly comparable due to inherent standardization) predicting grizzly bear detection from broader (level 1) to finer (level 3) spatial scales in the southern Coast Ranges, British Columbia, 2004 – 2007. Factors are those extracted from principal component analysis of original variables (Appendix 2).

	Level 1		Level 2		Level 3	
Factor	B	SE	B	SE	B	SE
1	-0.757	0.039	0.637	0.039	0.501	0.035
2	-0.349	0.043	-0.331	0.042	-0.083	0.034
3	0.161	0.036	-0.157	0.039	0.245	0.038
4	-0.464	0.040	-0.358	0.037	0.236	0.033
5	-0.053	0.042	-0.278	0.037	-0.300	0.036
6	0.284	0.027	-0.066	0.044	0.057	0.034
7	-0.013	0.040	-0.215	0.036	-0.115	0.031
8	0.042	0.040	-0.048	0.043	0.213	0.036
9	0.307	0.035	0.082	0.042	0.124	0.034
10	-0.297	0.042	0.158	0.025	0.061	0.034
11	-0.310	0.092	0.371	0.036	-0.063	0.033
12	0.148	0.035	-0.272	0.093	-0.065	0.035
13	-0.013	0.046	0.234	0.032	--	--
Constant	-0.427	0.042	-0.367	0.040	-0.226	0.035

Table 4-3b. Coefficients (directly comparable due to inherent standardization) predicting grizzly bear detection from broader (level 1) to finer (level 3) spatial scales in the Toba-Bute 2008-2010 combined survey area. Factors are those extracted from principal component analysis of original variables (Appendix 2).

	Level 1		Level 2		Level 3	
Factor	B	SE	B	SE	B	SE
1	-0.577	0.090	-0.495	0.083	0.233	0.087
2	0.101	0.075	0.234	0.084	0.405	0.076
3	0.102	0.087	0.178	0.081	-0.390	0.103
4	0.247	0.078	-0.186	0.072	0.343	0.076
5	-0.480	0.084	-0.136	0.085	0.014	0.081
6	0.174	0.083	0.349	0.085	0.510	0.080
7	0.024	0.086	-0.028	0.093	0.062	0.079
8	0.271	0.086	0.091	0.085	0.106	0.086
9			0.260	0.088	0.037	0.091
10			0.095	0.085	-0.119	0.094
11					0.055	0.076
12					0.056	0.080
Constant	-0.288	0.084	-0.231	0.082	-0.310	0.084

Table 4-4a. Predictive efficiency among models of grizzly bear detection derived at broader (level 1) to finer (level 3) spatial scales in the southern Coast Ranges, British Columbia, 2004 – 2007. Statistics given are the area under the receiver operating characteristic curve (AUC), model classification success (CS) at cutpoint P = 0.5, Nagelkerke R^2 coefficient of determination, model χ^2 and associated significance level, and predictive contribution (ΔAIC).

Scale-Specific Model	AUC	CS	R^2	χ^2	*P*	ΔAIC
Level-1	0.67	67.9	0.215	729.2	<0.001	57.6
Level-2	0.67	68.0	0.200	672.1	<0.001	7.9
Level-3	0.65	67.7	0.213	722.3	<0.001	1.2

Table 4-4b. Predictive efficiency among models of grizzly bear detection derived at broader (level 1) to finer (level 3) spatial scales in the Toba-Bute 2008-2010 combined survey area. Statistics given are the area under the receiver operating characteristic curve (AUC), model classification success (CS) at cutpoint $P = 0.5$, Nagelkerke R^2 coefficient of determination, model χ^2 and associated significance level, and predictive contribution (ΔAIC).

Scale-Specific Model	AUC	CS	R^2	χ^2	*P*	ΔAIC
Level-1	0.61	64.2	0.152	96.0	<0.001	8.9
Level-2	0.59	64.1	0.123	79.5	<0.001	1.1
Level-3	0.62	63.9	0.169	107.5	<0.001	23.4

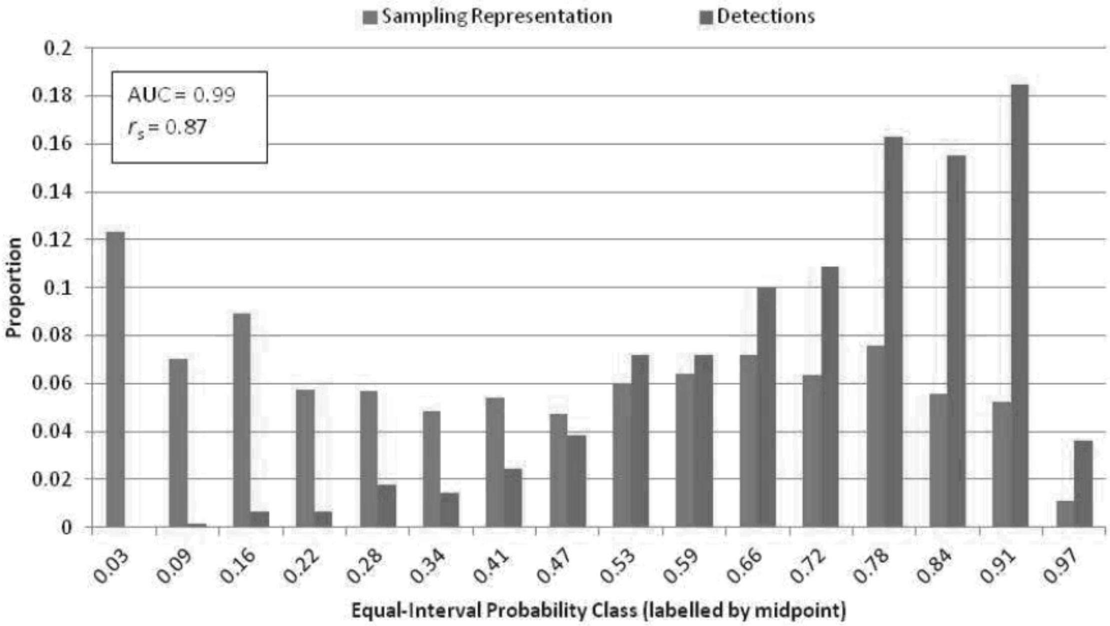


Figure 4-3a. Fit of a spatially-explicit model predicting grizzly bear detection across the southern Coast Ranges of British Columbia, based on representative sampling conducted during 2004 – 2007. Shown is the distribution of grizzly bear detections relative to sampling effort among equal-interval probability classes. Statistics indicated are the area under the receiver operating curve (AUC) and the Spearman-rank correlation coefficient (r_S).

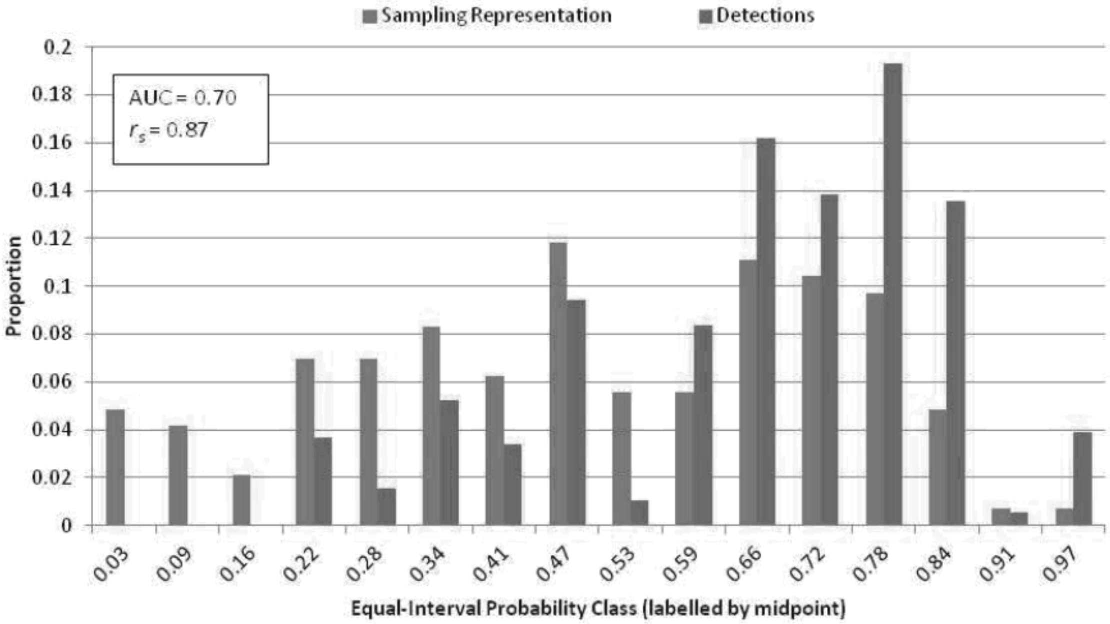


Figure 4-3b. Fit of a spatially-explicit model predicting grizzly bear detection across the Toba/Bute 2008/2010 combined survey area of southwest British Columbia. Shown is the distribution of grizzly bear detections relative to sampling effort among equal-interval probability classes. Statistics indicated are the area under the receiver operating curve (AUC) and the Spearman-rank correlation coefficient (r_S).

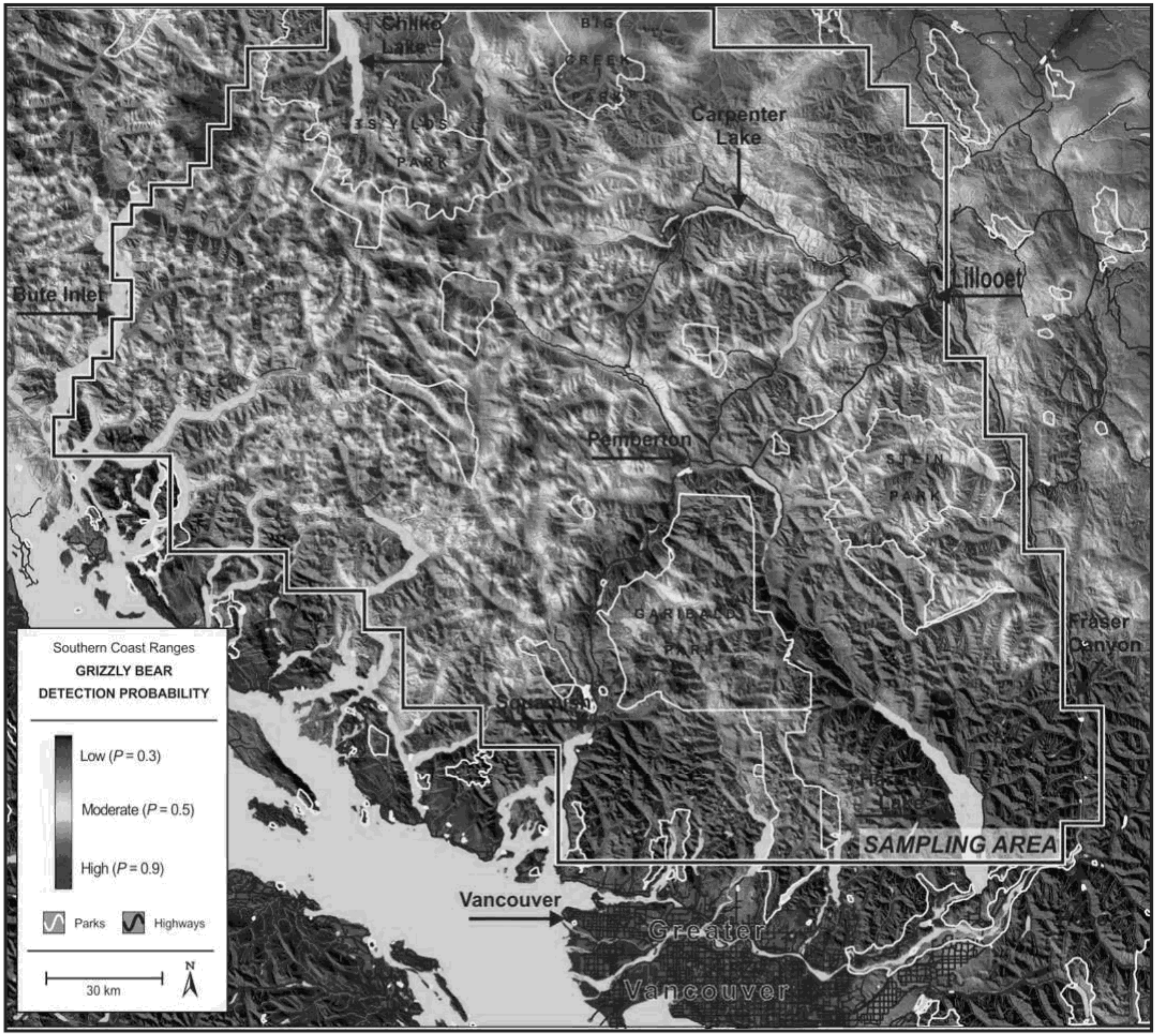


Figure 4-4. Grizzly bear <u>detection probability</u> across the southern Coast Ranges of British Columbia. Predictions are based on representative sampling conducted during 2004 – 2010. Predictions beyond the sampling area are based on extrapolation and should be considered with caution.

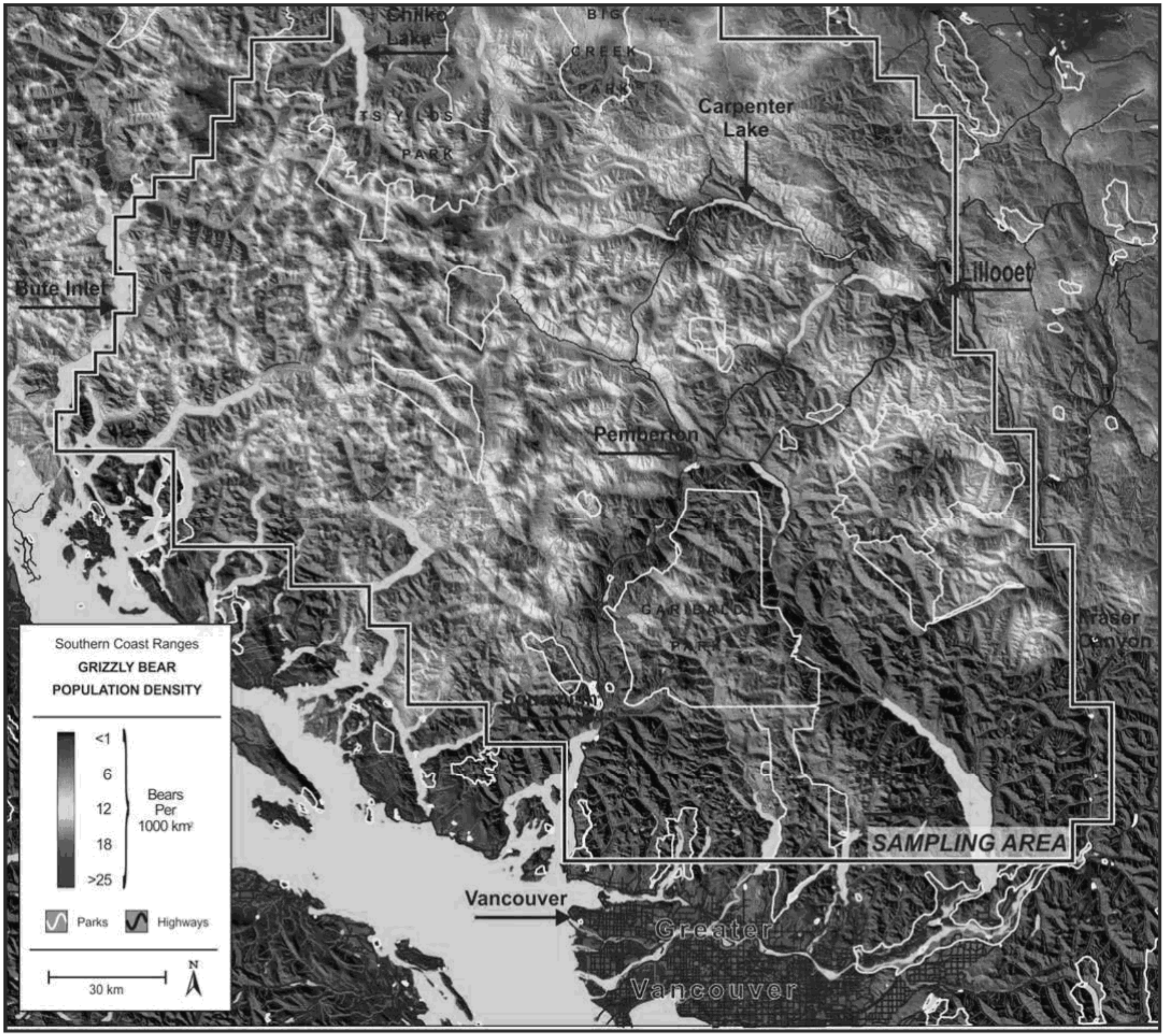


Figure 4-5. **Estimated grizzly bear <u>population density</u> across the southern Coast Ranges of British Columbia. Predictions are based on representative sampling conducted during 2004 – 2010. Predictions beyond the sampling area are based on extrapolation and should be considered with caution.**

Chapter 5

GENETIC STRUCTURE & FLOW: INFERENCES OF GRIZZLY BEAR POPULATION FRACTURE, CONTRACTION, SPREAD & CONNECTION

INTRODUCTION

Landscape factors can not only influence the distribution and size of localized grizzly bear subpopulations, but also the connectivity among those core areas. The continual or periodic population augmentation that connectivity facilitates can support peripheral populations that may not otherwise persist and can result in a stable and resilient regional metapopulation anchored by secure and productive habitat cores (Brown & Kodric-Brown 1977, Fahrig & Merriam 1994). Maintaining genetic flow among historically connected populations also contributes to localized adaptability in addition to the purging of deleterious alleles that can manifest in the reduction of individual fitness and ultimately population productivity and resilience (Schonewald-Cox et al. 1983, Frankham et al. 2002). From both perspectives (demographic and genetic), population connectivity can facilitate ecological and geographic shifts in response to a changing environment such as due to climate change (Root et al. 2003, Parmesan 2006).

Clearly, the current and potential pattern of regional grizzly bear distribution has important implications to the resiliency, viability, and conservation of localized subpopulations. In Chapter 4, we analyzed how landscape factors relate to and predict grizzly bear population abundance and distribution across the southern Coast Ranges. These results support the expectation that the regional population is very unevenly distributed at this southwestern range extent, and it is reasonable to expect some degree of population fragmentation due to a combination of and interaction among natural and human factors. Model output (Chapter 4) reflects the probabilistic spatial pattern of population distribution and extirpation. However, given the nature of the detection data, this analysis could not account for the influence of localized population isolation on the persistence and hence occurrence of individuals.

The history of connectivity within and among populations is reflected in the distribution of alleles (paired DNA sequences at specified genetic locations) among individuals across the larger region (Holderegger et al. 2009). This pattern can provide insight into current and historic population fracture, isolation, and contributing natural and human factors. An examination of the spatial distribution of individuals relative to ancestral landscapes, and the hybridization among ancestral groups can also suggest whether spatial expansion and/or reconnection since isolation has occurred and the process of this expansion.

In this chapter, we examine spatial patterns of genetic relatedness among individual grizzly bears relative to the geographic pattern of their occurrences. We test the general hypothesis that the regional grizzly bear population across the southern Coast Ranges has a history fragmentation as evidenced by significant genetic structure. Such a pattern we expect would relate to landscape factors of habitat and human influence that can be measured at present. Beyond this, our analyses are exploratory in that we refrain from *a priori* assumptions about the geography of genetic subpopulations or the location of potential fractures. Across the multi-year regional study area, we search for statistically significant clusters (groups) of genetically similar grizzly bears. Inferences of population isolation, connectivity and expansion are based on the probability of group membership, the geographic pattern of member detections, and the genetic variability within each group. Finally, we model the contribution of potentially-relevant landscape factors to the resistance of grizzly bear gene flow.

METHODS

Spatio-Genetic Population Structure

Using remote hair-snagging within a systematic design, we obtained 1828 georeferenced DNA samples from 411 grizzly bears across a 41,250 km^2 regional study area and over a nine year period (2004 - 2012; Chapters 1 & 2). For all individuals, 22-locus (21 plus sex) microsatellite genotypes were derived (Chapter 2). We investigated genetic population structuring across the regional study area by way of a model-based Bayesian cluster analysis (admixture model with no linkage among loci; Falush et al. 2007, Pritchard et al. 2000) using program STRUCTURE (Pritchard et al. 2010). We initially conducted the analysis with no *a priori* assumptions of population membership using random-seed simulation using 10,000 for both burnin length and run-steps (Pritchard et al. 2010). We assumed that the number of genetically discrete populations or groups (K) would range between 2 to 13, and we carried out 10 simulations for each K. For comparison to random-seeding, we applied a LOCPRIOR model (Pritchard et al. 2010) that modified the prior distribution of each individual's population assignment based on the wildlife management unit within which each individual was detected most frequently. Assuming there is geographic pattern to population membership, this allowed us to detect potentially meaningful structure based on lower levels of divergence while avoiding bias that could result in defined structure that is not real (Hubisz et al. 2009). We inspected genetic metrics to test underlying assumptions that mating was random (Hardy-Weinberg equilibrium) and that genetic markers were independent and non-linked (linkage dis-equilibrium) within subpopulations (Rousset 2008). We evaluated genetic relatedness among defined population clusters by way of a weighted analysis of variance (F_{ST}) statistic (Weir and Cockerham 1984, Hudson et al. 1992). We characterized genetic variability within defined subpopulation groups according to the frequency of heterozygotes among loci (expected Heterozygosity; H_e). We compared results at each K using the average of alpha values, admixture, among groups, H_e and F_{ST},

For each genetic cluster (defined at each K), we inferred a geographic origin and associated confidence on the basis of the spatial distribution of grizzly bear detections and the ancestral origin of those individuals. In doing so, each individual was weighted equally regardless of variation in the number of detection locations. On this basis, we used GSTAT to derive a kriged interpolation (Haining 1990, Pebesma 2004) of grizzly bear ancestry across the regional study area at a spatial scale matching that of our primary sampling effort (i.e., 100 km^2). We also plotted known movements between grizzly bear detections by sex to better understand the mechanism of genetic interchange among landscapes and the degree to which this may reflect demographic connectivity. Among ancestral groups, we combined the interpolated "centres of gravity" and the spatial spread of alleles to model the spatial distinctiveness of inferred ancestral landscapes among grizzly bears across the regional study area at each assumed K. Since females typically range and disperse over smaller distances than males, we additionally considered only females for inferring ancestral landscapes. Based on the STRUCTURE output and the spatial distinctiveness of inferred ancestral landscapes, we defined a maximum number of ancestral groups that are likely (K = *i*). We then averaged the images from K = 2 to K = *i*, weighting each according to evidence for population structure (α) We interpreted this output as a best model of grizzly bear isolation and gene flow history across the region.

Landscape Influences on Grizzly Bear Gene Flow

We evaluated the influence of landscape factors on historical gene flow among grizzly bears across the regional study area. Our intent was to model spatial disruptions to gene flow not genetic relatedness, recognizing that the latter is influenced by population size and associated genetic drift. Hence, differences in F_{ST} among genetic groups did not factor in this analysis.

We expected that grizzly bear gene flow would be explained, fundamentally, by (1) inherent landscape potential to support resident grizzly bears and (2) proximity to an occupied landscape. We further hypothesized that the continuity in gene flow has been interrupted by one or a combination of the following factors: (3) present human access and settlement, (3) major water bodies, (4) anticipated terrain barriers to movement, and (5) the historical pattern of human migration and settlement through the regional study area.

We accounted for landscape potential to support grizzly bears using our regional model of grizzly bear detection probability (Chapter 4; HABITAT). We measured proximity to an occupied landscape as the distance to a sampling cell with at least one grizzly bear detection (DISTANCE). We considered the density of existing roads, weighted according to traffic type and volume (ROADS; Chapter 4). Using 1:50,000 recreational opportunity spectrum data (Forest Practices Branch, 1998a), we derived a 7-class ordinal index of human accessibility (ACCESS), ranging from primitive to urban. From 1:250,000 baseline thematic mapping (BTM; Geographic Data BC 2001), we combined urban, settled, and agricultural lands into a single variable of human presence (HUMAN). We also used BTM data to define water bodies (WATER) and icefields (ICE). Using a digital elevation model with a native resolution of 25 m (Geographic Data BC 1996), we modeled assumed terrain barriers to movement as slopes exceeding 80% (SLOPE80). We saw no hypothetical mechanism for multivariate influence in a manner other than additive, and we did not consider interaction terms. In a future iteration of this analysis, we plan to consider the historic pattern of human presence and movement through the regional study area (HISTORIC) based in part on a 19th century human trail/route map from a time when there was fairly continuous human movement and migration through our study area for the gold rush (Begbie 1871).

We constrained this analysis to the 100 km^2 sampling scale, consistent with both the size of the largest grid-cell unit used for most of our field sampling and the scale at which we modeled the spatial distribution of ancestral groups (see above). Within each 100 km^2 grid cell across the regional study area, we extracted the average of the gene flow index described above as well as mean or proportional composition measures for each explanatory variable. We assessed data distributions of independent variables and applied logarithmic (HUMAN, WATER, ICE) or square-root (ROADS, DISTANCE) transformations to improve normality.

We modeled the influence of the above independent factors on grizzly bear gene flow using least-squares multiple linear regression (Seber & Lee 2003). We accounted for the potential influence of spatial autocorrelation in our model of genetic flow by including an autocovariate term representing, for each cell, the mean value of the eight adjacent cells (Lichstein et al. 2002). We inspected tolerance statistics to assess multicollinearity (Menard 1995). We then compared seven candidate models and used Akaike's Information Criterion (AIC) to rank these in terms of parsimony and prediction (Burnham & Anderson 2002). Two models consisted of HABITAT and DISTANCE independently, one included both terms, and six others also included both terms and each remaining variable independently. To account for model uncertainty, we used Akaike weights to average parameter coefficients among competing models such that each model's contribution to the explanation of grizzly bear gene flow was proportional to the evidence that it is best-fit to the data. We considered models with $\Delta AIC < 2$ as having strong support (*ibid.*). We further characterized the explanatory power of candidate models using a coefficient of determination (R^2).

RESULTS

Spatio-Genetic Population Structure

Our results indicate clear evidence for considerable genetic structure among grizzly bears across the southern Coast Ranges resulting from a recent history of isolation and inbreeding. The "correct" number of groups is not obvious, but is likely to range from 10 to 12 given our results across K = 2 to 13 (Figure 5-1). Following Pritchard et al. (2000) and considering within-group heterozygosity and spatial distinctiveness (Figure 5-2), we interpret the evidence to best support 11 genetically discrete population clusters among the 411 individual genotypes (mean log-liklihood -19257.8, P = 0.035; Figure 5-3, Table 5-1). Pairwise comparisons of genetic distance (F_{ST}) indicated considerable variation in genetic distinctiveness among groups (Table 5-2; Figure 5-4). Spatial interpolation of ancestry (including consideration of females only) gave a general indication of the degree to which each genetic grouping is (or has recently been) localized and panmictic (geographically discrete and reproductively independent) and we assigned geographic descriptors to each group on this basis.

The degree to which genetic clusters are geographically discrete (Figure 5-5) and restrictions in genetic flow among these groups (Figure 5-6) indicates a recent history of population contraction, fragmentation with the isolation of several small subpopulations. The degree to which genetic interchange has been more recently re-established appears to be largely a result of movements by males (Figure 5-7).

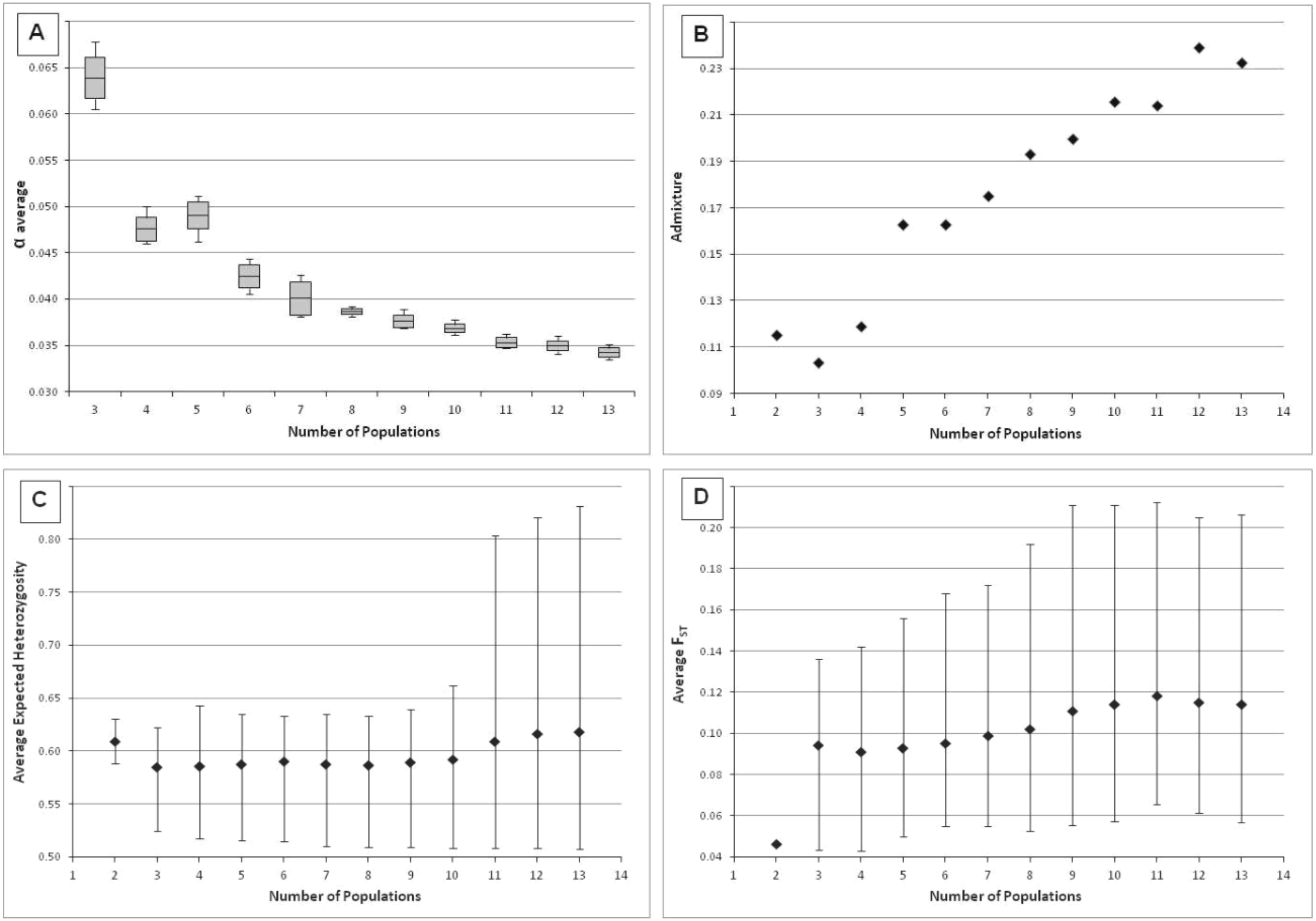


Figure 5-1. Results from Bayesian cluster analysis based on the assumption of 2 to 13 genetically distinct groups (K) among 411 grizzly bears sampled across the Southern Coast Ranges, British Columbia, 2004 - 2012. (A) Probabilities from program Structure are shown as boxplots (SD ±min/max) of 10 simulations at each K. Shown for the best simulation at each K is (B) average admixture among groups, (C) average expected heterozygosity (±min/max), and (D) average F_{ST} values(±min/max).

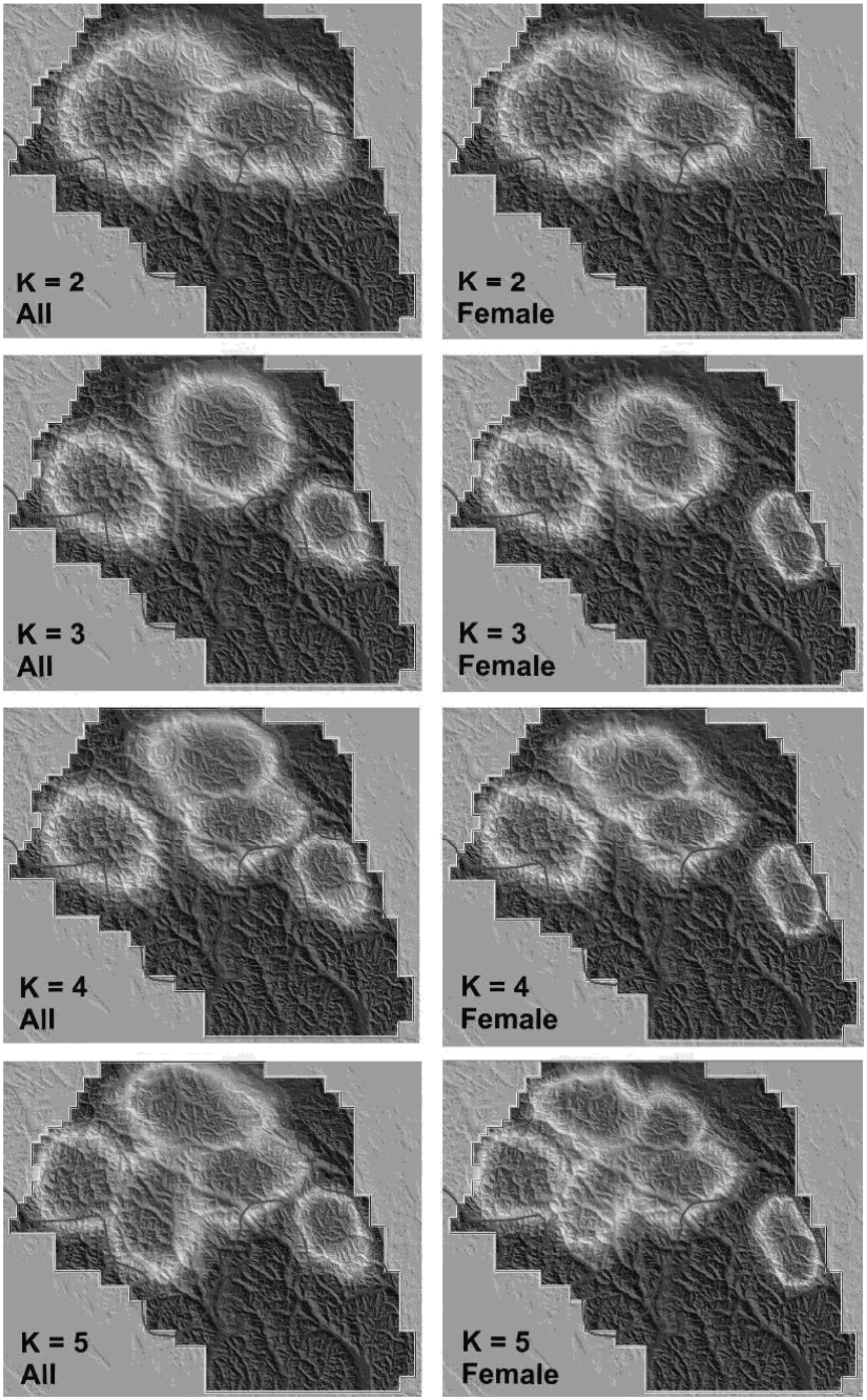


Figure 5-2. Present geographic distinctiveness among genetic clusters defined with groups (K) ranging from 2 - 13 among 411 grizzly bears across the Southern Coast Ranges, British Columbia, 2004 - 2012. The multi-year sampling area is shown in black, and landscapes where grizzly bears were detected (presumably occupied) are encompassed within the red line.

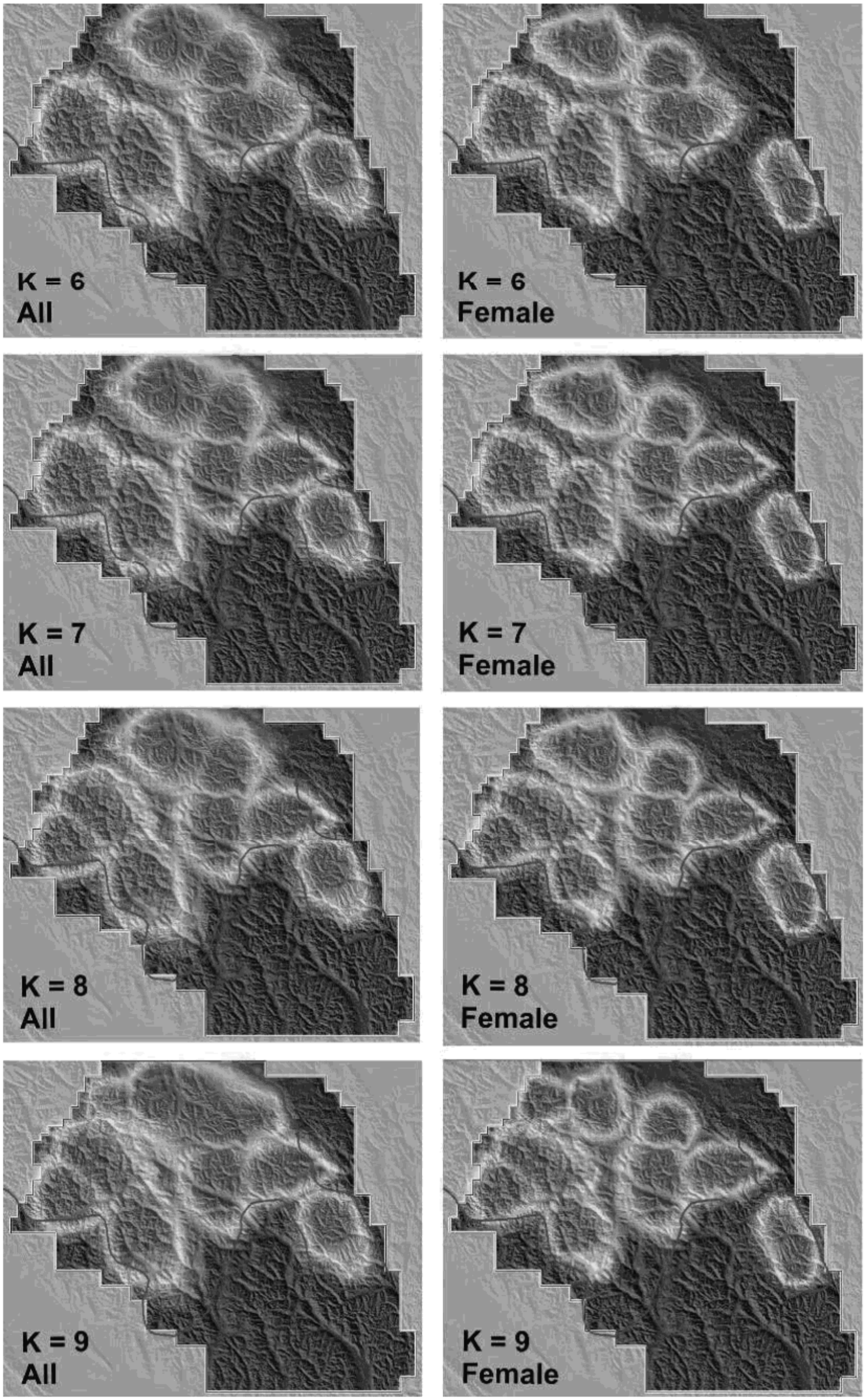
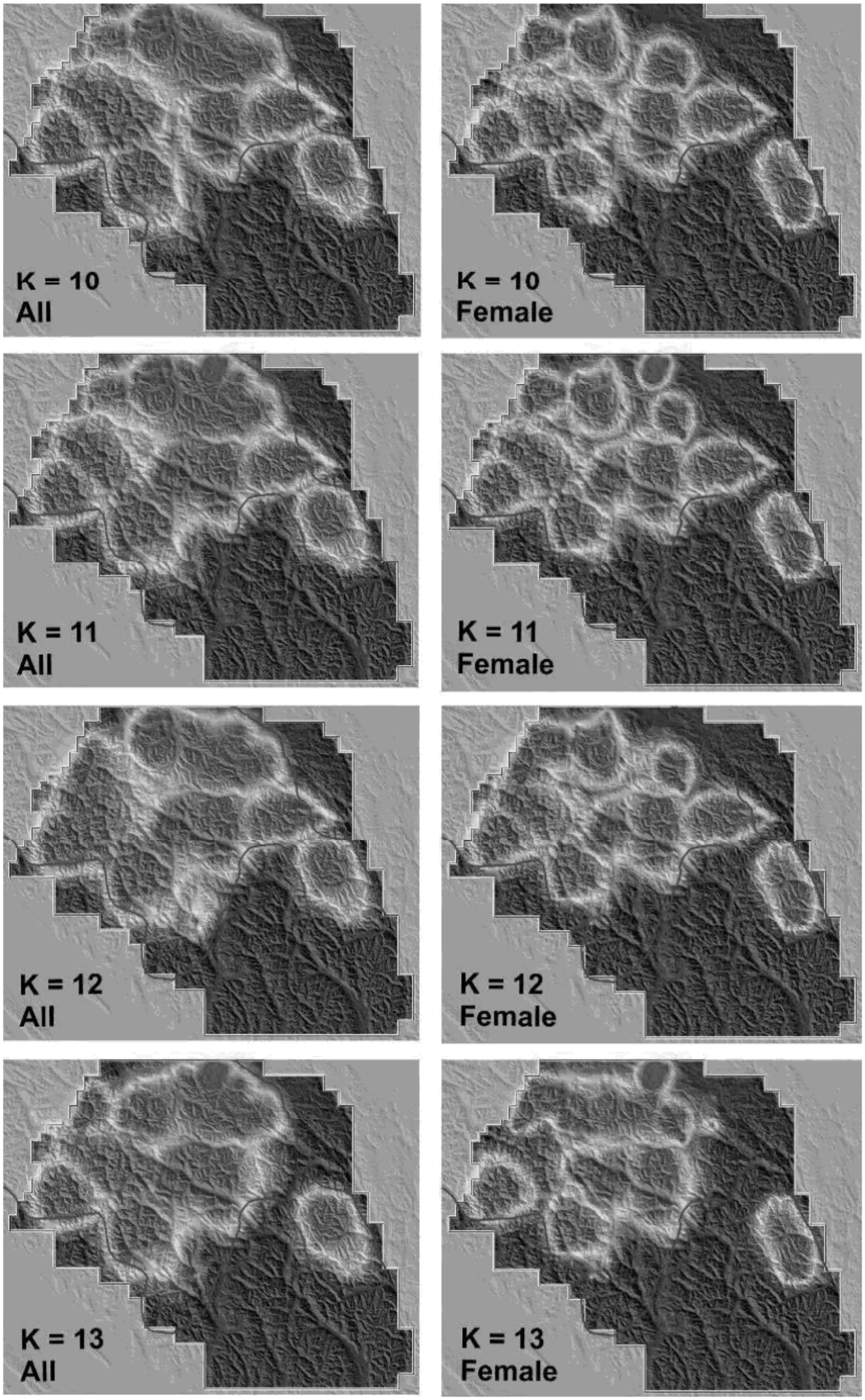


Figure 5-2. Continued.



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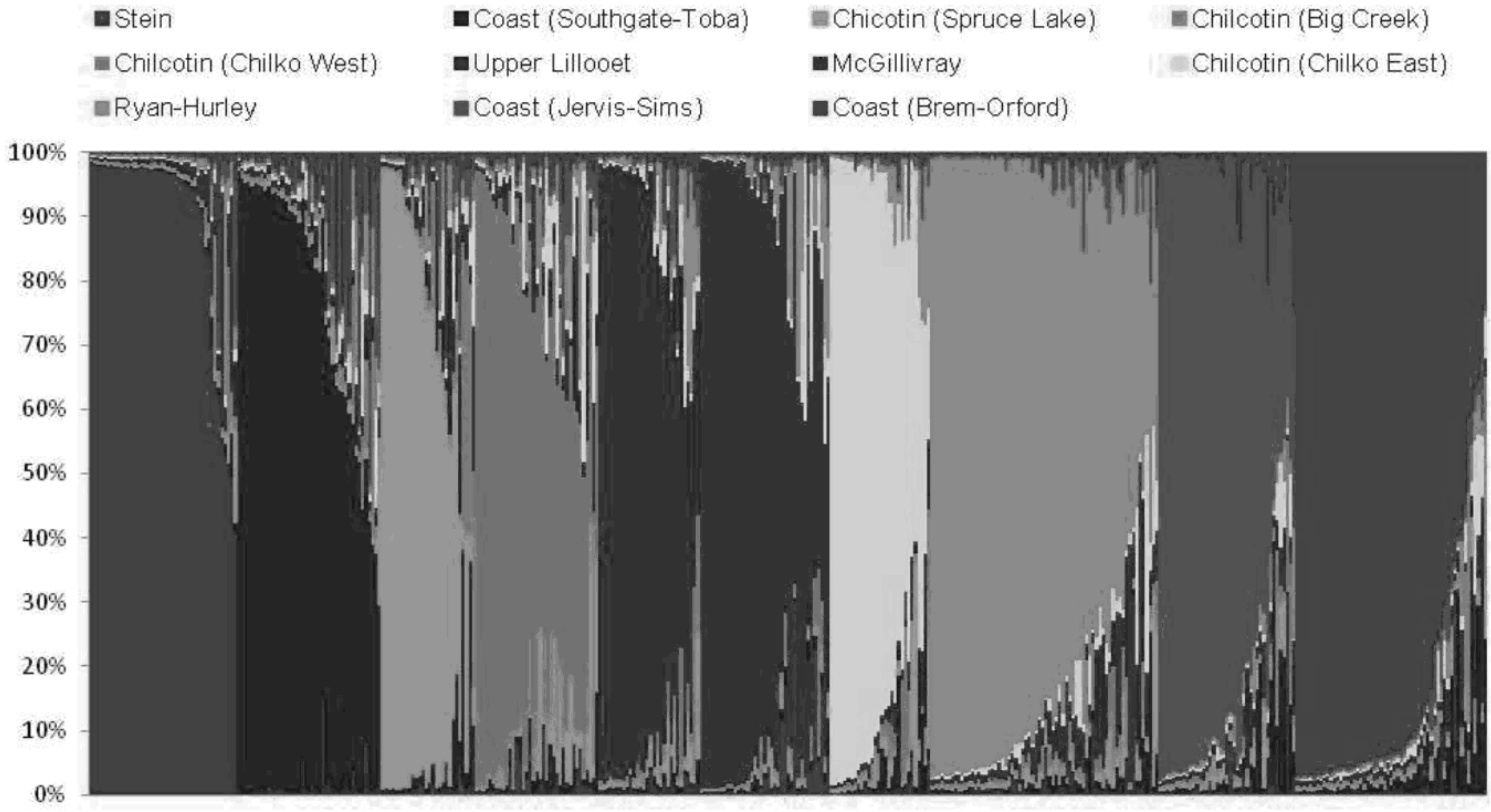


Figure 5-3. Proportional ancestry assigned to 411 individual grizzly bears (each represented by a column) among 11 genetically discrete population clusters across the southern Coast Ranges of British Columbia, sampled 2004-2012.

Table 5-1. Attributes of 11 genetically discrete population clusters among 411 individual grizzly bears genotyped from across the southern Coast Ranges, 2004-2012. Groups are ranked from highest to lowest genetic differentiation (mean F_{ST}) and are named by geographic association.

Cluster	Descriptor	Proportional Membership	F_{ST}	H_e	Shared Ancestry
1	Stein	0.106	0.174	0.508	0.886
4	Chilcotin (Big Creek)	0.137	0.140	0.804	0.829
7	McGillivray	0.058	0.137	0.559	0.764
11	Coast (Brem-Orford)	0.163	0.119	0.557	0.796
8	Chilcotin (Chilko East)	0.103	0.116	0.610	0.755
10	Coast (Jervis-Sims)	0.072	0.115	0.585	0.770
3	Chicotin (Spruce Lake)	0.094	0.108	0.639	0.787
2	Coast (Southgate-Toba)	0.010	0.099	0.618	0.371
5	Chilcotin (Chilko West)	0.072	0.097	0.639	0.784
6	Upper Lillooet	0.098	0.096	0.600	0.785
9	Ryan-Hurley	0.089	0.095	0.576	0.689

Table 5-2. Genetic distances (F_{ST}) among 11 genetically discrete subpopulation clusters sampled across the southern Coast Ranges, 2004-2012.

	Stein	Coast (Southgate-Toba)	Chicotin (Spruce Lake)	Chilcotin (Big Creek)	Chilcotin (Chilko West)	Upper Lillooet	McGillivray	Chilcotin (Chilko East)	Ryan-Hurley	Coast (Jervis-Sims)
Coast (Southgate-Toba)	0.169									
Chicotin (Spruce Lake)	0.164	0.100								
Chilcotin (Big Creek)	0.212	0.088	0.121							
Chilcotin (Chilko West)	0.149	0.091	0.089	0.120						
Upper Lillooet	0.126	0.079	0.077	0.127	0.080					
McGillivray	0.167	0.135	0.139	0.182	0.103	0.124				
Chilcotin (Chilko East)	0.203	0.096	0.105	0.119	0.066	0.100	0.140			
Ryan-Hurley	0.149	0.081	0.085	0.147	0.069	0.066	0.076	0.079		
Coast (Jervis-Sims)	0.199	0.078	0.085	0.133	0.105	0.084	0.164	0.122	0.090	
Coast (Brem-Orford)	0.198	0.071	0.115	0.155	0.098	0.095	0.136	0.129	0.105	0.091

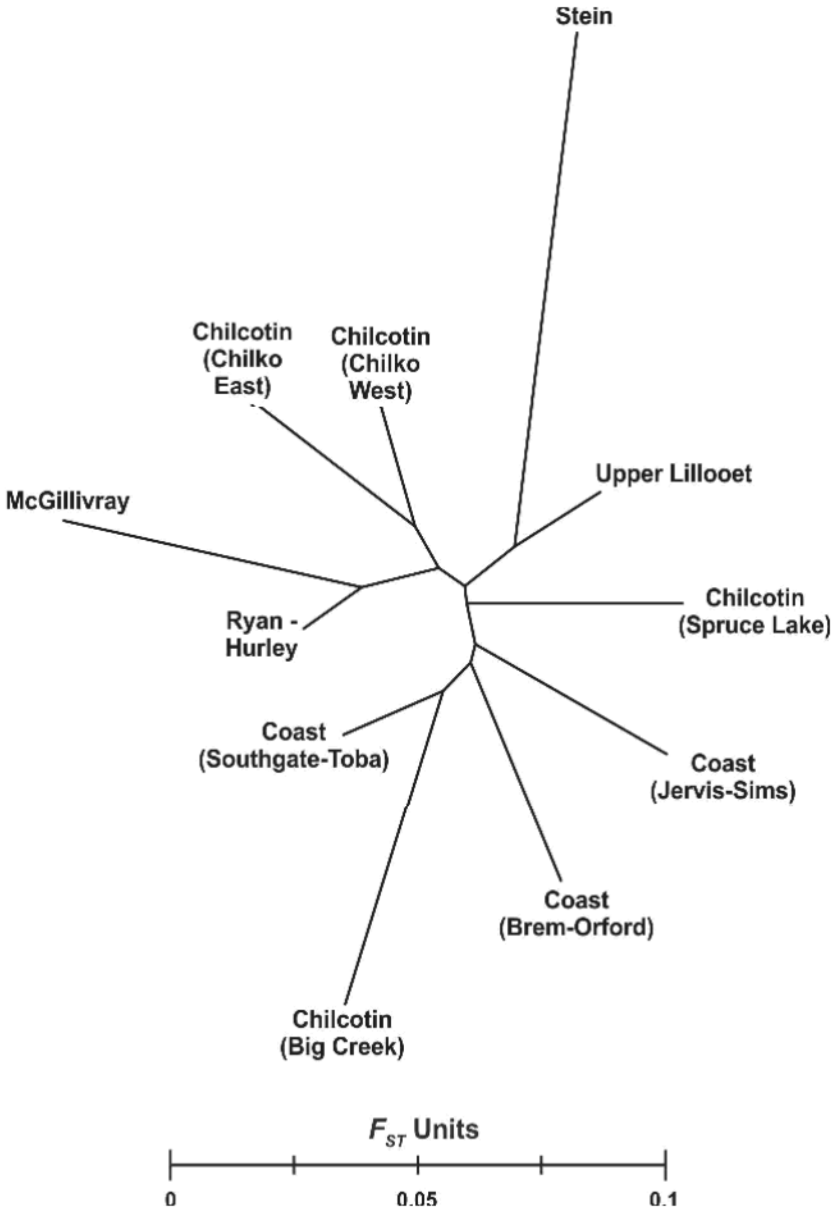


Figure 5-4. Fitch tree representing the genetic distance (F_{ST}) among discernible groups identified among grizzly bears across the southern Coast Ranges, British Columbia, based on sampling collected 2004-2012. Genetic distance (F_{ST}) between any two groups is the combined length of branches connecting them.

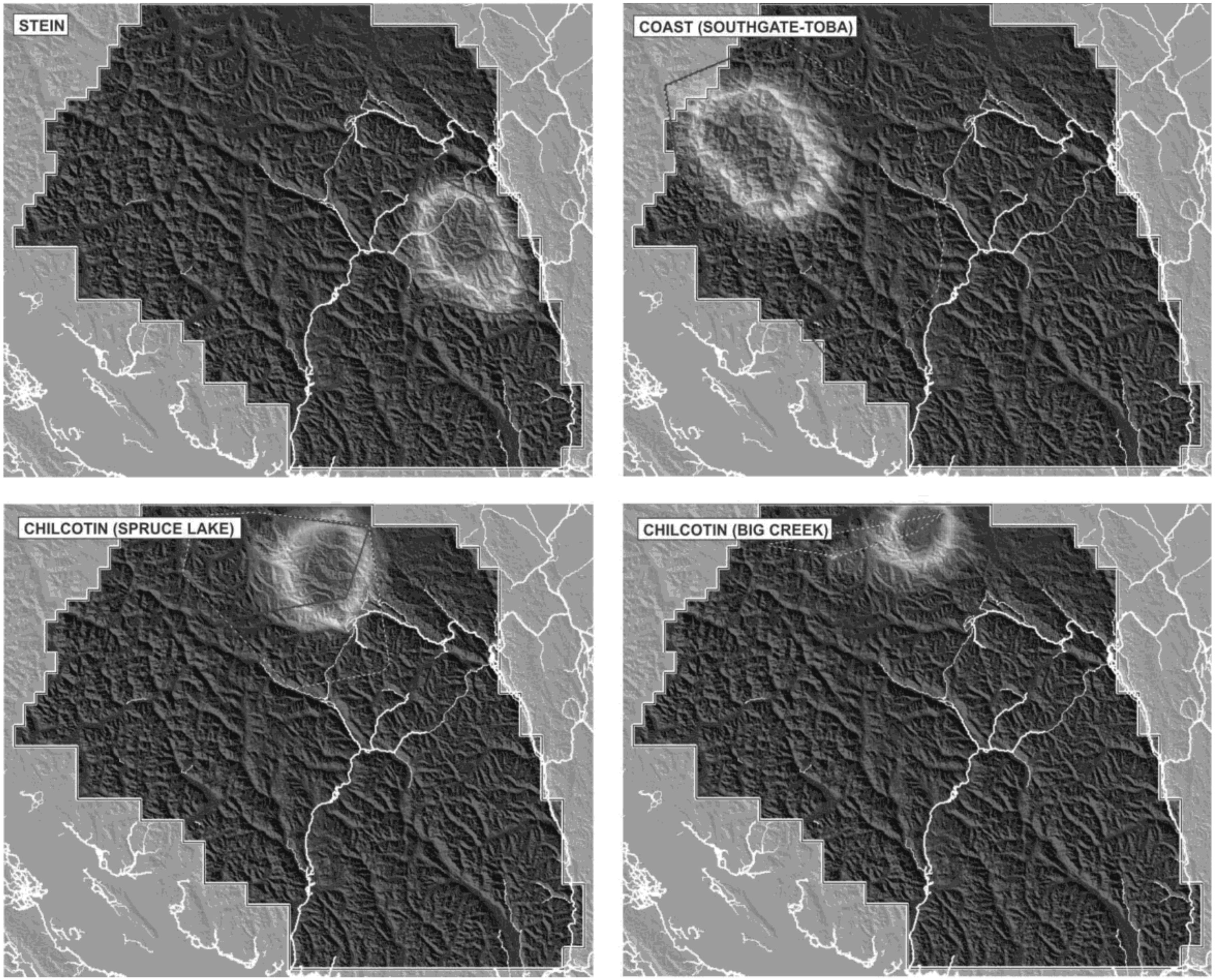


Figure 5-5. Inferred geographic origin of discrete genetic clusters identified among 411 grizzly bears across the southern Coast Ranges, 2004-2012. The "hot spot" depicts the centre of gravity of each geographically-named group based on spatial interpolation of proportional ancestry among individuals sampled. The spread of the hot spot reflects the degree of confidence in localized origin and not group size. Also depicted (red) are minimum convex polygons encompassing detections of individuals with 75% (solid red line), 50% (thin red line) and 25% (dotted red line) ancestry to the group – evidence of migration and gene flow. Major roads are depicted in white. Figure continues on following pages, showing additional groups.

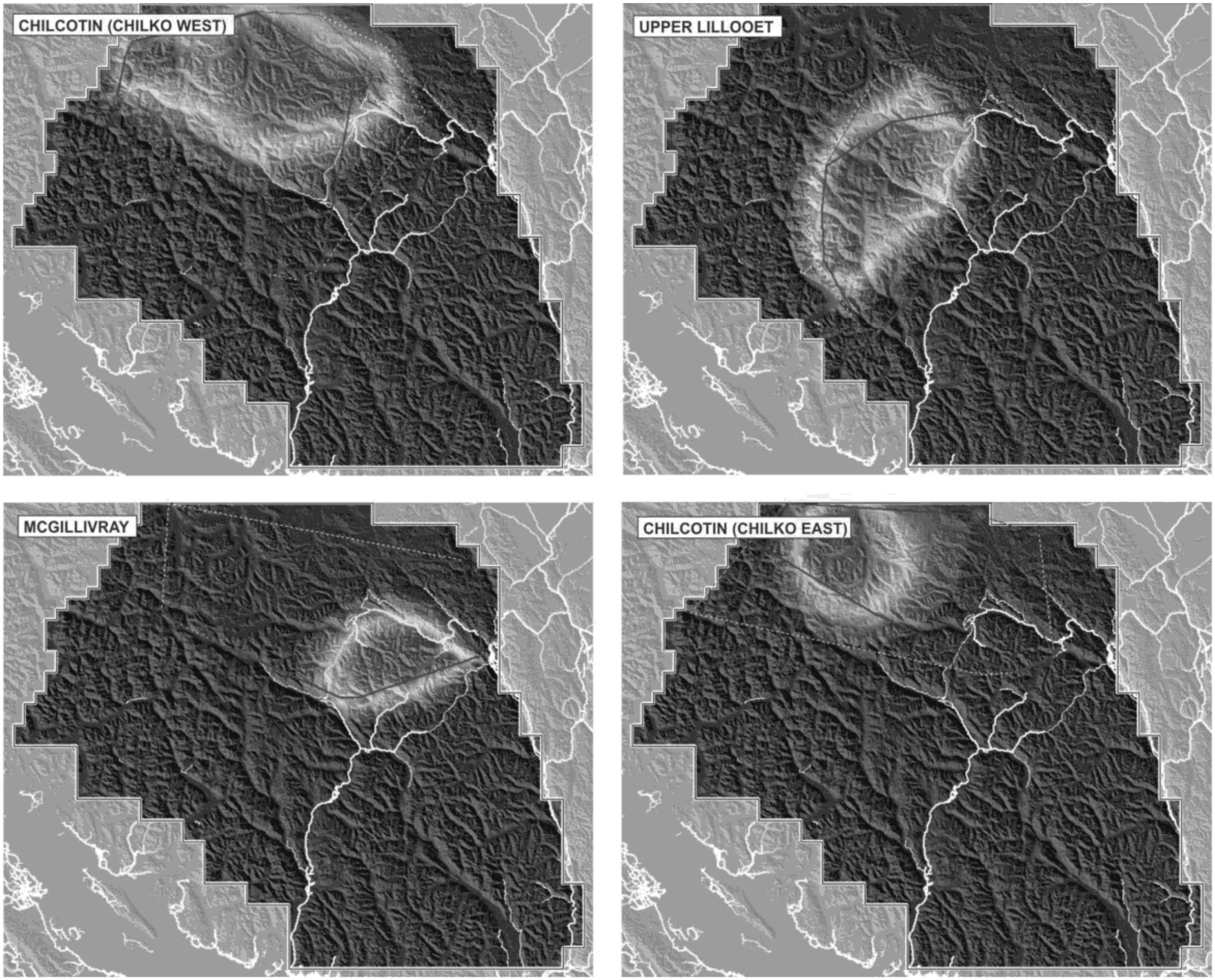
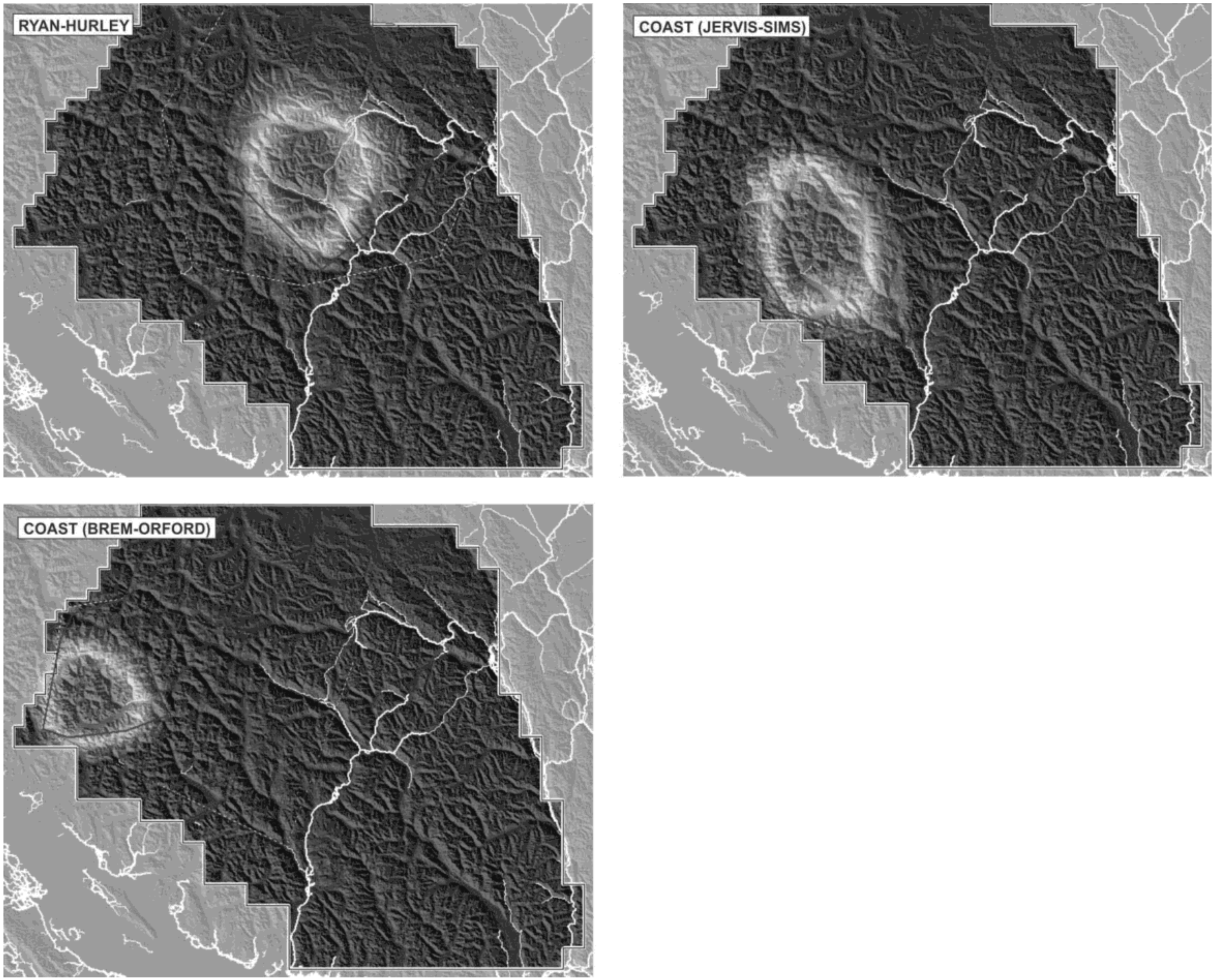


Figure 5-5. Continued.



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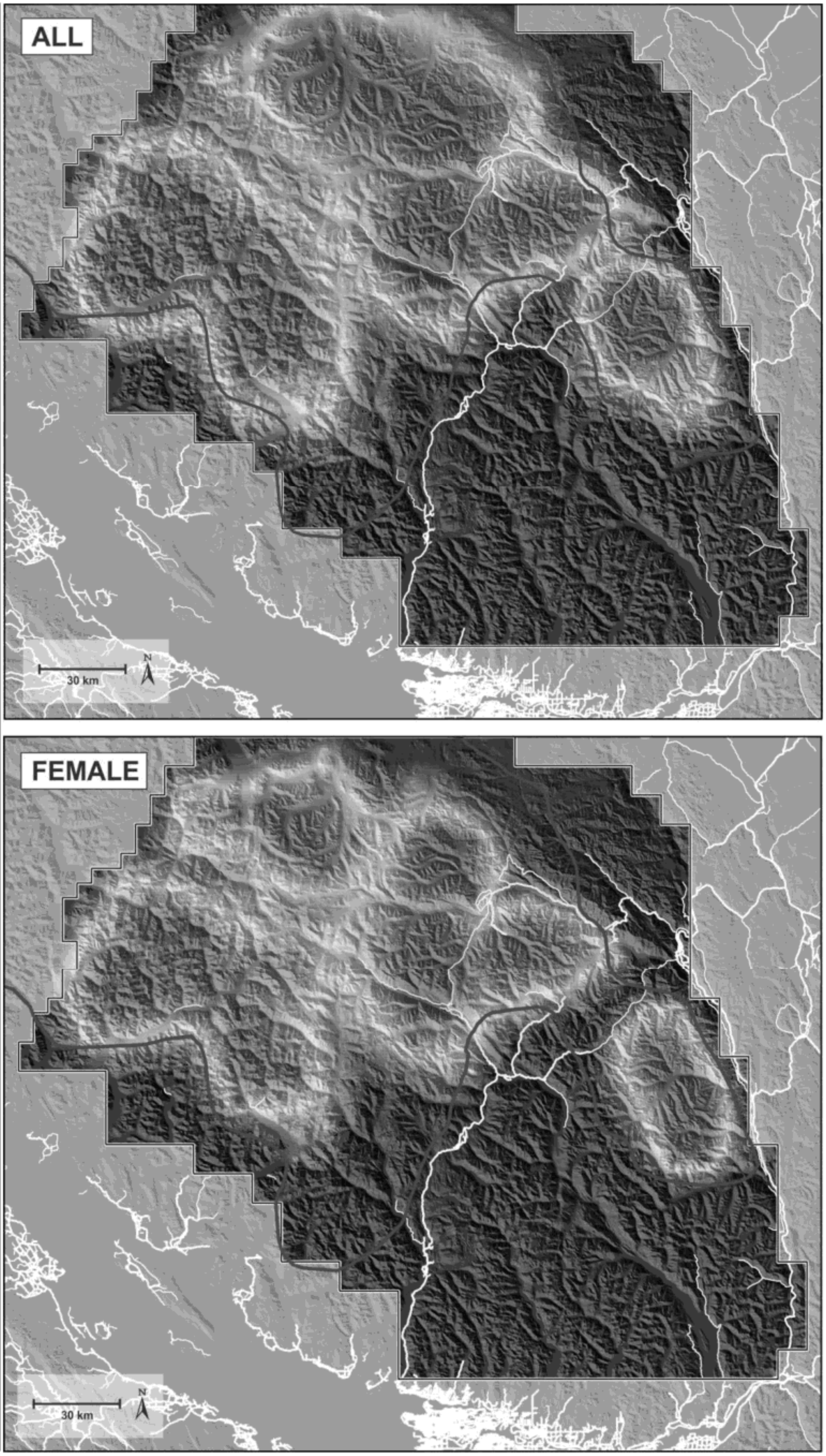

Figure 5-6. Relative isolation and gene flow among grizzly bear ancestral landscapes across the southern Coast Ranges, British Columbia, 2004 - 2012. The multi-year sampling area is shown in black, and landscapes where grizzly bears were detected (presumably occupied) are encompassed within the red line.

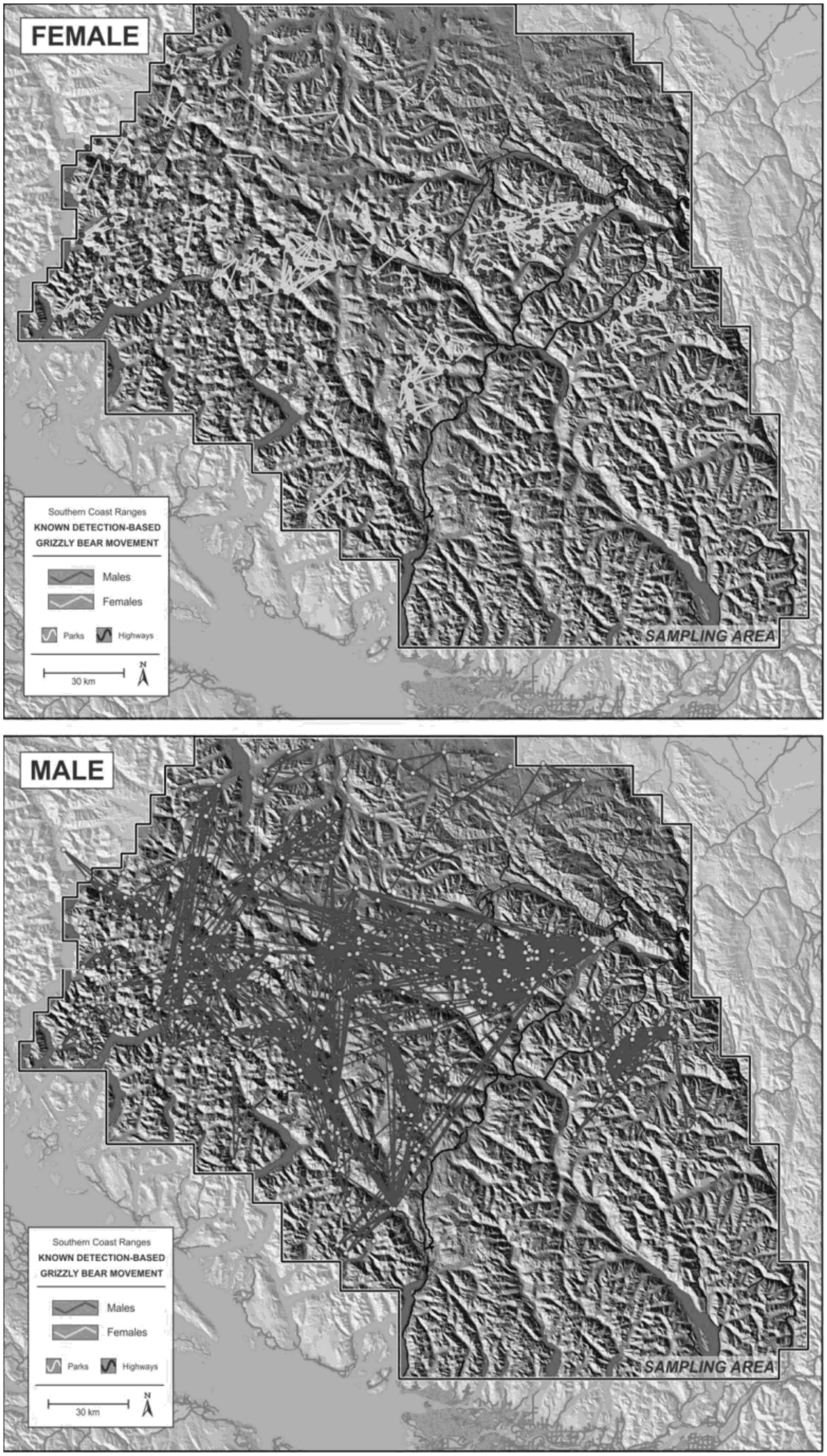

Figure 5-7. Coarse movements of male and female grizzly bears inferred from DNA-based remote detection across the southern Coast Ranges, British Columbia, 2004 - 2012. Each straight vector represents a connection between two detections of the same individual. Major differences between male and female movements are illustrated.

Landscape Influences on Grizzly Bear Gene Flow

As expected, much of the variation in grizzly bear gene flow across the regional study area was explained by the distance from an occupied landscape and landscape habitat potential as predicted by our detection probability model. However, permanent human activity and roads were both additional factors within the two top-ranked models best supported by our data (ΔAIC < 2). The zones of human access reflected in ROS data was also moderately predictive. Our data did not support icefields, water bodies, or very steep slope conditions as predictors of disruption to grizzly bear gene flow beyond what can be explained alone by landscape habitat potential and distance from occupied landscape.

Table 5-3. AIC ranking of models explaining disruption to grizzly bear gene flow across the southern Coast Ranges, British Columbia, based on sampling conducted 2004 – 2007. Covariates are represented in vertical text. Akaike weights (*w*) indicate the contribution of each to multi-model inference. Model fit is indicated by a coefficient of determination (R^2). A constant is included in all models.

Rank	DISTANCE	HABITAT	ROADS	ACCESS	HUMAN	ICE	WATER	SLOPE80	R^2	Δ AIC	*w*
1	X	X			X				0.871	0.0	0.506
2	X	X	X						0.871	0.7	0.349
3	X	X		X					0.868	3.1	0.106
4	X	X							0.863	6.8	0.017
5	X	X					X		0.863	8.3	0.008
6	X	X				X			0.863	8.5	0.007
7	X	X						X	0.863	8.8	0.006
8	X								0.787	75.1	0.000
9		X							0.560	190.5	0.000

Chapter 6

PEDIGREE CONSTRUCTION & THE CONTRIBUTION OF KNOWN GRIZZLY BEARS TO POPULATION PRODUCTIVITY & CONNECTIVITY

INTRODUCTION

In assessing and monitoring population trend and connectivity for grizzly bears across the southern Coast Ranges, understanding movements in association with breeding and the contributions of individual bears to gene flow is highly relevant. The basis for this understanding is knowledge of parent-offspring relationships among individual grizzly bears detected over time. Here, we describe methods, interpretation and outputs of pedigree analyses to characterize parental relationships among bears. These family relationships, considered in a spatial context, are an excellent indicator of functional population connectivity, including the ultimate success of dispersal movements (i.e., breeding). Such information can also be particularly powerful in explaining observed spatial patterns of genetic structuring across the larger regional population.

METHODS

As described (Chapter 2), we have systematically sampled grizzly bear occurrence across ~41,250 km^2 since 2004. These sampling efforts have been mostly for our regional population study with objectives pertaining to grizzly bear population abundance, distribution, connectivity and relatedness (Chapter 1). Resulting samples have been supplemented by other more geographically restricted sampling efforts for population monitoring (e.g., McLellan et al. 2011), samples associated with physical capture and collaring activities, and as well as opportunistic collection of grizzly bear hair and/or tissue samples (e.g., rub trees). Hence, the spatial and temporal intensity of which samples have been collected has varied across the region depending on the focus of specific research objectives.

All samples to date have been genotyped by Wildlife Genetics International (WGI) to facilitate the unambiguous identification and sexing of individual grizzly bears using consistent microsatellite markers established for the South Coast regional study. Individual genotypes were initially extended for analyses of population structure and relatedness among individuals (15 loci). These data are being used in efforts to estimate localized population abundance, trend, spatial/genetic structuring and associated current and historic connectivity. As of 2012, we had WGI extend multi-locus genotyping to 22 microsatellite loci in order to determine family relationships among the >400 individual grizzly bear detected across the region to date.

The probability of a parent-offspring relationship was calculated using PARENTE 1.2 software (Cercueil et al. 2002) which considers allele-matching patterns among potential parent-offspring triads. That is, a potential mother-father-offspring triad where the offspring has one allele from each parent at each of 21 loci is usually a strong indicator that the family relationship is real. More specifically, PARENTE can make use of data on allele frequencies, predicted error rates, mutation rates, sex, age, and known associations (if available) to test parent-offspring hypotheses. Given published estimates for error rate (Kendall et al. 2009) and re-analyses for mismatching markers conducted by WGI in parent-offspring pairs and triads that mis-matched at one or two loci, the error plus mutation rate was assumed to be 0.002. Based on this very low rate, it is virtually impossible for a parent and offspring to mismatch at >2 loci (i.e., will match across at least 19 of the 21 loci; D. Paetkau, WGI, pers. comm.). Under this scenario, 21 loci genotypes should provide sufficient power to unambiguously identify parent-offspring relationships given the typical heterozygosity within mainland grizzly bear populations. That is, where $H_E = 0.75$ across ~20 loci, siblings would be excluded as potential parents with high probability (D. Paetkau, WGI, pers. comm.).

However, given the low heterozygosity across the southern Coast Ranges (more so in some locales than others), *P*-values from PARENTE were not reliable on their own in differentiating parent-offspring from sibling relationships. Hence, only triads (both parents known) were considered in concluding relationships. But even perfectly compatible triads were problematic, especially for bears associated with the previously identified "Stein" and "McGillivray" population groups (defined in Chapter 5) that have very low heterozygosity. For example, based on triads, there are 29 competing hypotheses for the parentage of a single McGillivray male. Also, some triads involve the same individuals as others but with putative parent and offspring switched. For bears within at least the Stein and McGillivray groupings, one can only conclude parentage where the genotypes of at least two putative offspring are explained by the same putative mother and father (D. Paetkau, WGI, pers. comm). That is, a perfectly compatible triad is only suggestive of a parent-offspring relationship, not conclusive. Even with this highly conservative criterion for accepting the parent-offspring hypothesis, there is still a situation within the Stein group where two full siblings each occur within two fully compatible triads but with different putative mothers. In this case the correct mother cannot be known given the data. This issue should be less relevant elsewhere across the region where H_E is higher than within the Stein and McGillivray groups.

RESULTS

Pedigrees Related to Dominant Breeders

Because parent-offspring relationships can only be known through mother-father-offspring triads, much of a localized population needs to be genotyped for such an investigation to be worthwhile. Sampling efforts and other opportunistic collections have allowed us to obtain genotypes for most of the

South Coast grizzly bear population since 2004. Hence, we are able to describe family relationships in many localized areas of our larger regional study area. South of Carpenter Lake, in particular, the general pattern is one typical of few breeding males fathering many offpring, sometimes with close relatives (siblings, parents, offspring). This is a pattern typical of a population that is in the process of recovery and expansion. Below, I briefly summarize known family relationships, referencing unique identifiers assigned to individual animals as well as a name for those animals previously collared.

Within the Ashlu drainage and environs (Figure 6-1), M20 has fathered at least seven detected bears with three females, one of which has also successfully bred with M35. Another male, M56 (Keith) bred with F37 to produce two females, one of which is the collared study animal "Phantom" who herself has produced at least three cubs.

In landscapes largely defined by the Callaghan and Ryan drainages, many of the resident grizzly bears are members of a large family of patriarch M33 (Figure 6-2). He apparently has bred with at least nine different females, three of which were his daughters. This has resulted in at least 17 first generation offspring. Although several of these have themselves produced cubs, four of the seven of the apparent third generation bears were themselves fathered by M33. One of the daughters of M33, F89 (Power) did also breed with a separate male, M32 to produce F93 (Callie) who then successfully bred with M57. The male M57 has also been a dominant breeder within the larger Squamish-Lillooet GBPU, breeding with five females (including F93 "Callie" as noted above). In addition, other important breeders have been males M9 and M6, and females F2 and F21 (Figure 6-2).

Within an area roughly defined by the Ryan and Lillooet Valleys, female F81 has contributed significantly to the local population through matings with M33 and M57 (Figure 6-3). Important breeders have also been male M87 and female F259.

Within the southern South Chilcotin Ranges GBPU (south of Carpenter Lake), males M111 and M08 have been quite productive, successfully breeding with at least four and three females respectively (Figure 6-4). Dominant breeding females include F113 and F136. Within the central South Chilcotin Ranges (north of Carpenter Lake), our data suggest there have been at least two dominant breeding males, M114 and M163 (Figure 6-5). Two females, F197 and F213, have also been considerably productive.

Within the Toba-Bute GBPU, we detected bears across three generations that resulted from mating between F351 and M348 (Figure 6-6). Their son, M154, is a dominant breeder, successfully reproducing with at least four females. Male M318 and female F375, among others to a lesser degree, have also been important breeders within that GBPU.

The most complex family relationships that we resolved were within the McGillivray and Stein locales associated with defined genetic groups that are considerably more homozygous than elsewhere (Chapter 5). The root cause for such genetic similarity among animals is understandable considering known family relationships. Within the McGillivray group, much of the population is descended from male M125 (Bob) and female F108 (Jasmine) (Figure 6-7). Of the 15 known third-generation offspring in this family, five are the result of breeding between M125 (Bob) and his daughter F126 (Bernadet). In addition to M125 (Bob), another dominant breeder in the McGillivray locale has been M104 who has known to have successfully bred with five females. Finally, both M133, M105, and F139 have been contributing to population expansion in the McGillivray Range (Figure 6-8), with M105 (Huck) having dispersed from the Stein population (see below).

Finally, it appears that most of the current Stein grizzly bear population is descended from a single female, F406, and one or more undetected males (Figure 6-9). Normally a parent can only be established through a triad (where father is known). However, in this situation, F406 was identified through a historic sample obtained in 1998, and while her relationship as the mother of any given individual is therefore inconclusive, the fact that there is reasonable probability for a mother-offspring pairing with six different individuals (M65, M70 "Cod", M72 "Scud", F73 "Molly", F78, and M105 "Huck") suggests it is highly likely that she is in fact their mother. These offspring have themselves parented all of the known third generation offspring in the Stein population, many of which through breeding between siblings. While six of the eight females that M65 is known to have bred with are not his siblings, it is possible that they are his close cousins considering the low genetic variability in the Stein population. One of the sons of F406 (M105 "Huck") has only been detected north of the well defined Stein population (Stein-Nahatlatch GBPU) and so has presumably dispersed. His offspring are thus Stein hybrids.

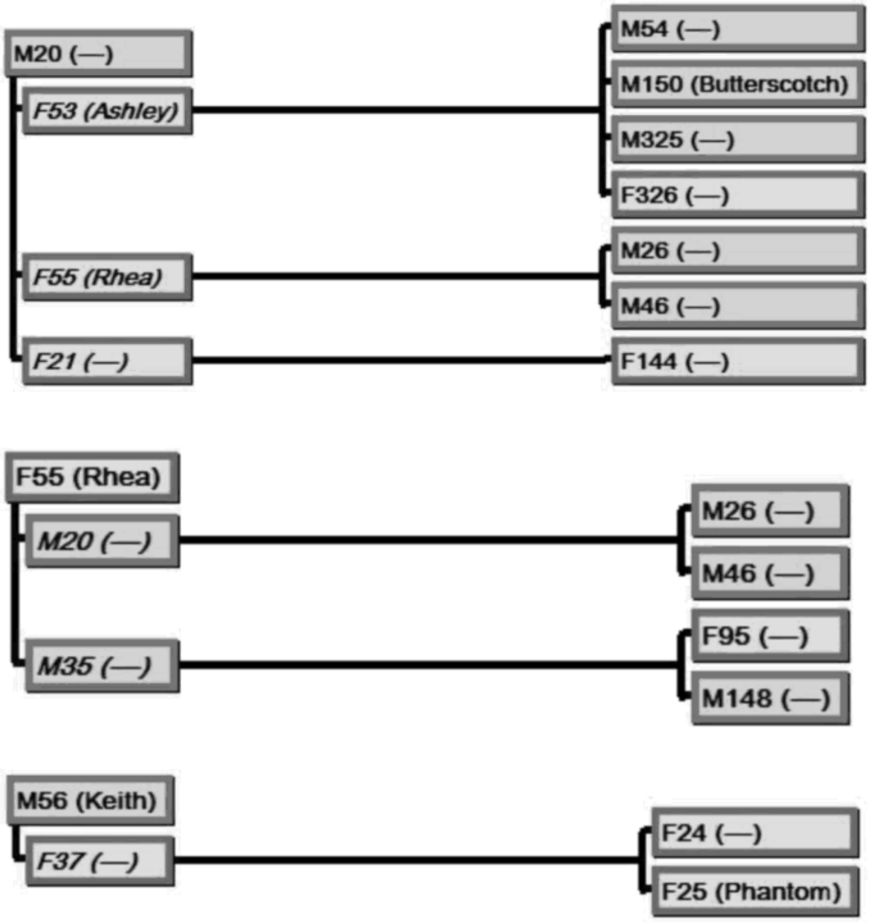

Figure 6-1. Known pedigrees related to dominant breeding grizzly bears detected primarily within the Ashlu drainage, 2004 - 2012.

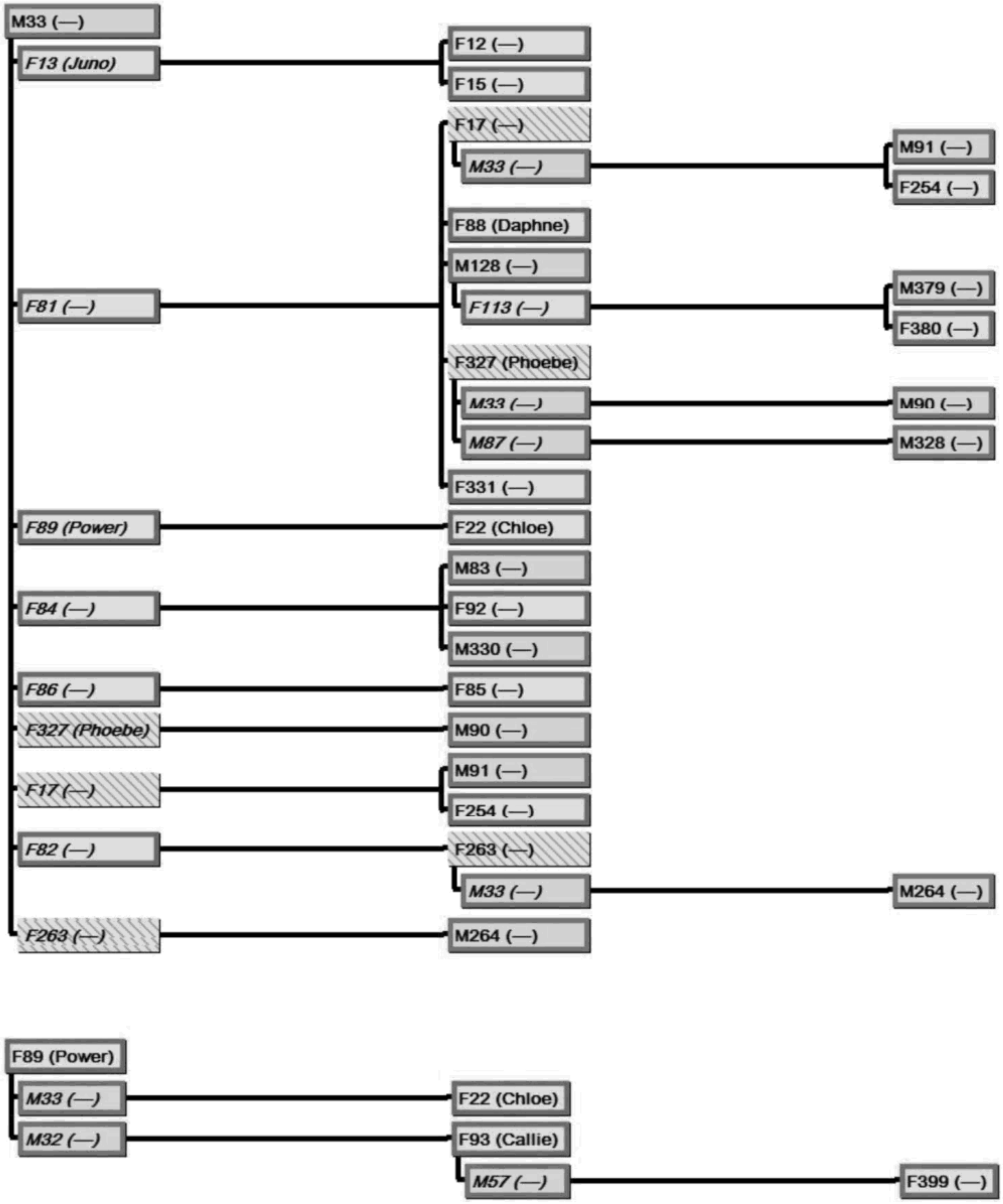

Figure 6-2. Known pedigrees related to dominant breeding grizzly bears detected primarily within the Callaghan and Ryan drainages, 2004 - 2012.

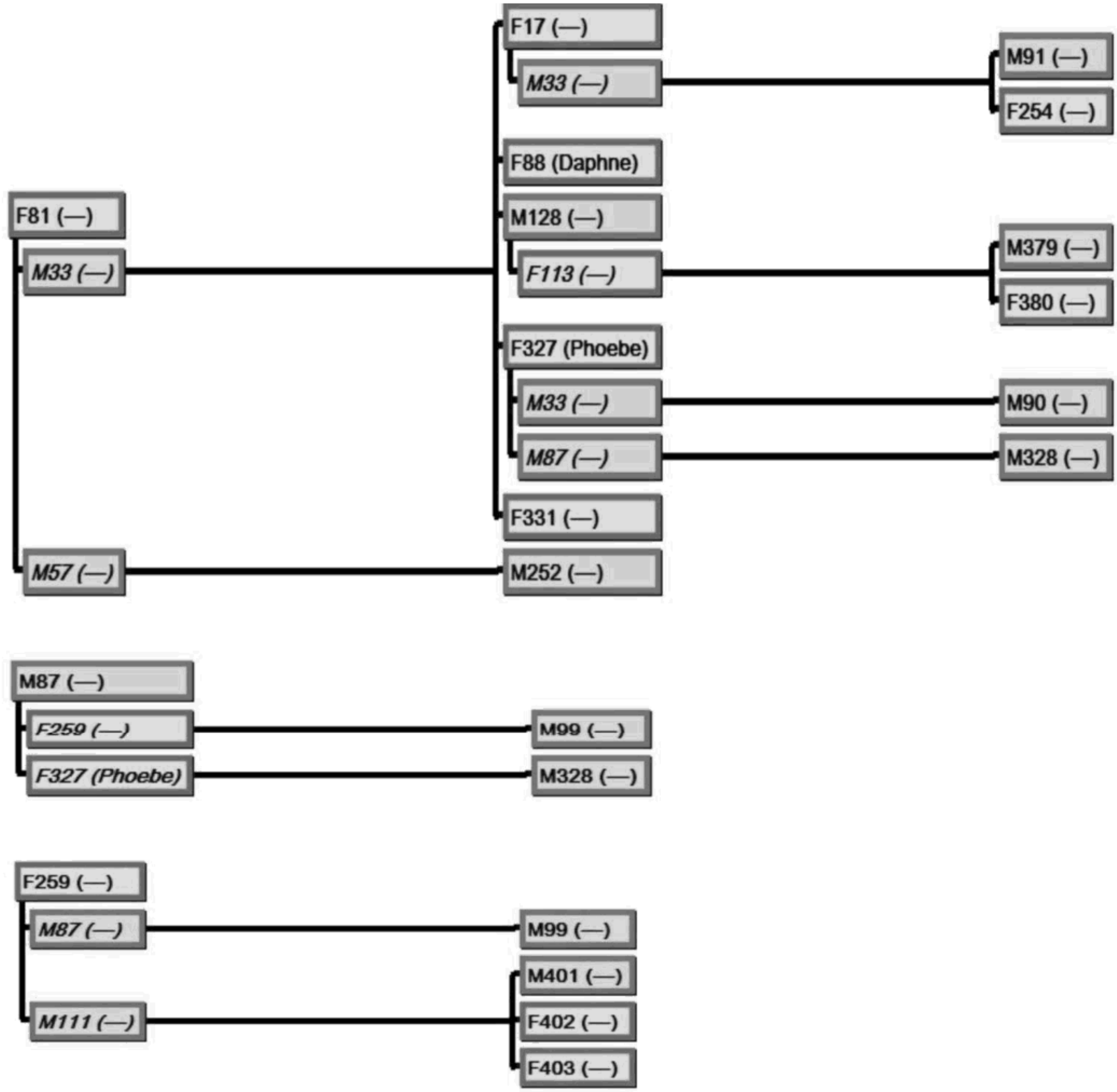

Figure 6-3. Known pedigrees related to dominant breeding grizzly bears detected primarily within the Ryan and Lillooet drainages, 2004 - 2012.

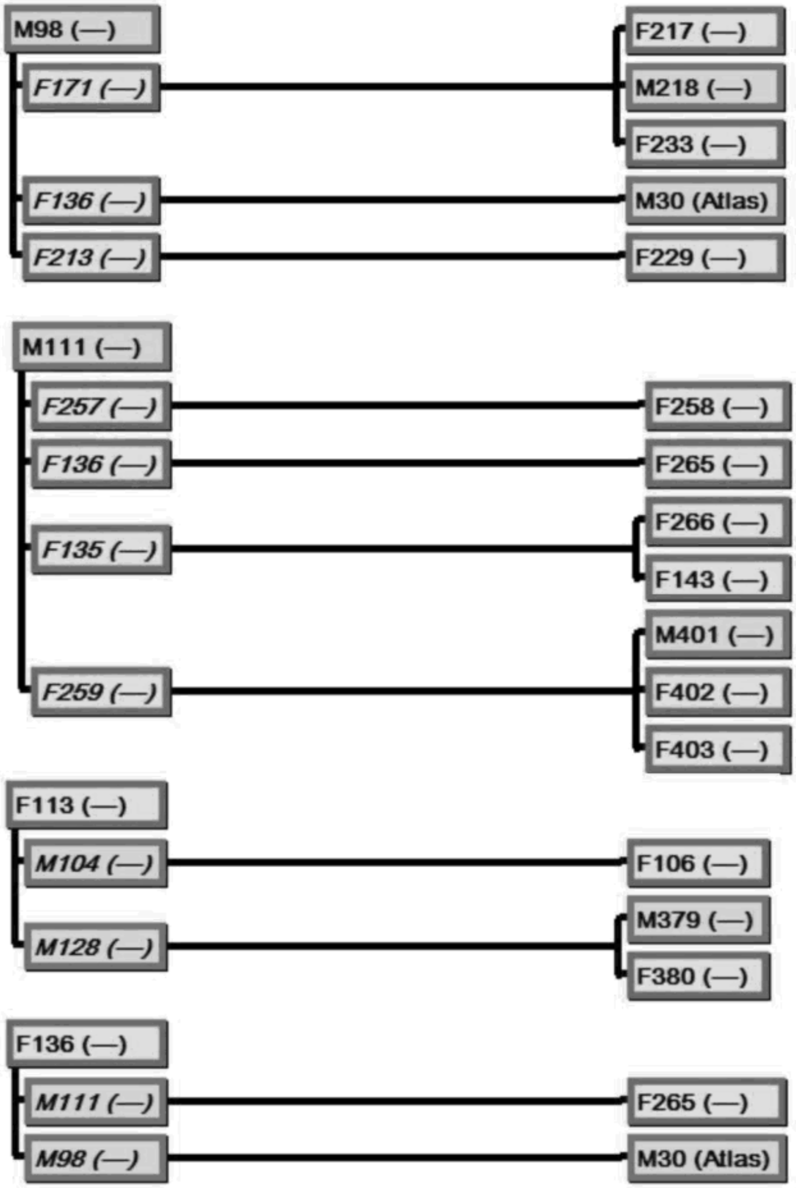

Figure 6-4. Known pedigrees related to dominant breeding grizzly bears detected primarily within the southern South Chilcotin Ranges GBPU, 2004 - 2012.

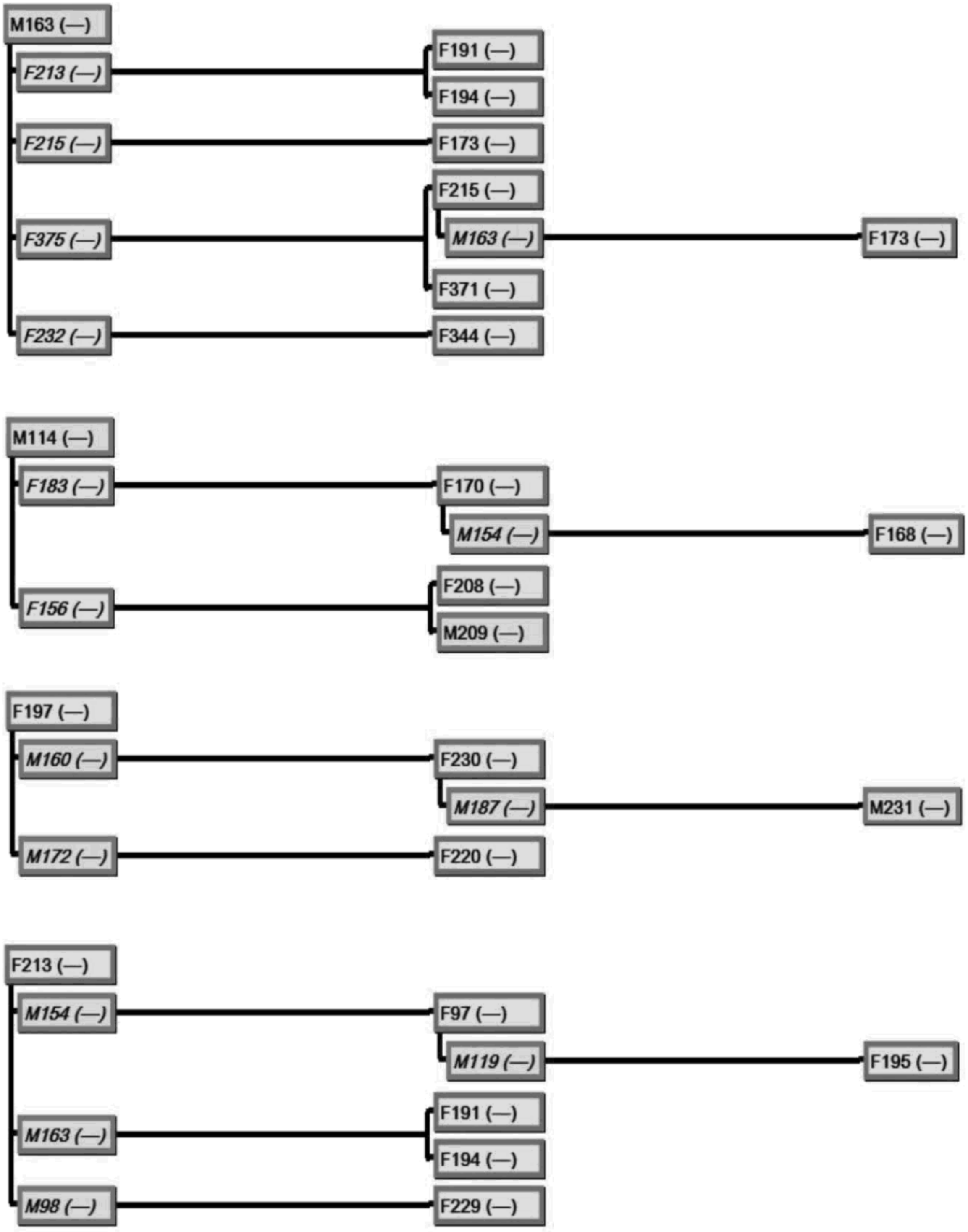

Figure 6-5. Known pedigrees related to dominant breeding grizzly bears detected primarily within the central South Chilcotin Ranges GBPU, 2004 - 2012.

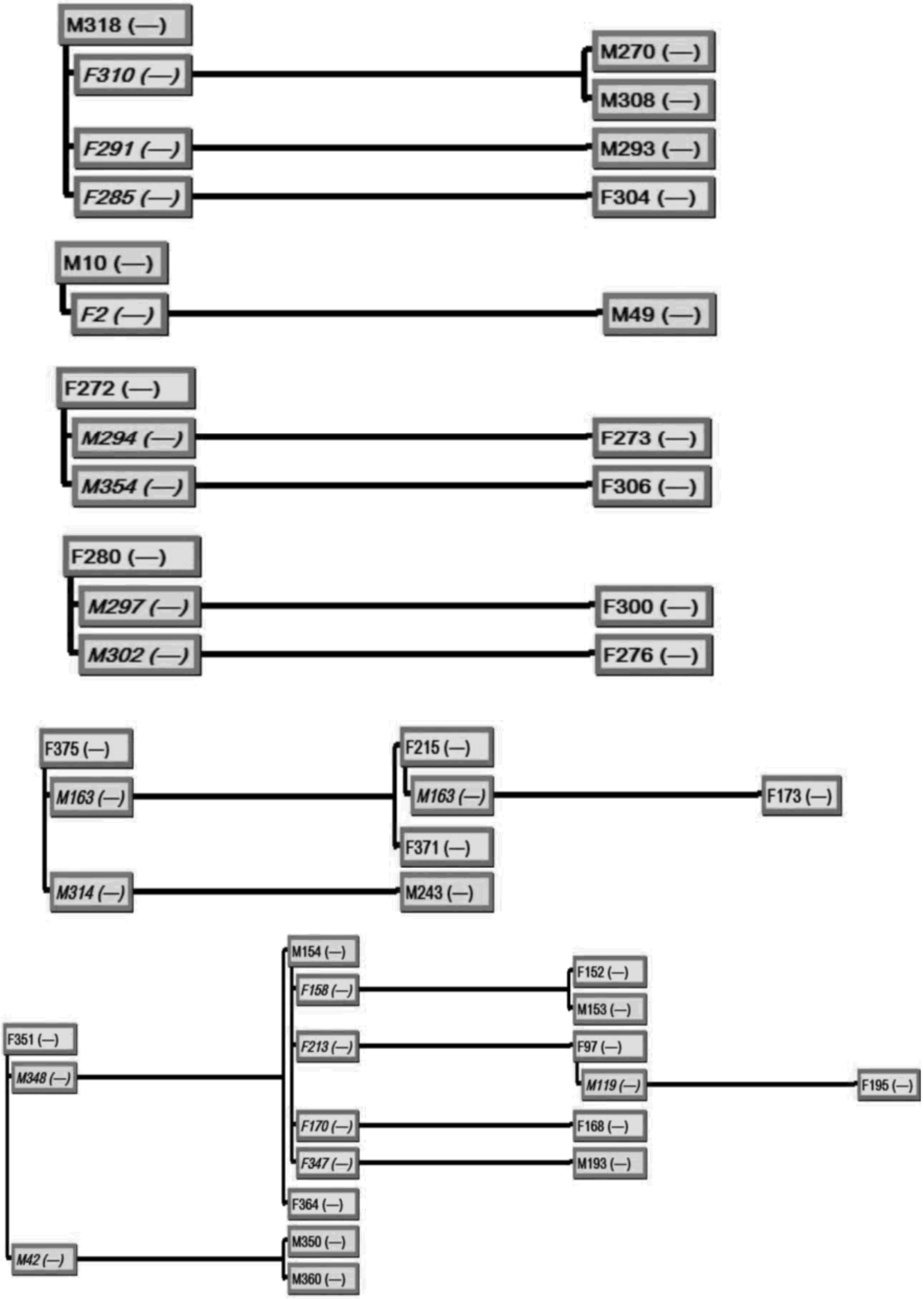

Figure 6-6. Known pedigrees related to dominant breeding grizzly bears detected primarily within the Toba-Bute GBPU, 2004 - 2012.

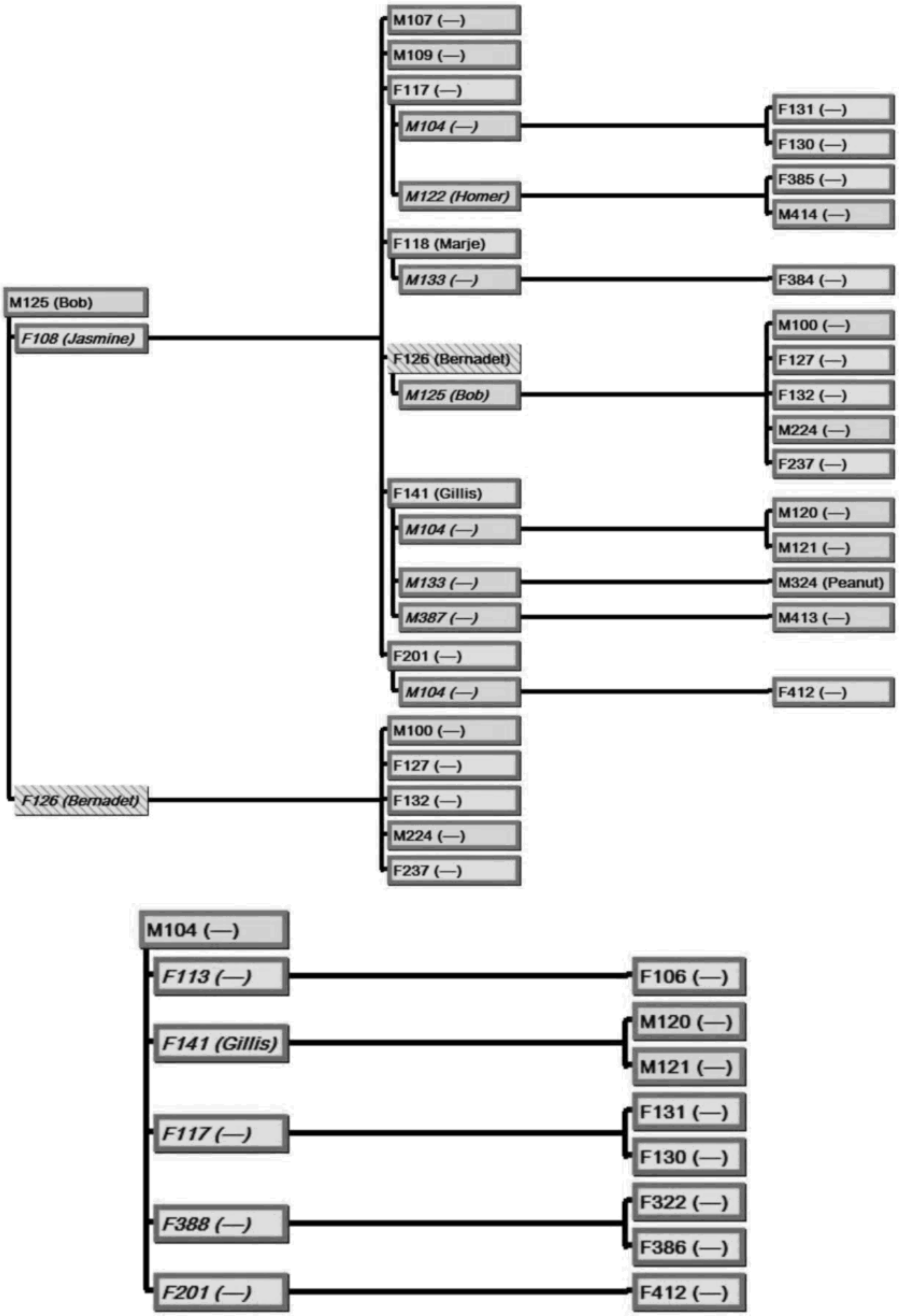

Figure 6-7. Known pedigrees related to dominant breeding grizzly bears M125 and M104 detected primarily within the McGillivray Ranges of the southern South Chilcotin Ranges GBPU,, 2004 - 2012.

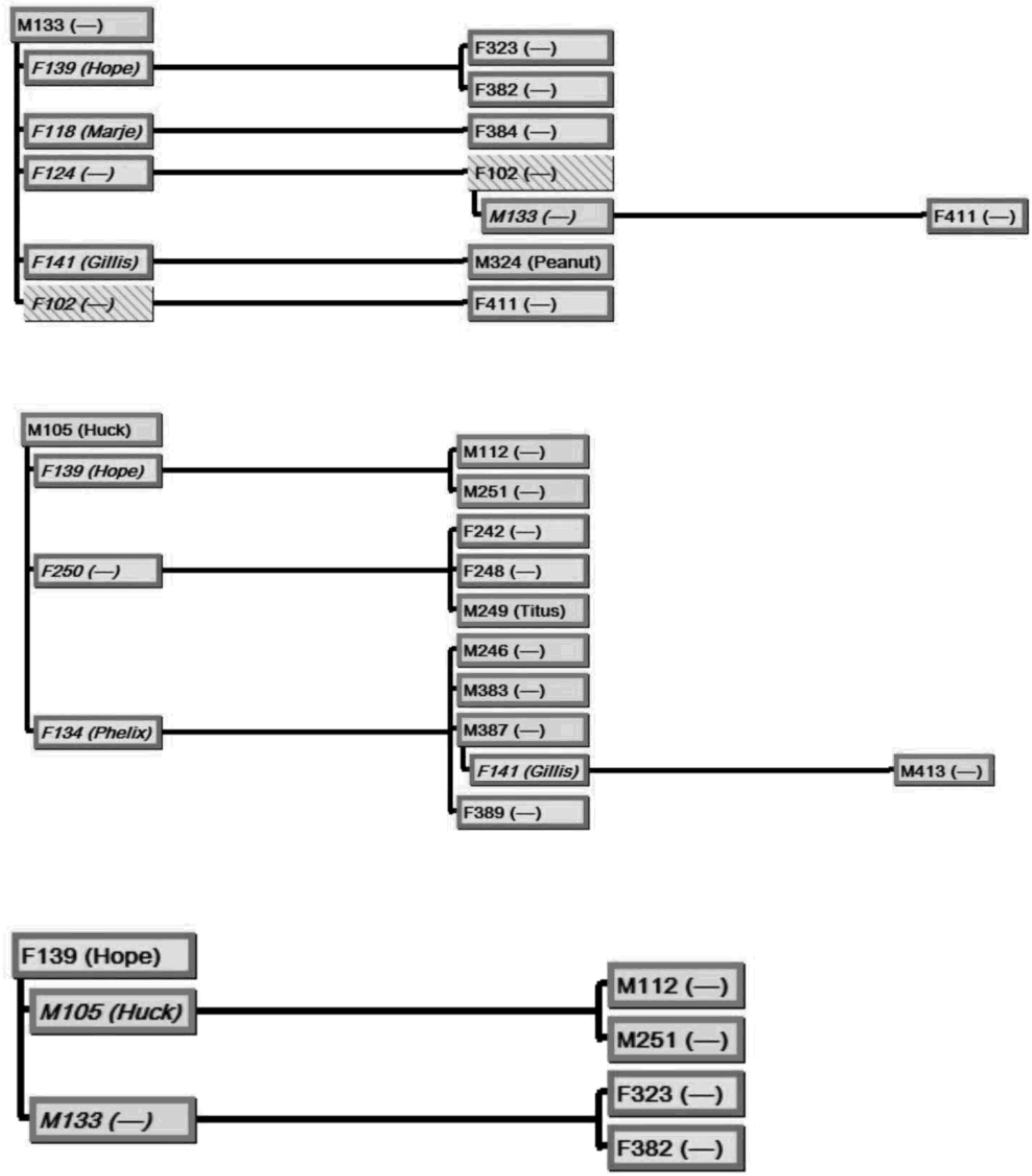

Figure 6-8. Known pedigrees related to select dominant breeding grizzly bears M133, M105 and F139, detected primarily within the McGillivray Ranges of the southern South Chilcotin Ranges GBPU, 2004 - 2012.

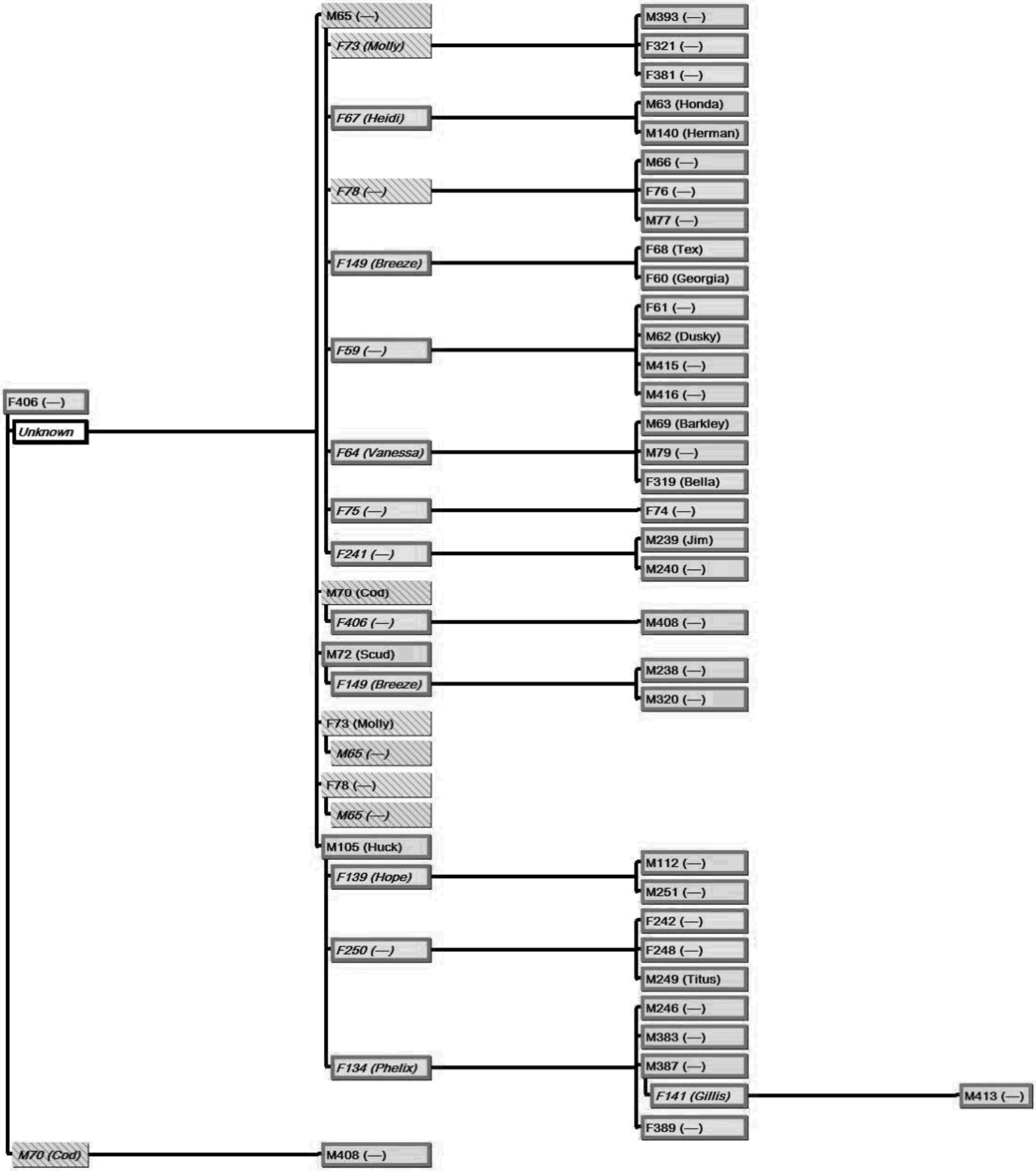

Figure 6-9. Known pedigrees related to dominant breeding grizzly bears detected within the "Stein Population" (Stein-Nahatlatch GBPU), southern Coast Ranges, British Columbia, 2004 - 2012.

Known Migration/Dispersal Events

Observed geographic patterns of genetic structuring among grizzly bears across the southern Coast Ranges do not correspond to GBPU boundaries, with the exception of the Stein population (situated exclusively within the northern portion of the Stein-Nahatlatch GBPU). Since the identification of putative migration requires the delineation of geographically discrete areas, I focus only on the Stein and McGillivray populations that can be quite clearly defined spatially based on present genetic structuring (Chapter 5). There are three known migration events specific to these populations for which there are no known records of human-assisted translocation. One female has emigrated to the Stein population (Stein-Nahatlatch GBPU). This female (F241) does not assign genetically to the Stein nor any other population cluster within the south Coast region and I speculate that she dispersed from east of the Fraser River. She successfully mated with male M65 producing two hybrid Stein offspring (M239, M240). One Stein male (M105; a.k.a., CM17 "Huck" from Squamish collaring project) has successfully dispersed to the southern portion of the South Chicotin Ranges GBPU including landscapes in associated with the McGillivray population group and has produced nine hybrid Stein offspring (M246, M249, M251, M383, M287, F242, F248, F389) with three McGillivray females (F134, F139, F250). One of these offspring (M249) is CM16 "Titus" from the Squamish collaring project who is known to range into the Ryan and Rutherford drainages. McGillivray females F117 and F141 (siblings) also successfully bred with a known male (M104) and an undetermined male both with neither McGillivray nor Stein ancestry, producing six 50% McGillivray hybrid offspring.

One very clear and interesting result from this current iteration of the grizzly bear parentage analysis across the south Coast Ranges is that, at least in some localized areas, many if not most bears are fathered by very few males. Specifically, Stein male M65 has fathered at least 18 offspring with eight females. Since these are concluded only from triads where the offspring and both parents are identified, it is quite possible that more offspring of this male existed during the period over which samples have been collected. The Stein emigrant to the McGillivray population (M105) produced at least nine offspring with at least three females. McGillivray male M125 (a.k.a, "Bob" from Lillooet collaring study) produced at least 12 offspring with two McGillivray females. In the Ryan/Callaghan/Squamish area, male M33 produced at least 17 offspring with nine females (including one that is likely also his daughter). While the above examples do not represent all of the known family relationships within the dataset, paternity is definitely skewed, at least in the southern landscapes occupied by grizzly bears within the larger region, a pattern that is likely indicative of a population undergoing expansion and recovery.

Chapter 7

GENERALIZED VARIATION & INFERENCES OF GRIZZLY BEAR DIET ACROSS THE SOUTHERN COAST RANGES

INTRODUCTION

The grizzly bear is adapted to a wide range of environmental conditions and potential foods (LeFranc et al. 1987, Schwartz et al. 2003). The ~50,000 km^2 of our greater regional study area encompasses tremendous variation in ecosystems as well as current and historic human activities across the southern Coast Ranges. These conditions potentially determine the availability of foods and also the accessibility of such foods in light of behavioral and population responses of bears to people. Understanding patterns of dietary variation among grizzly bears across the region may better highlight local foraging strategies and differences between sex that are useful in conservation planning and environmental assessment. Such variation may also help to explain forces that facilitate or hinder population connectivity as indicated by movements and genetic structuring (Chapter 5).

Dietary Inferences from Stable-Isotope Analyses of Hair

There are few options to effectively and systematically sample grizzly bear diet over such a huge regional area as addressed in this spatially extensive population study. Tied to the hair-snag sampling methods applied to detect individuals, the most promising approach to address dietary variation among grizzly bears across the southern Coast Ranges is the analysis of stable isotopes of assimilated nutrients within guard hairs of snagged samples. Stable isotope analysis is a well-established method for evaluating animal diets, and there are several examples of its application to infer the relative trophic positions of bears and their use of plants, terrestrial meat, and anadromous salmon in western North America (Hilderbrand et al. 1996, 1999; Jacoby et al. 1999, Hobson et al. 2000, Felicetti et al. 2003, Mowat & Heard 2006).

The methods, utility and limitations of stable-isotope analysis as applied in animal research are well-described elsewhere (Jianzhu et al. 2004, Ben-David & Flaherty 2012). Briefly, many elements of the same proton number vary in their neutron number and thus atomic weight and are either stable or not (radio-active). Rare stable isotopes of a given element occur naturally in specific ratios with their common isotope counterparts. These ratios change as the element moves through natural processes, known as "fractionation". Fractionation is expressed as the difference in ratio (δ) of a given stable isotope relative to a universally accepted environmental standard. The isotope ratios typically applied in wildlife diet studies are those of ^{13}C:^{12}C, ^{15}N:^{14}N, and ^{34}S:^{33}S. These isotope ratios are measured by a mass spectrometer which ignites a given sample and measures the ratio of heavy to light ions within the resultant gas.

Depending on the element, specific isotope ratios can be generally indicative of certain food types pertaining to trophic level. However, only broad generalizations are typically possible (e.g., vegetation, terrestrial meat or anadromous salmon). Marine-derived nutrients are apparently associated with distinct $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ signatures (Hilderbrand et al. 1999). Signatures of $\delta^{15}N$ are apparently indicative of trophic level, while $\delta^{13}C$ can be helpful in identifying source though relationships can be complex (Jacoby et al. 1999, Kelly 2000, Ben-David & Flaherty 2012). In the diet of bears, $\delta^{13}C$ may also indicate anthropogenic food items such as garbage (Hobson et al. 2000). Inferring higher levels of diet specificity is only possible where an individual food item exhibits a unique isotopic signature relative to other foods within the same environment. For example, whitebark pine nuts apparently have distinct sulphur signatures (Felcetti et al. 2003), while marine-derived nutrients such as salmon can result in significantly higher values for $\delta^{13}C$ and $\delta^{15}N$ (Hilderbrand et al. 1999). In discriminating the aforementioned food types, stable-isotope mixing models are applied to estimate the proportional contribution among sources with distinctive isotopic signatures. Required are the tissue/hair isotope ratios from the consumer, values from the food sources, and a discrimination factor that is specific to the tissue being analyzed. These models assume that the ratio of heavier isotopes (more protons) increase as elements move through trophic levels, and that the isotope ratio of the consumer is a linear combination of those from its diet. In applying mixing models, dietary composition of only n+1 nutrient sources can be estimated where "n" stable-isotopes are evaluated (Ben-David & Flaherty 2012). Where estimation is required for potential contributions from multiple nutrient sources, a probabilistic modeling approach may be possible (Phillips & Gregg 2003, Phillips et al. 2005).

Potentially important foods for grizzly bears across the southern Coast Ranges

Spawning anadromous salmon are a protein source of great potential importance to grizzly bears (Hilderbrand et al. 1999). However, a suite of scale-dependent factors may influence the availability of salmon to individual bears. Hence, the degree to which salmon are used and important in the life history of grizzly bears among landscapes of the southern Coast Ranges is highly uncertain. Estimating the use of salmon by grizzly bears across the diverse ecological and human conditions of our regional study area may allow testing of specific hypotheses. Particularly important factors may pertain to the distance to predictable locations of catchable salmon, associated abundance of salmon, and barriers to the movement by grizzly bears to such sites. Intra-specific relationships may also function, with females (and perhaps other subordinates) avoiding localized fishing sites to minimize risk and infanticide from interaction with large and potentially aggressive males (Ben-David et al. 2004) but with human activity mediating such interference (Nevin & Gilbert 2005a,b). Under natural circumstances, males may be more likely to benefit from salmon given their physically competitive advantage over females and their (related) observed propensity to travel long distances to predictable and productive fishing sites.

Sources of terrestrial meat protein for bears are also likely to vary across our study area. Moose (*Alces alces*) may be of considerable value where available to bears (Ballard 1992) and are more abundant on the Chicotin Plateau in the north/northeast of the study area (Shackleton 1999). Mountain goats are also reasonably widespread and there is anecdotal evidence to suggest they are occasionally hunted by grizzly bears. A reintroduced elk (*Cervus elaphus*) population is associated with some coastal watersheds (D. Reynolds, FLNRO, *pers. comm.*). Adult male grizzly bears can be expected to benefit disproportionately from ungulates considering that (1) they can be 1.2 - 2.2 times larger than adult females (Schwartz et al. 2003), (2) they are not hindered by the mobility and the energetic and security needs of dependent cubs, and (3) they are less vulnerable to interference from other bears at ungulate kill or scavenging sites. In addition to ungulates, the hoary marmot (*Marmota caligata*) occurs throughout much of the study area and appears to be a reasonably important food item to grizzly bears in at least one local area (McLellan 2007). There is presently no basis to expect differential use of marmots between male and female grizzly bears.

In addition to meat protein sources, there is available to grizzly bears a plethora of plant foods across the regional study area. These include, for example, cow parsnip (*Heracleum lanatum*), glacier lily (*Erythronium grandiflorum*), skunk cabbage (*Symplocarpus foetidus*), horsetail (*Equisetum* spp.), sedges (*Carex* spp.), nuts of whitebark pine (*Pinus albicaulis*), and a variety of fruiting shrubs such as huckleberry (*Vaccinium membranaceum*), buffaloberry (*Sheperdia canadensis*), saskatoon berry (*Amelanchier alnifolia*) and salmon berry (*Rubus spectabilis*) Undoubtedly, all grizzly bears make use of plant foods at least opportunistically in different seasons. But the importance plant foods may depend on availability of and access to meat protein, as well as seasonal and habitat factors influencing the distribution, concentration and nutritional value of such foods to bears.

Objectives

In this chapter, we present an exploratory analysis of variation in δ^{13}C, δ^{15}N, and δ^{34}S stable isotope measurements within hair samples from individual grizzly bears detected across the southern Coast Ranges study area to date. Of particular interest is apparent dietary variation across regional landscapes and differences between sympatric males and females. Results may illuminate grizzly bear foraging and life history strategies, their ecotypic variability across the region, and the potential influence of ecological and human factors. Such understanding may help to explain regional patterns of population abundance, distribution and connectivity, in addition to movements and habitat associations of genetically-tagged and GPS-collared study animals. In this context, our results will ultimately inform conservation planning as well as impact assessment and mitigation. At present, this chapter should be considered preliminary given that dietary inferences are informed only by isotope values for bear foods as sampled elsewhere, and samples for certain bears may require re-analysis (see Discussion).

METHODS

Sampling and Laboratory Work

We sampled grizzly bear occurrence throughout the 41,250 km^2 southern Coast Ranges regional study area using hair-snag/DNA detection sampling consistent with established methods (Chapter 2). From each individual bear detected, we selected a single sample with long guard hairs that was considered appropriate for isotope analyses. Laboratory work was carried out by the Stable Isotope Core Laboratory of Washington State University (WSU) under the direction of Benjamin Harlow. From each submitted sample, the lab selected two guard hairs with a range of material appropriate for the mass spectrometer. The entire hair-shaft was used, which we assume represents a dietary average during the active season of May - October when bear hair is expected to grow (Hobson et al. 2000). Samples were cleaned and washed in a chloroform/methanol solution, then dried and ground to a power in liquid nitrogen. Analyses for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ isotopic signatures were subsequently carried out (Appendix 6-1). For a smaller subsample of female grizzly bears, analyses for ^{13}C and ^{15}N had been previously completed at the Okanagan Regional Chemical Analysis Centre of the University of British Columbia under the direction of David Arkinstall. For consistency, guard hairs from these same samples were analyzed again at the Washington lab.

Exploring & Assessing Dietary Variation

Once our database was built, we evaluated bivariate relationships in the measured ratios among the stable isotopes considered by way of Pearson correlation coefficients. The isotope signatures considered in analyses of bear diet are generally correlated (Hobson et al. 2000, Mowat & Heard 2006) and deviations may indicate a unique diet.

We next described the dietary variation among grizzly bears across landscapes of the southern Coast Ranges as indicated by stable isotope measurements within hair samples. For each of the three isotopes considered, we calculated the mean value among sex-specific detections at each unique sampling site. For each sex, we then spatially interpolated these values with weightings that reflect the detection sample per site.

We evaluated differences in mean isotope values among specifically-defined geographic areas. Areas were subjectively delineated based on a combination of ecosystem variation and our knowledge of past and/or existing constraints to grizzly bear population distribution and connectivity (Chapters 4 & 5), using major landscape features (Figure 6-1). These areas are described as follows: (1) Chilcotin area north of Carpenter Lake, (2) Stein drainage and environs north of the Nahatlatch River, (3) eastern portion of the Squamish-Lillooet GBPU, east of the Squamish River, (4) coastal drainages, (5) Boulder-McParlon drainages south of Carpenter Lake and west of the Hurley River, and (6) McGillivray drainage and environs east of the Hurley River. Most bears occurred exclusively within a single area; those individuals that did not were assigned to a single area in which they spent the most time as estimated from our sampling data. We compared measured values for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ on the basis of these geographic areas using multivariate analysis of variance (MANOVA) and Bonferroni-adjusted confidence intervals while testing for interaction with sex.

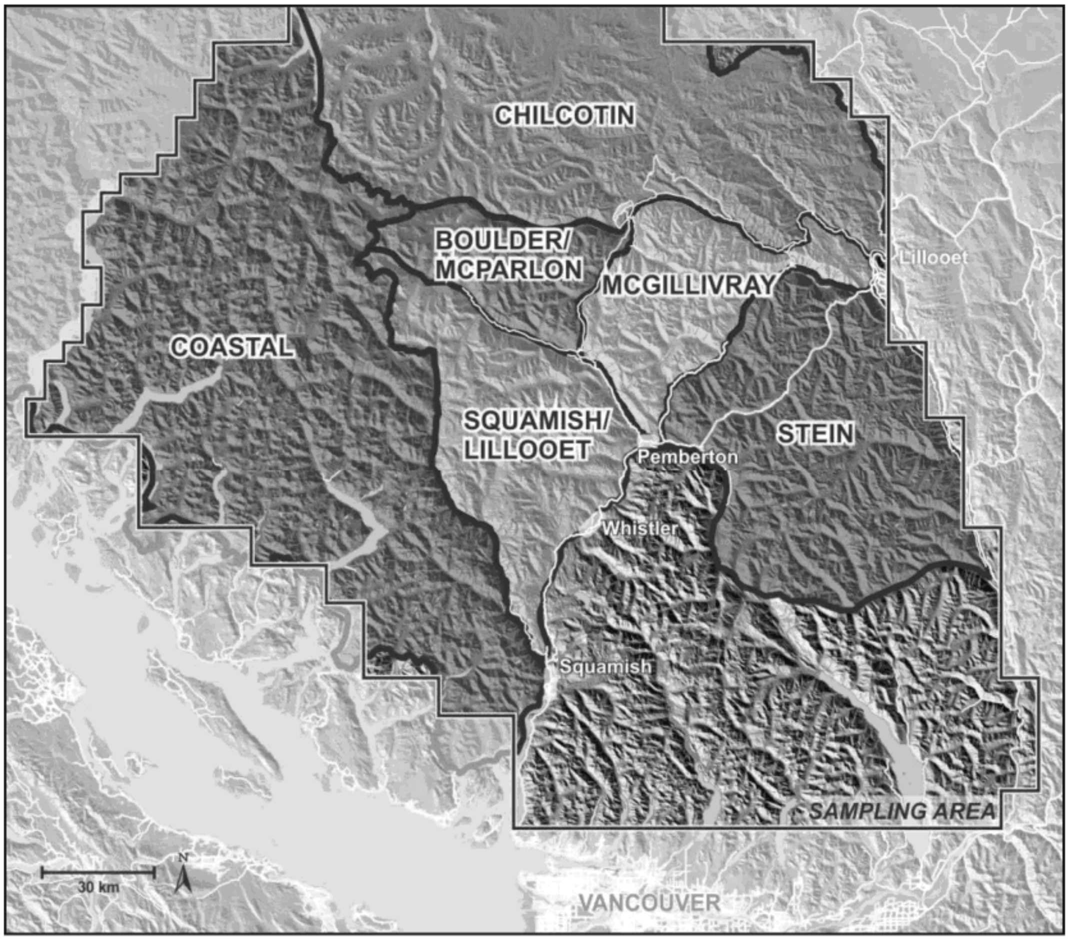

Figure 7-1. Geographic stratification for evaluating grizzly bear dietary variation based on stable isotope anlayses of hair samples across the southern Coast Ranges, southwestern British Columbia, 2004 - 2010.

For this exploratory analysis, we did not yet have isotope ratios as measured from potential grizzly bear foods gathered from across the regional study area. To infer dietary representation, we therefore relied on mean isotope ratios measured for bear foods elsewhere across British Columbia, with fractionation-adjusted estimates for $\delta^{13}C$, $\delta^{15}N$ derived from Mowat and Heard (2006) and those of $\delta^{34}S$ obtained from RTEC (2006). These figures constituted the isotope endpoints used to calculate diet proportions among three generalized food classes: (1) terrestrial meat, (2) anadromous salmon or other marine sources, and (3) plant foods (Table 7-1). Among these three classes, we obtained preliminary estimates of dietary proportions using a single isotope mixing model (Phillips & Gregg 2001) and we compared diet classes in a pair-wise fashion for each stable isotope. A final combined estimate of dietary proportion for each food class was based on the average of respective estimates among the three stable isotopes, weighted by the inverse of precision for each individual estimate[7]. On this basis, we evaluated dietary variation in a qualitative manner based on spatially interpolated isotopic ratios, and in a quantitative manner based on sample mean and standard deviations among specifically defined geographic areas described above.

Table 7-1. Mean isotopic ratios representing isotopic endpoints among generalized grizzly bear food classes with correction for trophic fractionation. Figures are from Mowat & Heard (2006) for $\delta^{13}C$ and $\delta^{15}N$, and from RTEC (2006) for $\delta^{34}S$.

Generalized Food Class	$\Delta^{13}C$	$\Delta\delta^{13}C$	SD	*n*	$\Delta^{15}N$	$\Delta\delta^{15}N$	SD	*n*	$\delta^{34}S$	SD	*n*
Terrestrial Meat	-24.8	-22.8	1	107	2.5	6.5	1	107	0.6	4.5	31
Salmon	-19.9	-18.9	1	338	12.5	15.2	1	338	19.1	0.5	21
Plant	-26.6	-24.6	2	200	-2.8	2.8	3	200	-2	4.2	44

RESULTS

Of 389 individual grizzly bears genetically identified from across the south Coast Ranges to March 2012, 327 had samples we judged as appropriate for isotope analyses. For these individuals, 478 samples were sent to the WSU lab for analyses. Duplicate samples were sent for 15 individuals. For these individuals, I averaged results between duplicate samples. for $\delta^{13}C$ and $\delta^{15}N$, seven samples contained no or insufficient material for reliable detection. For $\delta^{34}S$, five samples resulted in a high error of standards, five did not result in bracketing standards due to machine error , and 18 samples contained no or insufficient material for reliable detection.

Among hair samples from grizzly bears detected across the southern Coast Ranges, there were significant ($P < 0.001$) correlations among isotopic measurements (Figure 7-2). The correlation was particularly strong ($r = 0.91$) between $\delta^{13}C$ and $\delta^{15}N$ though this relationship did not hold for a large number of bears characterized by moderate to high $\delta^{13}C$ but little apparent change in $\delta^{15}N$. Correlations of both $\delta^{13}C$ and $\delta^{15}N$ with $\delta^{34}S$ were lower and were largely driven by samples with higher values of $\delta^{34}S$ and both $\delta^{13}C$ and $\delta^{15}N$.

Qualitatively, mean isotopic ratios for each element varied among landscapes across the regional study area, with apparent spatial trends (Figures 7-3 to 7-6). The $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values did vary among defined geographic areas and coincidentally between sex (MANOVA, Wilk's $\lambda = 0.920$, $F_{[15]}$ =

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[7] This analysis is being reserved until we have better information locally-relevant isotopic end-points for relevant diet classes.

2.53, *P* = 0.001). For all three isotopes, males were consistently enriched and especially so within coastal drainages, while both males and females were enriched within coastal drainages relative to other landscapes (Figure 7-7). The difference between sex appears to be greater for $\delta^{15}N$ and $\delta^{34}S$ than for $\delta^{13}C$. For $\delta^{34}S$, additional variation was also notable among landscapes, with the Stein and McGillivray areas being depleted relative to most other areas.

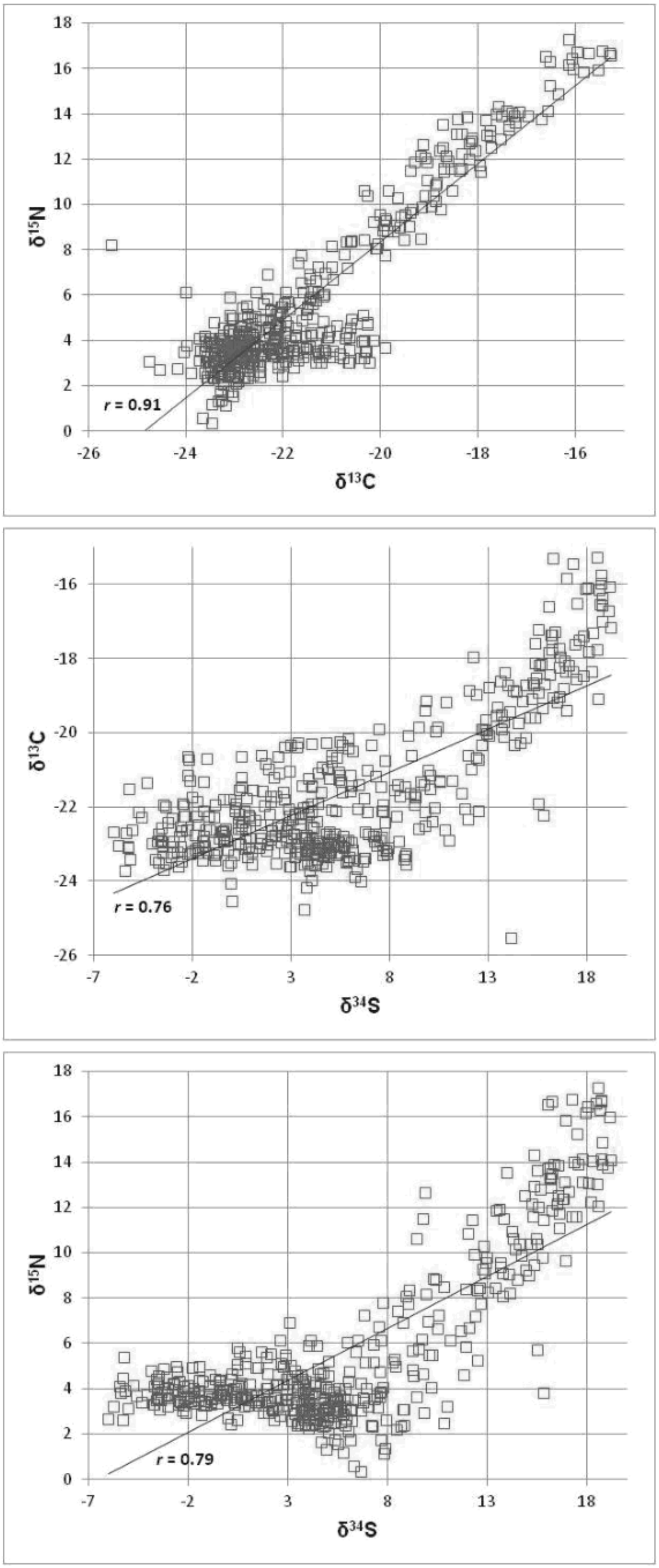

Figure 7-2. Bivariate relationships among $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ isotopic measurements from hair samples of grizzly bears detected across the southern Coast Ranges, southwestern British Columbia, 2004 - 2010.

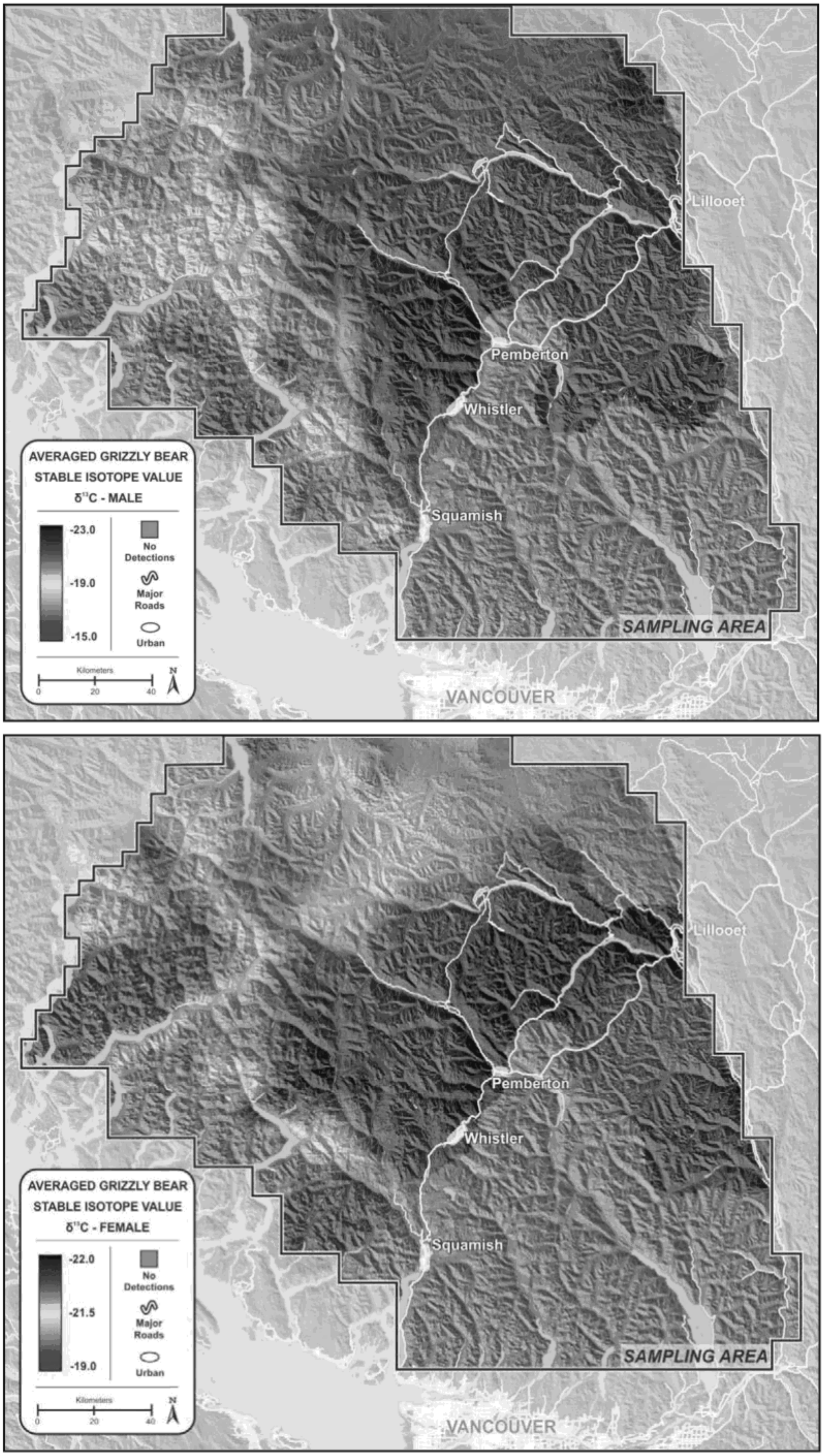

Figure 7-3. Landscape variation in isotopic measurements of δ^{13}C in hair of male (top) and female (bottom) grizzly bears sampled across the southern Coast Ranges, southwestern British Columbia, 2004 - 2010.

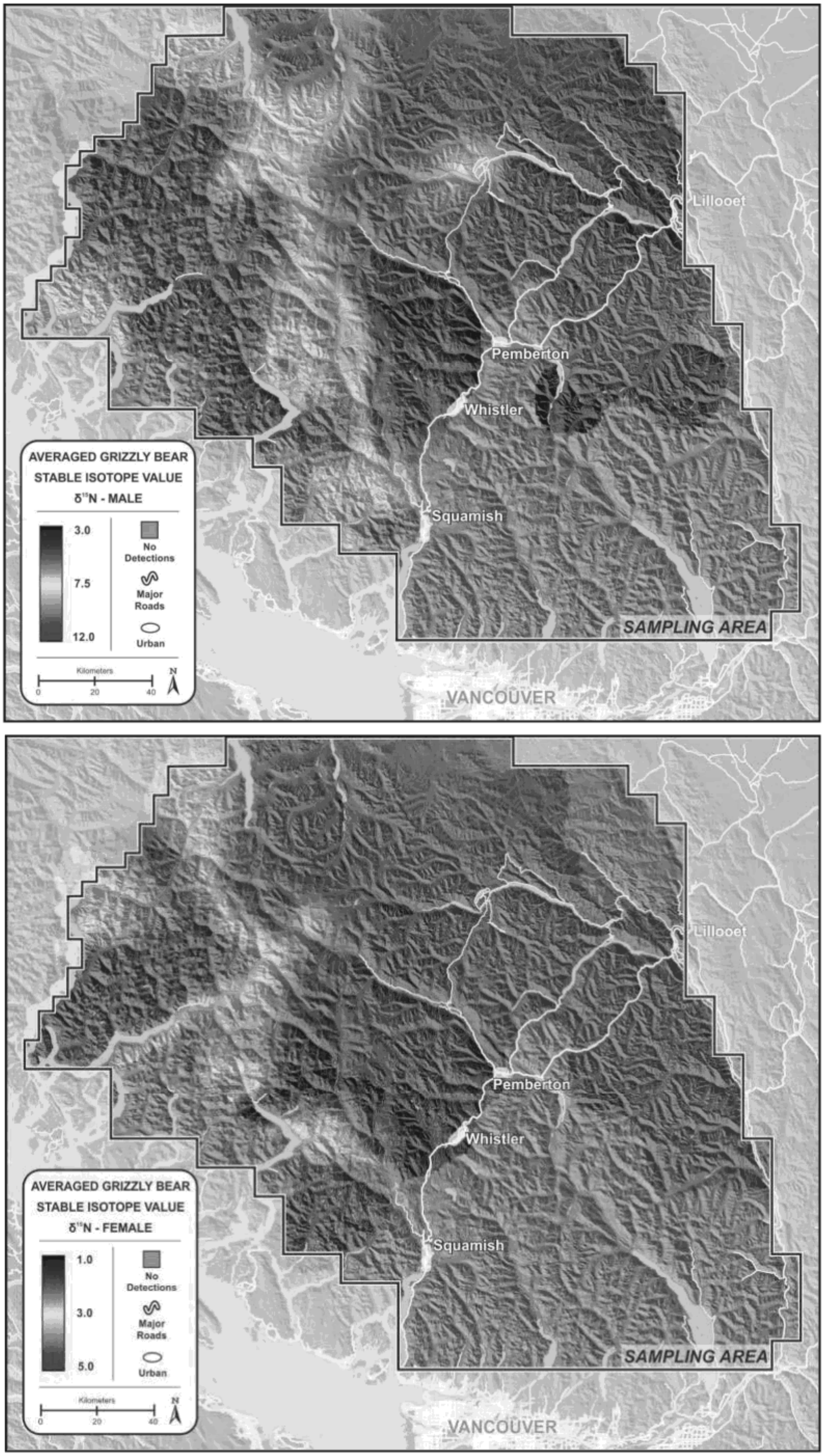

Figure 7-4. Landscape variation in isotopic measurements of $\delta^{15}N$ in hair of male (top) and female (bottom) grizzly bears sampled across the southern Coast Ranges, southwestern British Columbia, 2004 - 2010.

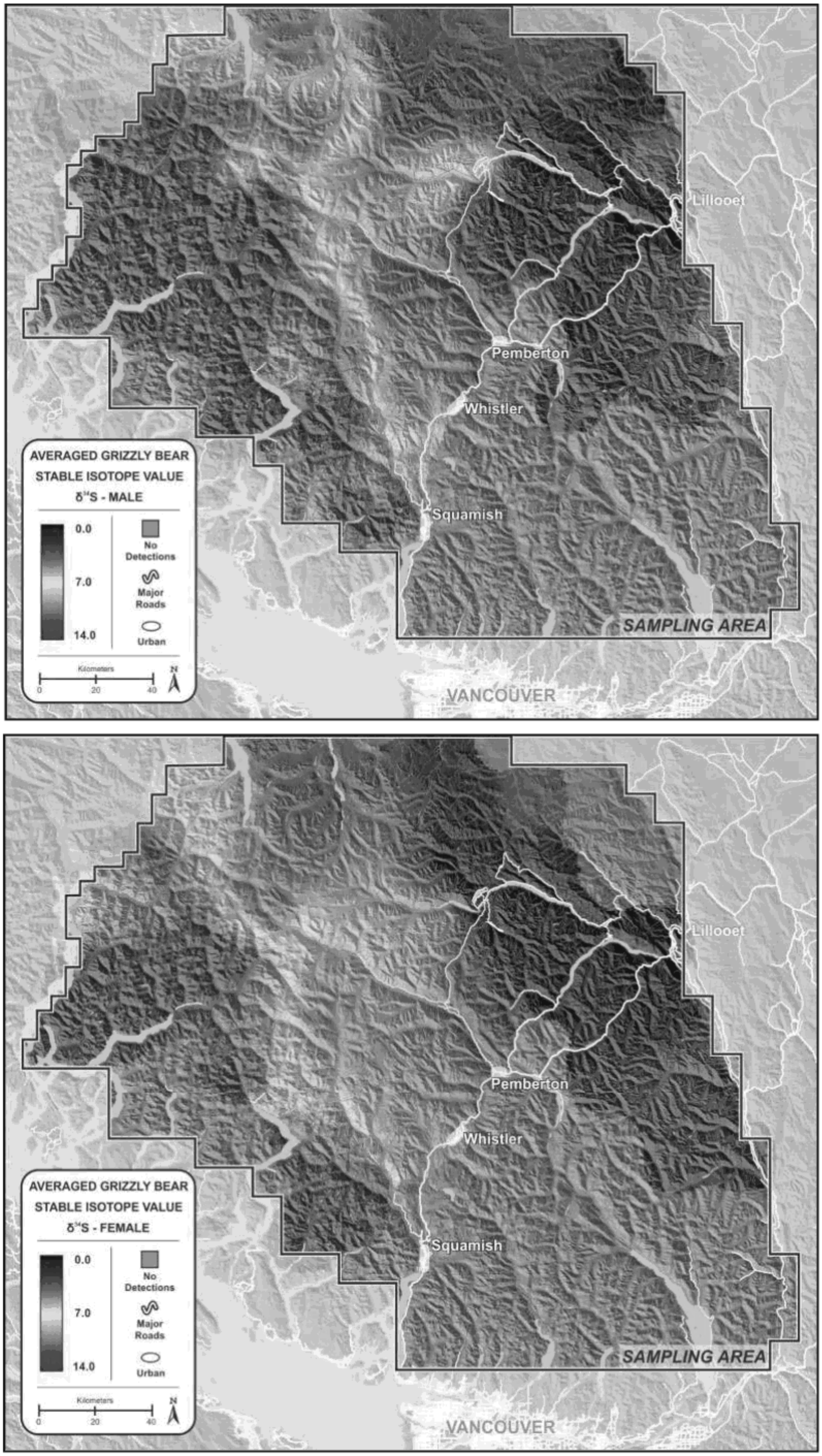

Figure 7-5. Landscape variation in isotopic measurements of $\delta^{34}S$ in hair of male (top) and female (bottom) grizzly bears sampled across the southern Coast Ranges, southwestern British Columbia, 2004 - 2010.

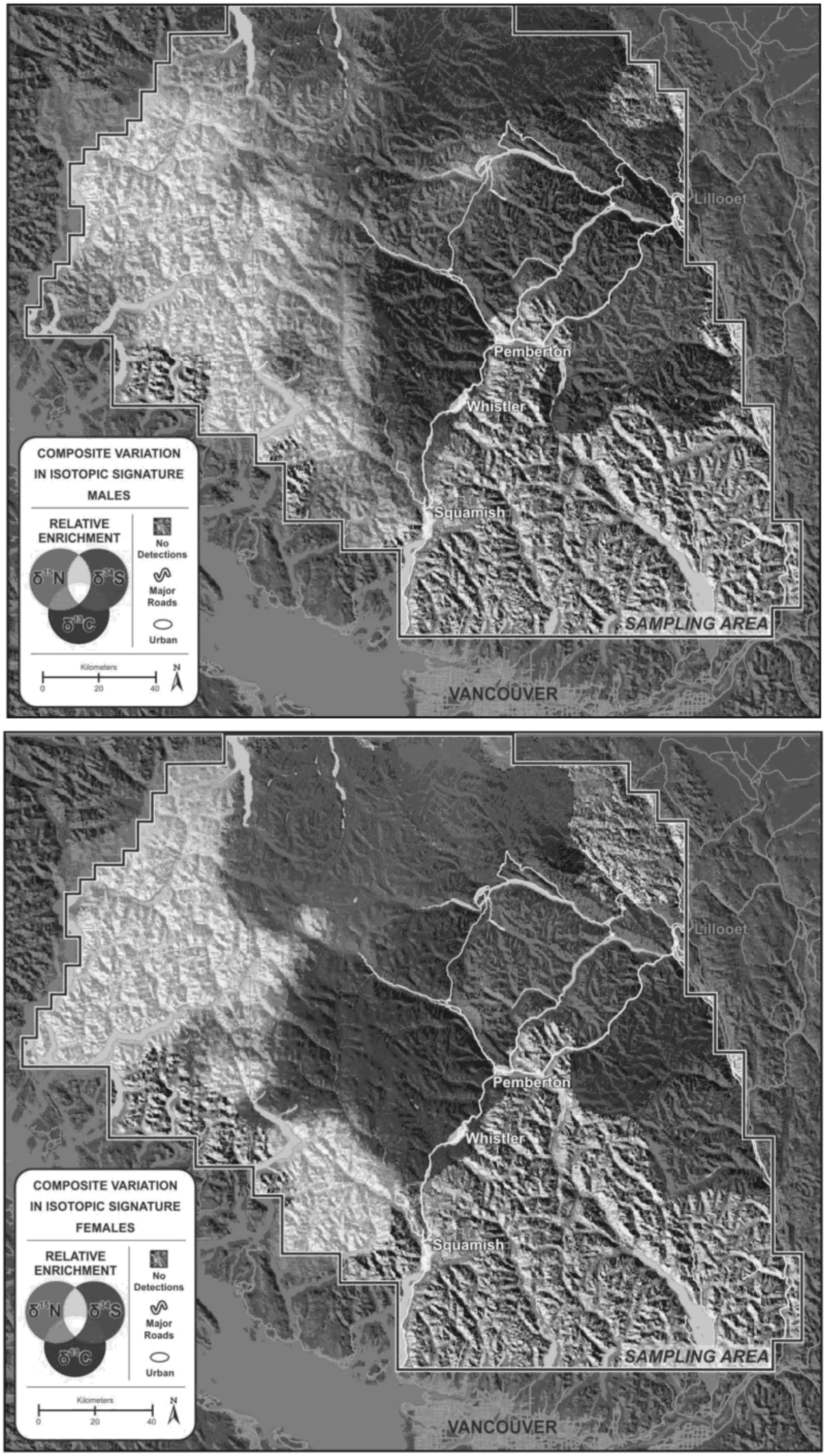

Figure 7-6. Landscape variation in composite isotopic signatures of hair from male (top) and female (bottom) grizzly bears sampled across the southern Coast Ranges, southwestern British Columbia, 2004 - 2010.

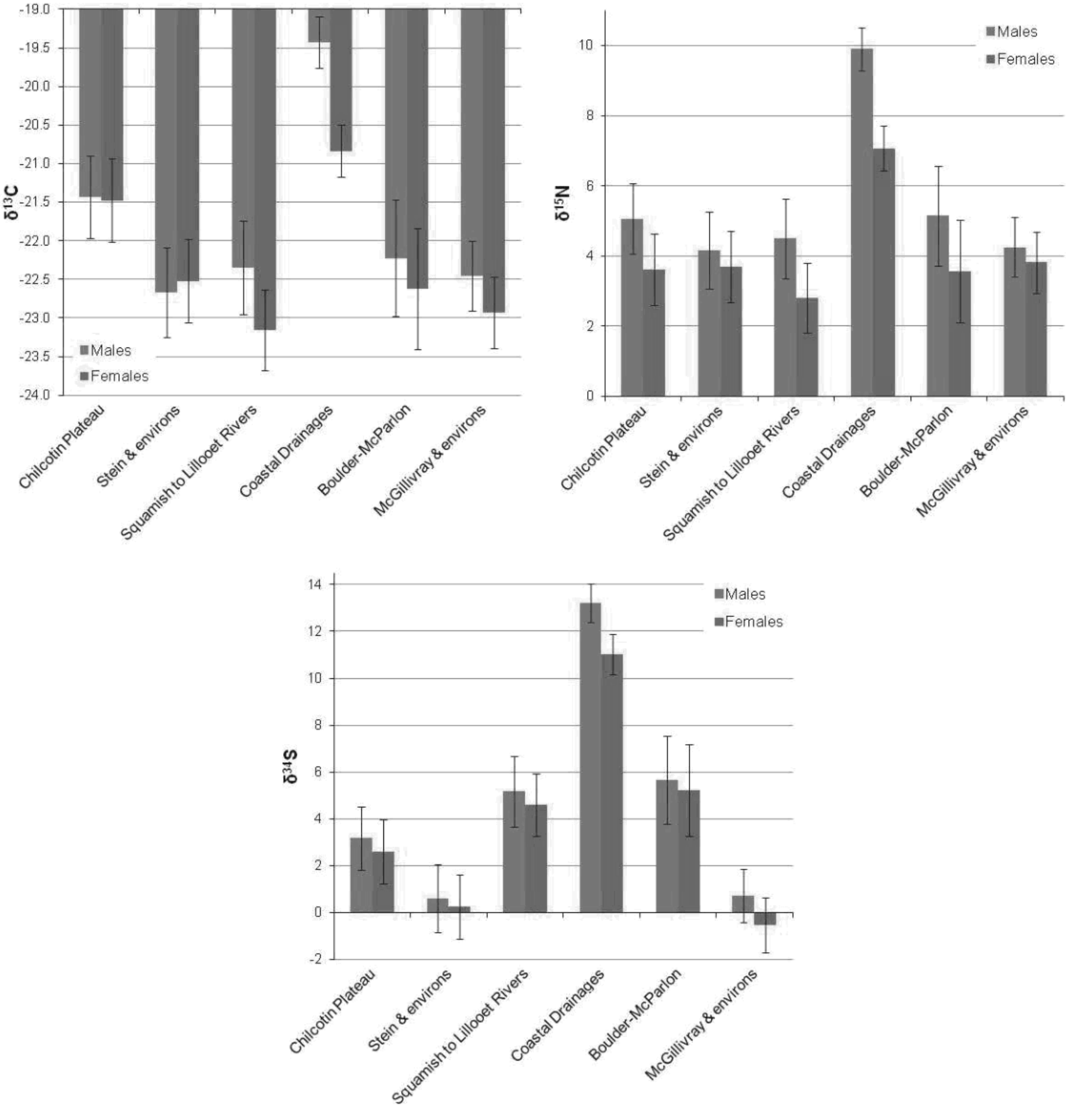

Figure 7-7. Variation in sex-specific isotopic values for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ within hair samples of grizzly bears representative of defined geographic areas across the southern Coast Ranges, southwestern British Columbia, 2004 - 2010. Error bars reflect 95% Bonferroni-adjusted confidence intervals within a multivariate analysis of variance.

DISCUSSION

There is clear and obvious variation in grizzly bear diet across the southern Coast Ranges. Considered in both a qualitative and quantitative sense, differences among geographic areas are apparent in measured ratios for each of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$. However, the specific foods to which these differences correspond are much less obvious. Stable isotope analyses can only broadly discriminate among a few main dietary components particularly in they involve differing trophic-levels (e.g., plant vs. meat). The isotopic endpoints we adopted among generalized food classes were defined from foods sampled from elsewhere in British Columbia (see Table 7-1). We expect that these endpoints and inferences resulting from their application will be revised in a future iteration of this chapter. This said, isotopic end-points for generalized plant and animal dietary classes can vary depending on specific foods sampled, and isotope mixing models that discriminate generalized classes can be extremely sensitive to these choices (Hobson et al. 2000). Thus, at this stage, we see the value of analyses herein mostly in the description of geographic variation of grizzly bear diet, though we offer some informed speculation of factors that contribute to that variation.

For their study area in northwestern British Columbia, RTEC (2006) describe $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ isotope ratios from samples of various food items potentially eaten by grizzly bears. They describe that salmon is generally enriched in all isotopes. This is most likely to explain the higher values we observed for coastal landscapes where grizzly bears are most likely to have access to spawning salmon. The fact that males occurring within landscapes further removed from salmon are more likely to travel to and make use of this important resource is also likely to explain the consistently higher values for males versus females across isotopes. However, this dichotomy between sex is especially pronounced within coastal landscapes where females should not have to travel long distances for salmon. This result is consistent with our expectation that some females, particularly those with dependent young, are likely to exhibit some spatial/temporal avoidance of localized fishing sites to minimize injury and infanticide risk from larger and potentially aggressive males (Ben-David et al. 2004). Finally, although our analyses do not specifically test this hypotheses of dietary differences between males and females at this stage, a cursory examination of Figure 7-7 suggests that inter-sex differences are less for $\delta^{13}C$ than for $\delta^{15}N$. If true, this result would indicate that males, on average, are consuming more meat since higher trophic levels are more likely to show in elevated measures of $\delta^{15}N$ than $\delta^{13}C$ (Kelly 2000).

Beyond coastal landscapes where isotope values are likely to be elevated due to salmon, there is elsewhere landscape variation in relative enrichment among the three isotopes considered. While these differences may or may not be statistically significant depending on specific geographic comparisons, there is an obvious level of geographic consistency that is especially apparent for females. Grizzly bears within Chilcotin landscapes north of Carpenter lake and east of Chilko Lake are relatively depleted in $\delta^{15}N$ and $\delta^{34}S$ while enriched for $\delta^{13}C$. This pattern is also apparent for females within the Stein area. McGillivray bears are relatively enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$ and $\delta^{34}S$. Whereas non-coastal Squamish/Lillooet bears are relatively enriched in $\delta^{34}S$ and depleted in $\delta^{13}C$ and $\delta^{15}N$. Any explanation for this variation is highly equivocal at this stage, but we offer some speculation.

Among bear plant foods, terrestrial plants generally have negative values for $\delta^{15}N$ (Felicetti et al. 2003, Mowat & Heard 2006) and values near 0 for $\delta^{34}S$ (Felicetti et al. 2003). Plants growing in water are apparently reduced for $\delta^{34}S$ and the lack of hygric plants available to bears may result in a positive mean value of $\delta^{34}S$ as is apparently the case for bear plant foods in the Yellowstone Ecosystem (Felicetti et al. 2003). It is possible that Squamish-Lillooet bears consume a greater proportion of their diet as terrestrial plants as compared to bears elsewhere in the region reflecting the high measures of $\delta^{34}S$ within bear hair from these landscapes relative to those of $\delta^{13}C$ and $\delta^{15}N$. However, our result for Squamish-Lillooet bears could also be influenced by marmots which have been shown to be somewhat elevated in $\delta^{34}S$ relative to other terrestrial meat (RTEC 2006), as well as whitebark pine nuts which are notably enriched in $\delta^{34}S$ relative to other grizzly bear plant and animal foods in the Yellowstone ecosystem (Felicetti et al. 2003).

Relative to terrestrial plants, RTEC (2006) report that moose, marmot and mountain goat hair and/or muscle are elevated in $\delta^{13}C$ and $\delta^{15}N$. However, values for $\delta^{34}S$ appear to vary considerably among these herbivore species, with moose being depleted in this isotope relative to terrestrial plants. We speculate that this apparent depletion of $\delta^{34}S$ within Chilcotin landscapes north of Carpenter Lake is in fact due to increased consumption of moose which are apparently abundant here relative to elsewhere across the region. The McGillivray and Stein bears may include more meat in their diet than do non-coastal Squamish-Lillooet bears but perhaps with less moose than Chilcotin bears.

There is, however, some anomaly with Stein females which may incite further investigation. In addition to a suite of terrestrial plant foods, McLellan (2007) described the use of both marmots and whitebark pine nuts by Stein grizzly bears. RTEC (2006) found mean $\delta^{34}S$ values for marmot hair and muscle to be similar to, if not slightly elevated over, terrestrial plants, but variation in marmot hair and muscle was quite high among 16 samples. As compared to other grizzly bear food sources, Felicetti et al. (2003) found whitebark pine nuts to be markedly elevated in $\delta^{34}S$. Hence, neither marmots nor whitebark pine appear to explain the isotopic signature of Stein grizzly bears.

Clearly, the next iteration of this chapter should include sampling from potentially important bear foods from across the region in order to define isotopic dietary end-points that are directly relevant to our study area. Moreover, there are additional samples from individual grizzly bears that need to be analyzed consistent with samples evaluated to date, and additional samples that require re-analysis.

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APPENDIX 4-1 – Loadings of Independent Variables on Principal Component Factors by Scale - Regional Sampling 2004 - 2007

The following three tables (for each analysis scale) show the direction, strength and absolute value of factor loadings among independent variables entered into an analysis and extraction of principal components (see Chapter 4). Strength is designated as + / - (loading > mean for the factor), ++ / - - (loading > 1 SD of mean), or +++ / - - - (loading > 1.5 SD of mean). Note, tables continue across pages.

LEVEL 1	Principal Component Factor												
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
BEC_ESSFxv1	0.01	0.12	0.10	0.01	0.07	+++ 0.80	0.04	0.03	0.09	0.02	0.01	0.07	0.07
BEC_ESSFxc	0.10	0.10	0.07	+ 0.19	+ 0.28	0.11	0.09	- 0.18	0.01	- 0.22	- 0.12	- 0.13	+ 0.13
BEC_MHmm1	0.08	+++ 0.89	0.10	0.02	0.06	0.05	0.08	0.08	0.04	0.12	0.01	0.01	0.10
BEC_IDFdk/unk	0.15	0.01	0.02	0.00	0.12	0.03	- - - 0.47	0.02	- 0.17	0.10	0.01	0.08	0.04
BEC_MSdc	0.05	0.01	0.01	0.03	0.01	+++ 0.77	0.02	0.02	0.03	0.04	0.02	0.01	0.05
BEC_IDFxh2	0.11	0.03	0.14	0.08	+++ 0.76	0.03	0.07	+ 0.16	0.09	0.09	0.07	+ 0.09	- 0.17
BEC_IDFww	0.17	0.13	0.02	0.12	0.12	0.04	0.09	+++ 0.76	0.11	- 0.17	0.07	0.04	0.05
BEC_CWHvm1	0.13	+++ 0.84	0.11	0.04	0.07	0.02	0.02	0.03	0.04	- 0.16	0.02	0.02	0.02
BEC_CWHvm2	0.16	+++ 0.89	0.12	0.07	0.08	0.05	0.07	0.07	0.07	- 0.15	0.04	0.00	+ 0.16
BEC_CWHms1	0.06	- 0.24	++ 0.44	+ 0.31	- 0.20	- 0.18	+ 0.25	0.02	0.02	+++ 0.55	0.08	0.02	- - - 0.31
BEC_CWHds1	0.20	0.20	0.10	+ 0.18	- 0.18	0.09	+ 0.17	+++ 0.50	0.07	+++ 0.50	0.09	- 0.14	0.04
BEC_CWHdm	0.14	+ 0.43	0.10	0.09	0.06	0.06	0.01	0.02	0.01	0.04	+++ 0.42	0.04	+++ 0.56
NDT_1	0.36	+++ 0.67	+ 0.22	+ 0.31	0.11	- 0.16	0.11	- 0.19	0.04	+ 0.20	0.00	0.07	- 0.16
NDT_2	0.19	- - 0.57	0.11	- 0.28	- - - 0.46	0.09	0.03	+ 0.15	0.10	0.06	0.06	0.08	+ 0.17
NDT_4	0.20	0.16	0.03	0.02	+++ 0.78	0.05	0.06	++ 0.32	0.10	- 0.15	0.04	0.03	0.04
ELEV	0.36	- - - 0.67	0.11	- 0.30	0.10	+ 0.17	- 0.19	- 0.24	0.11	- - 0.32	- 0.12	0.05	0.04
SLOPE	0.20	++ 0.49	0.03	- 0.19	0.07	- 0.15	0.11	0.08	- - - 0.63	++ 0.31	- 0.16	0.06	0.02
CURVA	0.22	0.10	- 0.30	- 0.19	- 0.20	0.13	0.13	- - - 0.38	- - 0.28	- - - 0.34	0.04	0.08	- 0.21
SOL_ENER	0.06	- - - 0.71	0.02	0.06	0.05	+ 0.14	0.02	- 0.21	+++ 0.40	- - - 0.39	0.01	0.06	0.01
ALPINE	- 0.49	- 0.41	0.04	- - - 0.57	- 0.28	0.12	0.12	- 0.18	0.11	0.13	0.09	0.06	0.09
ICE	- - - 0.88	0.11	0.04	++ 0.38	0.03	0.03	0.10	0.04	0.02	0.01	0.02	+ 0.11	0.00
FOR_LOG	0.35	0.21	0.12	0.15	0.05	- 0.22	+++ 0.66	0.01	0.04	0.13	0.06	- 0.12	+ 0.17
FOR_OLD	+ 0.60	+ 0.35	+ 0.20	+ 0.21	0.09	- 0.17	0.09	0.01	0.02	0.13	0.03	0.03	- - - 0.47
RANGE	0.08	0.05	0.02	0.01	+++ 0.76	0.02	0.10	0.02	0.04	0.01	0.01	0.01	0.09
WETLAND	0.08	0.08	0.08	0.02	0.09	0.09	0.08	0.02	+++ 0.85	0.04	0.07	0.05	0.02
FOR_YNG	+ 0.60	0.05	- 0.34	+ 0.26	++ 0.34	0.14	0.11	+ 0.25	0.09	0.14	+ 0.12	0.03	+++ 0.30
AGRI	0.05	0.08	0.04	0.09	+ 0.24	0.04	0.12	+++ 0.68	0.08	0.06	0.07	0.05	- 0.12
URBAN	0.07	0.02	0.03	0.01	0.03	0.04	0.04	+ 0.18	0.00	0.05	+++ 0.87	0.02	0.10
MUNI	0.11	0.10	0.01	0.12	0.04	0.02	0.07	0.08	0.02	0.03	+++ 0.89	0.05	0.03
ROAD_WT	+ 0.50	0.13	0.00	+ 0.30	+ 0.18	- 0.16	+++ 0.47	+ 0.28	- 0.14	0.11	+ 0.16	0.09	+ 0.19
ROADDST	- 0.54	0.15	0.13	0.08	0.10	+ 0.30	- - - 0.43	0.07	+ 0.24	0.06	0.03	+ 0.15	0.01
PRIMIT_2	- 0.39	0.15	0.08	0.11	0.11	0.03	- - - 0.69	- 0.23	+ 0.12	- 0.17	- 0.17	0.02	0.00
ACCESS	+ 0.50	0.20	0.06	0.11	0.10	0.08	+++ 0.69	+ 0.19	- 0.14	0.12	+ 0.13	0.01	0.04
CFRAG	+++ 0.86	0.14	0.11	0.12	0.14	+ 0.14	0.05	0.02	+ 0.13	+ 0.18	0.01	0.05	+ 0.18

LEVEL 1	**Principal Component Factor**												
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
ROOTDP	+ 0.63	0.18	0.02	+ 0.33	0.06	0.07	0.08	0.08	0.03	+++ 0.52	0.04	0.05	+ 0.15
KIND_IC	- - 0.78	0.14	0.13	+ 0.27	0.01	0.03	0.01	0.08	0.11	+ 0.16	0.02	+ 0.21	- 0.16
KIND_OR	0.03	+++ 0.75	0.11	0.07	0.11	0.06	+ 0.17	0.06	+ 0.24	0.05	+ 0.19	0.08	0.06
PARENT_C	++ 0.80	+ 0.25	0.01	+ 0.32	0.06	0.03	0.10	0.04	0.12	+ 0.23	0.08	0.01	0.05
PARENT_U	- 0.67	0.14	0.07	- - 0.37	- 0.21	- 0.15	0.12	0.02	- - - 0.35	- 0.24	0.07	0.01	0.09
KIND_R2	- - 0.80	+ 0.27	+ 0.21	+ 0.18	0.03	0.01	0.01	0.08	0.05	0.05	0.04	0.05	0.07
KIND_SO	+++ 0.86	0.08	0.13	0.16	+ 0.19	0.11	0.06	0.06	+ 0.18	0.11	0.03	- 0.10	+ 0.15
FISH	0.15	0.15	0.01	0.04	+ 0.32	0.07	0.01	+++ 0.68	0.02	+ 0.22	+ 0.22	- 0.18	0.08
HAB_1	++ 0.81	0.07	0.08	+ 0.28	0.09	0.07	0.03	0.01	+ 0.13	- 0.23	0.06	0.06	- - 0.24
HAB_3	0.27	++ 0.54	0.04	+ 0.31	- 0.25	0.10	++ 0.31	0.11	- 0.13	++ 0.31	+ 0.17	0.05	+++ 0.33
HAB_4	- 0.63	- 0.29	0.07	- - - 0.56	0.07	0.02	0.13	- 0.14	0.06	0.07	0.08	0.06	+ 0.12
HAB_5	++ 0.71	0.12	- 0.19	0.03	+ 0.22	- 0.31	0.02	0.09	++ 0.29	- 0.19	0.07	0.00	- 0.22
HAB_6	0.08	- 0.29	0.08	- - - 0.45	+++ 0.44	+++ 0.54	0.12	0.12	0.05	- 0.18	0.06	- 0.11	0.01
HAB_7	0.24	- 0.25	0.09	- - - 0.55	+++ 0.45	++ 0.36	0.12	0.07	+ 0.18	0.08	0.02	0.06	- 0.15
HAB_8	- - - 0.91	0.08	0.07	+ 0.34	0.03	0.04	0.09	0.04	0.03	0.02	0.03	+ 0.11	0.00
HAB_9	0.14	+ 0.38	+ 0.28	- 0.29	- 0.25	0.02	+ 0.27	0.09	+++ 0.38	++ 0.32	0.06	0.05	+++ 0.32
HAB_12	0.20	0.15	0.01	0.00	0.08	+++ 0.89	0.03	0.07	+ 0.14	0.07	0.03	0.09	0.02
HAB_13	+ 0.61	0.09	0.16	0.03	0.10	- 0.27	- 0.18	+ 0.23	- - - 0.35	0.03	0.04	+ 0.09	- - - 0.32
BVI	- - - 0.93	0.15	0.15	0.12	0.05	0.06	0.05	0.09	0.08	0.03	0.05	0.07	0.10
BVI_SD	- 0.53	0.21	+++ 0.74	0.05	0.01	0.01	0.14	0.06	0.01	0.08	0.01	+ 0.18	0.05
BVI_X	- - 0.74	0.20	+++ 0.56	0.07	0.03	0.01	0.12	0.08	0.05	0.07	0.01	+ 0.14	0.01
GVI	+++ 0.91	+ 0.24	0.06	0.01	0.05	0.13	+ 0.19	0.10	0.02	0.08	0.05	0.08	0.01
GVI_SD	- - 0.71	0.10	+++ 0.66	0.10	0.04	0.00	0.04	0.04	0.01	0.01	0.03	0.05	0.00
GVI_X	0.32	0.00	+++ 0.92	0.04	0.07	0.03	0.05	0.00	0.00	0.08	0.02	0.00	0.03
NDVI	++ 0.76	+ 0.35	0.01	+ 0.22	- 0.18	- 0.23	+ 0.26	0.12	0.03	+ 0.17	0.08	0.08	0.04
NDVI_SD	- 0.56	0.08	+++ 0.79	0.03	0.03	0.01	0.02	0.00	0.07	0.02	0.06	0.09	0.01
NDVI_X	0.12	0.19	+++ 0.87	0.06	0.09	- 0.16	+ 0.22	0.12	0.07	0.12	0.01	0.05	0.01
WVI	0.10	0.23	0.12	+++ 0.88	0.09	+ 0.14	0.11	0.03	0.04	0.07	+ 0.13	0.09	0.02
WVI_SD	0.26	0.00	0.09	- 0.20	0.07	0.04	0.13	0.09	0.04	0.04	0.06	+++ 0.91	0.01
WVI_X	0.33	0.06	0.13	0.08	0.04	0.00	0.10	0.08	0.04	0.03	0.03	+++ 0.90	0.02

LEVEL 2	**Principal Component Factor**												
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
BEC_ESSFxv1	0.01	0.10	0.07	0.07	0.02	0.07	0.11	0.04	0.01	+++ 0.47	0.09	0.02	+++ 0.62
BEC_MHmm1	0.14	+++ 0.87	0.09	0.04	0.03	0.08	0.06	0.08	0.01	0.01	0.06	0.01	0.04
BEC_IDFdk/unk	0.13	0.07	- 0.33	0.03	0.09	+ 0.14	0.13	0.01	0.09	0.06	- 0.22	0.02	0.01
BEC_MSdv	0.05	0.04	0.04	0.05	0.02	0.03	0.01	0.05	0.01	+ 0.19	0.12	0.04	+++ 0.78
BEC_MSdc	0.03	0.01	0.05	0.07	0.02	0.00	0.05	0.06	0.04	+++ 0.80	0.01	0.04	0.10
BEC_IDFxh2	0.10	0.04	0.01	0.02	0.05	+++ 0.75	0.03	0.10	0.03	0.07	0.12	0.01	0.06
BEC_IDFww	0.11	0.07	0.12	0.00	0.05	0.03	0.06	+++ 0.77	0.06	0.04	0.00	0.01	0.01
BEC_CWHvm1	0.17	+++ 0.78	0.02	0.05	0.01	0.07	0.01	0.01	0.08	0.05	0.11	0.02	0.07
BEC_CWHvm2	0.22	+++ 0.89	0.10	0.01	0.05	0.10	0.11	0.07	0.07	0.04	0.10	0.03	0.00

LEVEL 2	**Principal Component Factor**												
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
BEC_CWHms1	0.19	- 0.29	+ 0.28	+ 0.34	+ 0.19	- 0.19	+++ 0.63	0.04	0.04	0.03	0.02	0.05	- 0.24
BEC_CWHds1	0.05	0.20	+ 0.19	+ 0.33	0.10	- 0.16	+ 0.17	+++ 0.55	+ 0.22	0.03	- 0.15	- 0.10	0.03
BEC_CWHdm	0.17	+ 0.22	0.01	0.07	+ 0.16	0.00	- 0.18	0.10	+++ 0.62	- 0.15	0.07	+++ 0.40	0.09
NDT_1	+ 0.44	+++ 0.72	0.08	0.11	+ 0.23	0.11	0.15	- 0.14	0.09	0.06	0.05	0.00	- 0.20
NDT_2	0.18	- - - 0.62	0.06	0.00	- 0.18	- - - 0.43	0.04	0.10	+ 0.22	0.01	0.03	0.04	0.08
NDT_4	0.20	0.12	0.02	0.02	0.04	+++ 0.80	0.07	+ 0.25	0.05	0.07	0.02	0.03	0.04
ELEV	0.19	- - - 0.57	- 0.28	- 0.32	- 0.23	0.10	- - 0.36	- 0.22	- - 0.33	0.09	+ 0.17	- 0.10	0.10
SLOPE	0.29	+ 0.40	0.07	0.03	0.08	0.07	0.01	0.06	0.08	0.04	- - - 0.73	- 0.16	- 0.19
SOL_ENER	0.07	- - - 0.58	0.08	0.15	0.11	0.07	- 0.21	- 0.17	- - 0.30	0.03	+++ 0.54	0.02	+ 0.13
ALPINE	+ 0.43	- 0.36	- 0.20	- 0.32	- - - 0.42	- 0.25	- - - 0.41	- 0.17	0.10	0.08	0.10	0.06	0.04
ICE	+ + 0.74	0.03	- 0.22	0.11	+++ 0.47	0.01	- 0.26	0.00	- 0.17	0.03	0.06	0.01	0.04
FOR_LOG	0.20	0.15	+++ 0.74	+ 0.22	0.11	0.03	0.01	0.00	0.10	0.07	0.04	0.08	- 0.19
FOR_OLD	- 0.37	+ 0.25	0.00	0.15	0.10	0.09	+++ 0.79	0.04	0.08	0.05	0.01	0.03	0.08
RANGE	0.06	0.03	0.12	0.06	0.04	+++ 0.71	0.05	0.09	0.01	0.05	0.07	0.00	0.08
WETLAND	0.10	0.07	- 0.18	0.16	0.02	0.06	0.09	0.09	+ 0.22	0.09	+++ 0.71	- 0.11	0.10
FOR_YNG	- 0.59	0.06	0.12	+ 0.18	+ 0.22	+ + 0.35	- 0.22	+ 0.24	+ 0.18	0.05	0.07	+ 0.13	+++ 0.32
AGRI	0.04	0.02	0.12	0.02	0.09	+ 0.23	0.02	+++ 0.73	0.04	0.08	0.11	+ 0.16	0.05
URBAN	0.04	0.02	0.09	0.05	0.03	0.00	0.01	+ 0.28	0.04	0.05	0.03	+++ 0.86	0.07
MUNI	0.07	0.02	0.07	0.03	0.06	0.02	0.03	0.08	0.11	0.01	0.02	+++ 0.91	0.00
ROAD_WT	- 0.38	0.09	+++ 0.61	+ 0.18	+ 0.24	+ 0.15	0.03	+ 0.28	+ 0.19	0.10	0.06	+ 0.13	0.08
ROADDST	0.36	0.08	- - - 0.59	0.06	0.07	0.10	- 0.16	0.02	0.04	+++ 0.38	+ 0.22	0.01	0.05
PRIMIT_2	0.19	0.08	- - - 0.77	0.15	0.09	0.08	0.13	- 0.21	0.08	0.02	0.08	- 0.13	0.08
ACCESS	0.29	0.15	+++ 0.79	0.15	0.07	0.07	0.13	+ 0.18	0.04	0.00	0.08	+ 0.12	+ 0.15
CFRAG	- 0.62	0.09	0.15	+++ 0.68	0.05	0.12	0.08	0.04	0.04	0.06	0.07	0.00	+ 0.15
ROOTDP	0.35	0.12	0.16	+++ 0.81	0.13	0.07	0.11	0.00	0.02	0.03	0.08	0.07	0.09
KIND_IC	+ + 0.73	0.17	0.13	0.16	+ 0.30	0.01	0.05	0.03	0.09	0.03	+ 0.15	0.00	0.06
KIND_OR	0.00	+++ 0.65	0.14	0.01	0.07	0.09	+ 0.26	0.04	+ + 0.29	0.04	+ 0.15	0.07	0.01
PARENT_C	- 0.51	+ 0.25	+ 0.21	+++ 0.68	0.11	0.06	+ 0.24	0.05	0.07	0.01	0.06	0.02	0.10
PARENT_U	+ 0.45	0.19	0.16	- - - 0.70	0.15	- 0.16	0.15	0.05	0.05	0.07	- 0.26	0.05	- 0.13
KIND_R2	+ + 0.74	+ 0.26	0.10	- 0.24	+ 0.29	0.00	0.02	0.06	0.02	0.02	0.06	0.03	0.07
KIND_SO	- - 0.67	0.03	0.16	+++ 0.64	0.01	0.14	0.06	0.06	0.03	0.05	0.13	0.03	+ 0.13
FISH	0.14	0.06	0.07	0.02	0.14	+ 0.28	0.08	+++ 0.55	+++ 0.47	0.05	0.11	+ 0.19	0.03
HAB_1	- - 0.69	0.08	0.04	0.10	+ 0.19	0.09	+++ 0.46	0.07	- 0.21	- 0.16	+ 0.14	0.03	+ 0.24
HAB_3	0.15	+ 0.43	+ 0.34	+ 0.29	+ 0.30	- 0.23	0.08	+ 0.15	+++ 0.46	+ 0.15	- 0.14	+ 0.13	0.00
HAB_4	+ 0.56	- 0.24	- 0.20	- 0.29	- - - 0.41	0.09	- - - 0.42	- 0.13	0.05	0.02	0.05	0.04	0.09
HAB_5	- - 0.67	0.04	0.02	0.13	0.10	+ 0.24	0.16	0.10	- - 0.30	- - 0.28	+ + 0.31	0.03	- 0.12
HAB_6	0.05	- 0.31	0.15	- 0.26	- - 0.36	+ + 0.36	- 0.26	- 0.14	0.04	+++ 0.44	0.06	0.06	+ 0.20
HAB_7	0.13	0.21	- 0.18	0.08	- - - 0.62	+++ 0.40	0.07	0.05	0.11	+ 0.26	+ 0.21	0.00	0.06
HAB_8	+ + 0.79	0.02	- 0.21	0.13	+++ 0.43	0.02	- 0.24	0.01	0.13	0.03	0.06	0.00	0.06
HAB_9	0.24	+ 0.22	+ 0.23	0.10	- 0.16	- 0.21	0.06	0.10	+++ 0.68	0.03	+ + 0.29	0.02	- 0.14
HAB_12	0.14	0.15	0.08	0.07	0.03	0.09	0.11	0.05	0.06	+++ 0.76	0.12	0.04	+++ 0.43
HAB_13	- 0.49	0.03	0.10	+ 0.17	- 0.19	0.13	+ 0.18	+ 0.20	- - - 0.41	- 0.26	- - 0.33	0.04	0.10
BVI	+++ 0.84	0.12	0.16	- 0.22	0.04	0.06	- - 0.36	0.06	0.04	0.08	0.11	0.04	0.10
BVI_SD	+++ 0.85	- 0.23	0.08	0.08	0.14	0.07	0.08	0.05	0.01	0.00	0.08	0.00	0.09
BVI_X	+++ 0.91	0.18	0.13	0.14	0.02	0.07	0.12	0.06	0.02	0.02	0.01	0.01	0.02
GVI	- - 0.74	0.20	+ 0.32	+ 0.27	0.08	0.06	+ + 0.35	0.09	+ 0.16	0.10	0.03	0.03	0.03

LEVEL 2	Principal Component Factor												
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
GVI_SD	+++ 0.94	0.09	0.05	0.11	0.05	0.05	0.05	0.08	0.03	0.04	0.07	0.08	0.05
GVI_X	+++ 0.81	0.06	0.15	0.01	- 0.18	0.08	+ 0.21	0.10	+ 0.17	0.04	- 0.13	- 0.12	0.07
NDVI	- 0.57	+ 0.29	+ + 0.37	+ 0.33	0.14	- 0.17	+ + 0.36	0.12	+ 0.19	- 0.16	0.02	0.05	0.11
NDVI_SD	+++ 0.89	0.08	0.06	0.06	0.15	0.02	0.00	0.06	0.05	0.04	- 0.18	- 0.10	0.02
WVI	0.03	0.21	0.15	+ 0.23	+++ 0.81	0.04	+ 0.29	0.03	0.09	+ 0.12	0.06	0.08	+ 0.15
WVI_SD	+ + 0.70	0.04	- 0.24	0.03	- - - 0.42	0.06	0.05	0.07	0.08	- 0.21	0.04	0.06	+ 0.17
WVI_X	+ + 0.76	0.10	- 0.21	0.03	- 0.16	0.06	+ 0.16	0.09	0.07	- 0.18	0.05	0.08	+ 0.23

LEVEL 3	Principal Component Factor											
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
BEC_ESSFxv1	0.00	0.21	0.01	+ 0.30	- 0.32	+ 0.22	0.08	0.08	- 0.21	+ + 0.24	0.03	- 0.10
BEC_MHmm1	0.11	+ 0.38	- - - 0.56	0.21	0.11	0.15	0.06	+ 0.23	0.04	0.09	+ 0.15	+++ 0.25
BEC_MSdv	0.12	0.21	0.08	+ + 0.34	- 0.20	0.15	0.01	+ + 0.27	- 0.15	0.02	- - - 0.34	+++ 0.38
BEC_IDFww	0.11	0.01	0.13	0.15	+ 0.32	0.14	0.01	- 0.24	+++ 0.42	0.03	- 0.16	+ 0.13
BEC_CWHvm1	0.27	+ 0.45	- - 0.39	0.09	0.14	0.14	- 0.22	0.07	0.09	- - 0.21	0.01	- - - 0.31
BEC_CWHvm2	0.24	+ + 0.47	- - - 0.56	0.16	0.14	0.17	0.10	+ + 0.26	0.11	0.02	0.11	0.05
BEC_CWHms1	0.31	0.19	+++ 0.43	0.17	- - 0.38	- - - 0.33	+ 0.23	- 0.24	0.02	+ 0.16	0.02	0.03
BEC_CWHds1	0.28	0.17	+ 0.33	+ 0.26	0.05	0.05	0.05	- - 0.30	0.05	- - - 0.28	+ + 0.25	+++ 0.31
NDT_1	0.13	+++ 0.61	- - - 0.56	0.16	0.00	0.02	+ 0.24	+ 0.20	+ 0.14	0.05	0.02	0.02
NDT_2	0.05	0.17	+++ 0.68	0.02	- 0.25	- 0.18	- 0.21	0.12	- 0.20	- 0.14	+ 0.20	0.06
NDT_4	0.17	- 0.30	0.07	0.14	+ + 0.36	+ 0.25	0.10	- - - 0.33	+ + 0.27	+ 0.21	- - 0.21	- - - 0.26
ELEV	+ 0.65	- - - 0.64	0.08	0.11	0.03	0.08	0.00	+ 0.24	0.11	0.05	0.01	0.00
SLOPE	0.36	+++ 0.57	0.16	- - 0.38	0.05	0.14	0.02	- - - 0.33	- 0.22	0.01	0.11	0.02
CURVA	0.27	- - 0.47	0.14	- 0.23	+ + 0.35	0.15	+ 0.14	+ + 0.30	0.11	0.06	0.03	+ + 0.21
ASPECT_S	0.08	0.21	+ 0.22	0.11	0.15	0.09	0.03	+++ 0.43	+++ 0.30	- 0.15	0.06	- - - 0.42
SOL_ENER	0.17	- - - 0.68	+ 0.21	0.06	0.07	- 0.19	0.07	+++ 0.54	+ 0.17	0.02	0.06	- 0.14
ALPINE	+ + 0.87	0.19	0.11	0.01	0.11	0.02	0.04	0.12	- 0.15	- 0.14	0.09	0.03
AVAL	0.42	+ 0.32	0.09	- - 0.35	- 0.28	+ 0.20	0.07	0.07	0.04	0.09	- - - 0.30	+ 0.11
ICE	+ 0.51	0.10	0.17	+ + 0.35	0.03	- 0.25	+++ 0.53	0.04	0.01	- 0.19	0.02	0.01
FOR_LOG	0.44	+ 0.30	+ 0.27	0.06	+ + 0.39	0.11	0.13	0.13	0.08	+++ 0.38	+ 0.15	- 0.09
FOR_OLD	0.45	0.02	- 0.23	- - 0.34	- - - 0.40	- - 0.28	0.07	- 0.24	+ 0.16	+ 0.14	+++ 0.30	0.01
WETLAND	0.21	0.09	0.14	+ + 0.36	- 0.30	+ 0.19	0.09	+ 0.17	+++ 0.37	0.08	0.02	+++ 0.32
FOR_YNG	- 0.53	0.17	0.08	+++ 0.42	+ 0.28	+ 0.22	0.04	0.08	0.09	- - 0.25	- - - 0.31	- 0.11
ROAD_WT	- 0.56	0.25	+ 0.24	+ 0.26	+++ 0.46	0.06	0.03	0.08	0.00	0.08	0.09	- 0.11
ROADDST	0.34	0.13	0.03	0.10	- - - 0.57	+ + 0.26	0.03	0.04	+ 0.14	0.09	+ 0.13	- 0.09
PRIMIT_2	+ 0.54	0.24	- 0.26	0.21	- - - 0.40	+ 0.20	0.10	0.03	+ 0.21	- - 0.25	0.10	- 0.10
ACCESS	- 0.58	0.23	+ 0.20	0.20	+++ 0.46	- 0.17	0.12	0.12	- 0.21	+ 0.21	0.04	+ 0.14
CFRAG	- 0.75	0.23	0.20	0.20	0.08	+++ 0.34	+++ 0.33	0.02	0.11	0.04	0.01	0.03
ROOTDP	- 0.59	0.02	+ 0.30	- 0.29	0.12	+ 0.21	+++ 0.48	0.08	0.05	0.05	0.07	0.01
KIND_IC	+ 0.52	0.27	- 0.26	+ 0.26	0.15	- 0.20	+ 0.19	0.10	+ + 0.26	+++ 0.28	0.09	0.04
KIND_OR	0.33	+ + 0.47	- 0.28	0.03	0.09	0.11	0.05	0.08	0.01	- 0.12	+++ 0.44	+ 0.12
PARENT_C	- - 0.80	0.03	0.03	0.21	0.10	+ + 0.31	+++ 0.36	0.04	0.03	0.05	0.07	0.02

LEVEL 3	**Principal Component Factor**											
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
PARENT_U	+ + 0.79	0.05	0.03	0.08	0.13	- - - 0.34	- - - 0.41	0.01	0.01	0.02	- 0.12	0.02
KIND_R2	+ 0.53	+ 0.39	- 0.30	+ 0.29	0.12	- 0.23	0.13	0.10	+ 0.21	+ 0.17	0.10	0.02
KIND_SO	- - 0.80	0.22	0.16	0.17	0.05	+++ 0.34	+ + 0.30	0.03	0.08	0.05	0.05	0.02
FISH	0.29	0.25	0.17	+ + 0.37	+ 0.22	0.10	- 0.18	- - 0.28	+ 0.16	- - - 0.32	0.03	0.02
HAB_1	- 0.56	- - 0.46	- 0.25	0.12	- 0.29	- - - 0.31	0.06	0.10	0.10	0.00	0.11	0.04
HAB_3	- 0.51	+++ 0.62	0.08	+ 0.26	0.06	0.08	0.09	0.08	0.10	0.07	0.00	- 0.13
HAB_4	+++ 0.90	0.02	0.07	0.05	0.09	0.06	0.11	0.07	0.03	- 0.13	+ 0.15	0.05
HAB_5	0.32	- - - 0.54	0.13	- 0.30	+ 0.31	0.03	0.06	0.05	+++ 0.37	0.02	0.08	0.05
HAB_6	+ 0.57	- 0.38	0.06	0.19	0.13	+ 0.26	- 0.14	- 0.16	- 0.17	+ + 0.23	0.08	0.05
HAB_7	0.47	- 0.45	0.03	0.04	+ 0.27	+ + 0.28	0.07	0.03	+ 0.19	+ + 0.25	+ + 0.23	0.04
HAB_8	+ 0.61	0.14	0.14	+ 0.33	0.01	- 0.23	+++ 0.54	0.02	0.02	- 0.19	0.01	0.00
HAB_9	0.03	+ + 0.52	+ + 0.38	+ 0.25	0.11	+ + 0.28	0.12	+ 0.20	+++ 0.33	0.10	0.09	+ 0.14
HAB_12	0.15	0.20	0.07	+++ 0.56	- 0.27	+ + 0.28	0.00	0.04	- 0.22	+++ 0.31	0.01	0.01
HAB_13	0.13	- 0.35	0.09	- - - 0.49	+ + 0.39	0.05	0.00	- 0.20	+ 0.18	0.06	0.07	+ 0.12
BVI	+ + 0.84	0.21	0.19	+ 0.24	0.05	0.11	+ 0.19	+ 0.16	0.12	0.00	+ 0.14	0.02
BVI_SD	+ + 0.81	0.17	0.19	- 0.31	0.08	0.09	0.06	0.10	- 0.14	0.06	0.04	0.01
BVI_X	+++ 0.92	0.20	0.19	0.05	0.07	0.09	0.07	0.02	0.04	0.00	0.05	0.02
GVI	- - 0.84	0.23	0.16	- 0.27	0.01	0.01	- 0.23	0.12	0.09	0.10	- 0.14	0.00
GVI_SD	+ + 0.89	0.25	+ 0.22	0.06	0.03	0.02	0.07	0.07	0.01	0.05	0.06	0.01
GVI_X	+ 0.67	+ 0.39	+ + 0.38	- 0.26	0.07	0.08	0.10	0.13	0.06	0.06	- 0.16	0.03
NDVI	- - 0.79	+ 0.41	0.17	0.19	0.05	0.10	0.09	+ 0.17	0.13	0.03	- 0.13	0.02
NDVI_SD	+ + 0.76	+ 0.29	+ 0.28	- 0.29	0.06	0.11	0.11	0.02	0.05	0.04	- 0.14	0.05
WVI	- - 0.78	0.21	0.14	+ 0.23	- 0.29	- 0.22	0.05	0.07	0.13	0.01	- 0.14	0.02
WVI_SD	+ + 0.86	0.17	0.07	0.14	0.09	0.16	0.10	0.10	0.04	0.04	+ 0.11	0.00
WVI_X	+ + 0.79	+ 0.31	0.04	0.11	0.01	0.12	+ 0.16	- 0.17	0.08	0.01	0.07	0.01
BEC_ESSFxv1	0.00	0.21	0.01	+ 0.30	- 0.32	+ 0.22	0.08	0.08	- 0.21	+ + 0.24	0.03	- 0.10

APPENDIX 4-2 – Loadings of Independent Variables on Principal Component Factors by Scale - Toba/Orford & Southgate/Chilko (Toba-Bute) Sampling 2008 & 2010

The following three tables (for each analysis scale) show the direction, strength and absolute value of factor loadings among independent variables entered into an analysis and extraction of principal components (see Landscape Distribution Methods). Strength is designated as + / - (loading > mean for the factor), ++ / - - (loading > 1 SD of mean), or +++ / - - - (loading > 1.5 SD of mean). Note, tables continue across pages.

LEVEL 1	**Principal Component Factor**							
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
ALPINE	- - 0.92	0.13	0.02	0.18	0.07	0.14	0.09	0.03
ASPECT_S	0.05	+ 0.27	0.12	0.14	0.06	0.07	0.08	+++ 0.84
ASPECT_W	0.53	+++ 0.71	0.14	0.14	0.13	- 0.18	0.01	+ 0.19
AVAL	0.32	0.22	0.21	0.06	- - - 0.41	- 0.19	- 0.14	- - - 0.47
BARREN	0.14	0.22	0.15	0.03	+++ 0.89	0.05	0.02	0.08
BEC_ATp	- - 0.96	0.19	0.14	0.05	0.03	0.03	0.08	0.02
BEC_MHmm1	0.51	+ 0.33	- 0.38	+++ 0.64	0.01	+ 0.19	0.08	0.03
BEC_MHmm2	0.49	- 0.31	+ 0.32	- - - 0.61	0.08	0.11	0.05	+ 0.13
BEC_CWHdm	+ 0.86	0.20	0.19	0.04	0.13	- 0.21	0.00	- 0.15
BEC_CWHds1	0.03	0.03	+ 0.41	- - - 0.60	0.02	+++ 0.41	- 0.25	0.08
BEC_CWHms1	0.39	0.01	0.21	- - - 0.81	0.12	0.06	0.01	+ 0.18
BEC_CWHvm1	+ 0.67	+ 0.29	0.07	++ 0.49	0.03	- - - 0.37	0.04	0.04
BEC_CWHvm2	+ 0.65	+ 0.33	- 0.26	+++ 0.60	0.06	0.03	0.01	0.01
BVI	- - 0.95	0.14	0.08	0.05	0.13	0.09	+ 0.15	+ 0.13
BVI_SD	0.51	0.05	+++ 0.76	0.21	0.00	0.10	+ 0.13	- 0.20
BVI_X	- 0.77	0.17	++ 0.54	0.16	0.04	0.01	+ 0.14	0.07
COMPLEX	0.16	0.01	+++ 0.75	- 0.35	++ 0.32	0.02	0.08	0.07
CURVA	0.33	0.18	- 0.42	++ 0.53	0.04	+ 0.15	0.04	0.05
ELEV	- - 0.94	- 0.26	0.12	0.01	0.08	0.04	0.09	0.06
FISH	0.39	0.12	+ 0.42	0.18	0.14	+++ 0.47	- - - 0.39	0.09
GVI	++ 0.92	+ 0.29	0.08	0.12	0.09	0.10	- 0.12	0.05
GVI_SD	- 0.73	0.06	+++ 0.63	0.17	0.01	0.13	0.07	0.01
GVI_X	0.15	+ 0.37	+++ 0.89	0.13	0.01	0.05	0.07	0.08
HAB_1	+ 0.87	0.12	0.03	0.08	- 0.18	0.11	- 0.19	- - - 0.31
HAB_10	0.07	+++ 0.78	0.12	+ 0.42	+ 0.23	++ 0.28	0.01	0.06
HAB_11	0.43	+++ 0.67	0.13	0.20	- - 0.32	0.02	0.11	+ 0.12
HAB_12	- 0.68	0.02	0.13	0.03	+++ 0.48	- - - 0.37	0.10	+ 0.16
HAB_13	0.59	+ 0.29	- 0.33	+ 0.29	- - - 0.40	+++ 0.38	+ 0.16	0.00
HAB_3	++ 0.94	0.16	0.20	0.06	0.02	0.09	- 0.15	0.01
HAB_4	- 0.81	+ 0.39	0.06	0.09	++ 0.34	0.05	0.12	0.02
HAB_5	+ 0.72	0.18	- 0.35	+ 0.27	- - 0.34	++ 0.33	0.00	0.01
HAB_6	0.51	+ 0.28	+ 0.35	0.19	+++ 0.56	0.13	- 0.16	0.09
HAB_7	0.09	++ 0.60	0.09	++ 0.53	++ 0.33	+++ 0.35	0.04	- 0.11
HAB_8	- 0.87	- 0.41	0.06	0.14	0.03	0.11	+ 0.14	0.08

LEVEL 1	**Principal Component Factor**							
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
HAB_9	0.53	++ 0.51	+ 0.33	0.16	+ 0.30	0.13	- 0.13	+++ 0.33
ICE	- 0.79	- - 0.52	0.03	0.11	- 0.15	0.06	+ 0.18	0.05
FOR_LOG	+ 0.62	0.05	0.13	0.11	- - 0.35	- - - 0.42	+ 0.14	- - 0.28
NDT_1	0.52	0.19	0.14	+++ 0.80	0.06	0.03	0.09	0.05
NDT_2	0.52	0.19	0.14	- - - 0.80	0.06	0.03	0.09	0.05
NDVI	++ 0.94	0.19	0.11	0.09	- 0.16	0.10	0.10	0.03
NDVI_SD	0.51	0.11	+++ 0.80	0.15	0.03	0.08	0.03	0.07
NDVI_X	0.46	+ 0.42	+++ 0.72	0.06	- 0.15	0.07	0.05	- 0.14
FOR_OLD	+ 0.68	0.21	0.20	0.11	0.03	+++ 0.49	- 0.17	0.08
PRIMIT_2	0.60	0.02	0.06	- 0.28	0.02	++ 0.33	0.09	- 0.23
ROADDST	- 0.77	0.14	0.17	- 0.27	0.02	- 0.15	+ 0.17	0.07
ROAD_WT	+ 0.84	0.13	- 0.26	0.15	- 0.16	0.09	- 0.19	+ 0.22
ACCESS	+ 0.88	0.14	0.06	+ 0.30	0.12	- 0.21	0.01	0.09
CFRAG	++ 0.98	0.01	0.01	0.03	0.04	0.09	0.08	0.01
ROOTDP	++ 0.98	0.01	0.01	0.03	0.05	0.10	0.08	0.01
KIND_IC	- - 0.98	0.01	0.01	0.03	0.04	0.09	0.08	0.01
KIND_OR	++ 0.97	0.01	0.02	0.02	0.06	0.12	0.08	0.02
PARENT_C	++ 0.98	0.01	0.01	0.03	0.05	0.10	0.08	0.01
PARENT_U	- - 0.97	0.01	0.02	0.03	0.05	0.10	0.08	0.01
KIND_R2	- - 0.97	0.01	0.02	0.03	0.05	0.10	0.08	0.01
KIND_SO	++ 0.98	0.01	0.01	0.03	0.04	0.09	0.08	0.01
SLOPE	0.22	+++ 0.92	0.02	0.02	0.06	0.12	0.08	+ 0.18
SOL_DURA	0.29	- - - 0.88	0.20	0.12	0.00	0.05	0.05	- 0.19
SOL_ENER	0.50	- - - 0.79	0.04	0.04	0.01	0.08	+ 0.13	+ 0.15
WETLAND	0.21	0.08	+++ 0.65	0.20	+++ 0.44	++ 0.30	0.10	0.06
WVI	0.07	- - - 0.85	0.03	- 0.30	- 0.28	- 0.20	0.04	0.06
WVI_SD	0.47	0.04	0.06	0.14	0.01	0.04	+++ 0.84	0.07
WVI_X	0.50	0.23	0.03	0.06	0.09	0.08	+++ 0.80	0.05
FOR_YNG	+ 0.86	0.19	- 0.34	0.04	0.06	- 0.19	- 0.12	0.02

LEVEL 2	**Principal Component Factor**									
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
BEC_ESSFxv1	0.01	0.10	0.07	0.07	0.02	0.07	0.11	0.04	0.01	+++ 0.47
BEC_MHmm1	0.14	+++ 0.87	0.09	0.04	0.03	0.08	0.06	0.08	0.01	0.01
BEC_IDFdk/unk	0.13	0.07	- 0.33	0.03	0.09	+ 0.14	0.13	0.01	0.09	0.06
BEC_MSdv	0.05	0.04	0.04	0.05	0.02	0.03	0.01	0.05	0.01	+ 0.19
BEC_MSdc	0.03	0.01	0.05	0.07	0.02	0.00	0.05	0.06	0.04	+++ 0.80
BEC_IDFxh2	0.10	0.04	0.01	0.02	0.05	+++ 0.75	0.03	0.10	0.03	0.07
BEC_IDFww	0.11	0.07	0.12	0.00	0.05	0.03	0.06	+++ 0.77	0.06	0.04
BEC_CWHvm1	0.17	+++ 0.78	0.02	0.05	0.01	0.07	0.01	0.01	0.08	0.05
BEC_CWHvm2	0.22	+++ 0.89	0.10	0.01	0.05	0.10	0.11	0.07	0.07	0.04
BEC_CWHms1	0.19	- 0.29	+ 0.28	+ 0.34	+ 0.19	- 0.19	+++ 0.63	0.04	0.04	0.03

LEVEL 2	**Principal Component Factor**									
Variable	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
BEC_CWHds1	0.05	0.20	+ 0.19	+ 0.33	0.10	- 0.16	+ 0.17	+++ 0.55	+ 0.22	0.03
BEC_CWHdm	0.17	+ 0.22	0.01	0.07	+ 0.16	0.00	- 0.18	0.10	+++ 0.62	- 0.15
ALPINE	- - 0.86	0.20	0.06	0.06	+ 0.30	0.03	- 0.20	0.08	0.06	0.02
ASPECT_S	0.05	0.04	0.07	0.08	0.04	0.05	0.05	+++ 0.91	0.06	0.10
ASPECT_W	0.21	0.04	0.00	+ 0.29	- 0.33	+ 0.20	- 0.17	- - - 0.56	0.08	0.05
AVAL	0.52	0.09	0.15	- - - 0.68	+ 0.21	0.14	0.04	0.12	- 0.13	0.03
BARREN	0.20	0.14	0.01	0.11	+ 0.29	- - - 0.66	+++ 0.43	0.06	0.06	0.02
BEC_ATp	- - 0.91	+ 0.29	0.05	0.17	0.00	0.08	0.07	0.03	- 0.12	0.10
BEC_MHmm1	0.33	- 0.44	+++ 0.52	0.05	+++ 0.49	+ 0.15	0.06	0.02	+++ 0.28	- 0.19
BEC_MHmm2	0.33	+ 0.39	- - - 0.66	0.15	- 0.26	0.03	0.05	0.06	0.04	+ 0.12
BEC_CWHdm	+ 0.67	- 0.43	0.16	0.17	- 0.32	0.07	+ 0.23	0.09	- 0.19	- 0.13
BEC_CWHds1	0.22	+ 0.33	- - - 0.62	0.04	0.03	0.08	++ 0.30	0.09	0.09	0.03
BEC_CWHms1	0.15	+ 0.25	- - - 0.82	- 0.24	0.17	0.04	- 0.17	0.12	0.02	+ 0.17
BEC_CWHvm1	0.52	0.08	+++ 0.67	- 0.29	0.07	0.09	0.08	0.04	0.03	0.01
BEC_CWHvm2	0.46	- 0.30	+++ 0.66	0.15	+ 0.30	+ 0.20	0.06	0.06	+ 0.12	0.09
BVI	- - 0.88	+ 0.25	0.04	0.05	0.01	- 0.21	0.07	+ 0.24	- 0.10	+ 0.19
BVI_SD	0.49	+++ 0.77	- 0.21	0.14	0.10	0.09	0.03	- 0.14	0.04	0.01
BVI_X	- 0.70	+++ 0.62	0.16	0.19	0.11	0.14	0.02	0.00	0.02	0.05
COMPLEX	0.10	+++ 0.72	- 0.29	0.07	- 0.23	0.14	++ 0.35	0.03	+ 0.16	+ 0.12
CURVA	0.37	0.15	+ 0.26	++ 0.43	+ 0.31	+ 0.15	- 0.23	0.05	0.05	- 0.20
ELEV	- - 0.88	+ 0.30	0.05	+ 0.26	0.02	0.00	- 0.15	0.10	0.01	0.09
FISH	0.42	0.11	0.16	0.14	0.06	0.10	+++ 0.71	- 0.14	+++ 0.31	0.03
GVI	++ 0.88	- 0.23	0.12	0.19	0.14	+ 0.22	0.07	0.08	0.08	- 0.14
GVI_SD	- 0.66	+++ 0.69	0.16	0.04	0.11	0.12	0.04	0.09	- 0.10	0.09
GVI_X	0.06	+++ 0.91	0.13	- 0.31	0.12	0.01	0.03	0.03	0.10	0.00
HAB_1	+ 0.69	0.19	0.16	0.13	0.14	+ 0.18	0.07	- - - 0.51	+ 0.11	- 0.23
HAB_10	0.02	0.02	+ 0.28	- 0.39	+++ 0.80	0.04	0.11	0.10	0.09	0.03
HAB_11	0.39	0.14	+ 0.29	- - - 0.52	0.13	+++ 0.45	0.06	+ 0.18	- 0.14	+ 0.16
HAB_12	0.53	0.16	0.06	0.06	0.02	- - - 0.71	0.12	0.12	0.06	+ 0.18
HAB_13	0.41	- 0.36	0.19	0.01	+ 0.36	+++ 0.61	0.11	0.09	0.07	0.07
HAB_3	++ 0.88	- 0.27	0.03	0.18	- 0.20	0.03	0.03	0.03	0.08	- 0.18
HAB_4	- 0.76	0.14	0.02	- 0.29	+ 0.34	- 0.27	0.09	+ 0.20	0.08	0.10
HAB_5	0.53	- - 0.47	0.15	0.05	+ 0.27	+++ 0.51	0.06	0.06	++ 0.23	- 0.17
HAB_6	0.46	0.16	0.05	0.10	++ 0.43	- - - 0.62	0.00	0.10	- 0.12	0.08
HAB_7	0.01	0.02	+ 0.23	0.12	+++ 0.90	0.10	0.07	0.03	0.03	0.01
HAB_8	- 0.84	+ 0.24	0.10	+ 0.29	- 0.26	0.09	0.07	0.10	0.08	+ 0.16
HAB_9	+ 0.57	0.07	0.13	- 0.35	+ 0.22	0.12	+++ 0.53	++ 0.29	0.04	0.10
ICE	- 0.76	+ 0.24	0.09	++ 0.42	- 0.29	0.02	0.08	0.08	0.07	+ 0.19
FOR_LOG	+ 0.58	0.17	+ 0.21	0.03	- 0.25	0.12	- - - 0.42	- - 0.32	0.06	+ 0.23
NDT_1	0.55	0.03	+++ 0.68	0.03	+ 0.35	0.05	- 0.23	0.04	+ 0.13	0.01
NDT_2	0.55	0.03	- - - 0.68	0.03	- 0.35	0.05	+ 0.23	0.04	- 0.13	0.01
NDVI	++ 0.89	- 0.23	0.10	0.10	0.05	+ 0.28	0.05	0.06	0.08	- 0.14
NDVI_SD	0.36	+++ 0.88	0.10	0.04	0.03	0.02	0.00	0.12	- 0.10	0.08
NDVI_X	+ 0.66	+++ 0.56	0.02	- 0.25	0.19	+ 0.29	0.11	0.04	0.02	0.02
FOR_OLD	+ 0.61	0.05	- 0.33	0.09	+ 0.29	+ 0.16	+ 0.28	- 0.14	+++ 0.32	0.02
PRIMIT_2	0.42	0.02	- 0.34	0.11	0.05	0.03	+ 0.19	0.07	- - - 0.39	- - - 0.44

LEVEL 2	Principal Component Factor									
Variable	1	2	3	4	5	6	7	8	9	10
ROADDST	- 0.73	0.06	- 0.22	0.06	- 0.22	0.05	0.02	+ 0.18	- 0.17	+ 0.18
ROAD_WT	+ 0.70	- 0.27	+ 0.19	0.11	0.18	0.11	0.01	0.09	+++ 0.51	0.08
ACCESS	+ 0.80	0.14	+ 0.38	0.04	0.07	+ 0.15	0.05	- 0.18	0.08	0.06
CFRAG	++ 0.97	0.06	0.01	0.09	0.01	0.06	0.10	0.03	0.07	0.01
ROOTDP	++ 0.97	0.05	0.01	0.09	0.01	0.06	0.10	0.03	0.07	0.01
KIND_IC	- - 0.97	0.06	0.01	0.09	0.01	0.06	0.10	0.03	0.07	0.01
KIND_OR	++ 0.97	0.06	0.01	0.09	0.01	0.06	0.10	0.03	0.07	0.01

LEVEL 3	Principal Component Factor											
Variable	1	2	3	4	5	6	7	8	9	10	11	12
ALPINE	++ 0.72	+ 0.36	+ 0.22	0.13	0.01	0.15	+ 0.30	0.01	0.09	0.03	0.02	+ 0.14
ASPECT_S	0.06	0.16	- 0.37	0.05	0.06	+ 0.30	++ 0.32	0.09	+++ 0.67	0.06	++ 0.21	0.07
ASPECT_W	0.06	0.17	0.10	- 0.24	+ 0.17	0.01	0.06	- 0.20	- - - 0.72	0.04	0.06	0.03
AVAL	++ 0.73	+ 0.40	0.17	- 0.18	0.11	0.08	0.10	0.00	0.01	0.09	0.01	- 0.14
BARREN	0.04	0.16	0.07	- 0.25	0.07	- - 0.41	- - 0.35	0.02	+++ 0.43	+ 0.19	+ 0.17	0.00
BEC_ATp	++ 0.71	+ 0.45	0.15	- 0.17	0.00	- 0.17	+ 0.22	0.04	0.11	0.02	0.00	++ 0.28
BEC_MHmm1	0.12	0.02	+++ 0.68	0.15	+++ 0.54	0.03	0.01	+ 0.15	0.00	0.03	+ 0.10	0.08
BEC_MHmm2	0.23	0.32	- 0.34	0.06	- - 0.38	0.12	+++ 0.48	++ 0.27	- 0.15	0.09	0.00	0.10
BEC_CWHdm	- 0.52	0.22	0.11	+ 0.24	0.04	0.16	0.04	- - - 0.65	0.02	0.06	+ 0.13	0.03
BEC_CWHds1	0.24	0.10	0.03	0.10	- - - 0.45	0.11	0.13	+ 0.18	0.10	+++ 0.52	0.08	+ 0.16
BEC_CWHms1	0.10	0.03	- 0.26	- 0.17	- - - 0.74	0.10	- 0.15	++ 0.28	0.07	- 0.21	0.07	- 0.17
BEC_CWHvm1	0.25	0.31	- 0.24	+++ 0.37	+++ 0.56	0.11	- 0.24	0.01	0.12	- 0.13	- - - 0.29	0.11
BEC_CWHvm2	0.04	0.09	+ 0.19	0.01	+++ 0.80	+ 0.26	- 0.20	0.06	0.01	0.09	0.05	- 0.13
BVI	++ 0.77	+ 0.42	0.18	0.07	0.01	0.11	0.07	0.10	++ 0.32	0.02	0.09	+ 0.15
BVI_SD	++ 0.82	+ 0.37	0.03	0.15	0.04	0.14	0.12	+ 0.12	0.05	- 0.17	+ 0.12	0.08
BVI_X	+++ 0.84	+ 0.43	0.10	0.13	0.02	0.03	0.06	0.00	0.10	- 0.12	0.04	+ 0.16
COMPLEX	++ 0.71	0.18	0.02	0.13	0.11	+ 0.20	- - 0.41	0.02	+ 0.15	- - 0.27	0.08	0.09
CURVA	0.19	0.10	+++ 0.71	- 0.21	+ 0.24	0.10	0.14	- 0.21	0.07	- 0.19	0.03	+ 0.16
ELEV	+ 0.64	+ 0.45	0.15	- 0.24	0.12	0.09	++ 0.35	+ 0.22	0.10	- 0.18	0.05	+ 0.15
FISH	0.34	0.26	0.11	+ 0.24	- 0.18	0.05	- 0.16	0.12	+ 0.18	+++ 0.56	+++ 0.27	+ 0.12
GVI	- 0.66	- 0.48	0.10	+ 0.16	0.04	+++ 0.43	0.07	0.02	0.08	0.03	0.02	- - - 0.29
GVI_SD	++ 0.78	+ 0.51	0.06	- 0.16	0.01	0.03	0.11	0.05	0.03	0.04	0.01	+ 0.19
GVI_X	++ 0.75	+ 0.40	0.00	- 0.16	0.03	++ 0.37	0.10	+ 0.14	0.04	0.03	0.03	0.04
HAB_1	- 0.56	0.15	0.16	0.06	0.06	0.10	0.07	++ 0.27	- - - 0.63	0.00	0.09	0.02
HAB_10	++ 0.79	0.15	+ 0.33	- 0.16	0.13	0.09	0.01	0.03	0.04	0.02	0.01	- - 0.24
HAB_11	0.04	0.09	- 0.20	0.14	0.08	+++ 0.74	0.08	0.03	+ 0.28	0.06	- - - 0.36	0.08
HAB_12	+ 0.47	0.29	- - 0.43	0.06	0.11	- - - 0.48	0.04	+ 0.14	0.03	0.07	- 0.14	- 0.18
HAB_13	0.07	0.20	+++ 0.82	0.04	0.07	0.07	0.04	0.07	0.08	0.04	0.02	- 0.13
HAB_3	- - 0.78	0.34	0.17	+ 0.20	0.12	0.00	0.13	- 0.15	+ 0.16	0.10	0.01	- 0.15
HAB_4	++ 0.84	0.34	0.05	0.12	0.01	- 0.20	0.02	0.05	+ 0.14	0.12	0.06	0.08
HAB_5	0.17	0.19	+++ 0.85	0.04	+ 0.22	0.10	0.09	0.10	0.05	0.11	+ 0.11	0.02
HAB_6	+ 0.57	+ 0.42	0.02	- 0.20	0.01	- - - 0.44	0.11	0.04	0.10	0.07	- 0.12	0.00

LEVEL 3	**Principal Component Factor**																							
Variable		**1**		**2**		**3**		**4**		**5**		**6**		**7**		**8**		**9**		**10**		**11**		**12**
HAB_7	+	0.66		0.22	++	0.41	-	0.17		0.05	-	0.23		0.11	+	0.15		0.01		0.02		0.03	- - -	0.29
HAB_8		0.45	+	0.54		0.11		0.06		0.02	-	0.24		0.12		0.09		0.03		0.01		0.06	+++	0.58
HAB_9		0.06		0.13	-	0.34		0.04		0.05	+	0.17		0.06	-	0.16	+++	0.45	+++	0.52		0.02	- - -	0.30
ICE		0.36	+	0.39		0.13		0.03		0.04	-	0.18	+	0.24		0.01		0.09		0.01		0.01	+++	0.60
FOR_LOG		0.31		0.26		0.15	+	0.22		0.13	+	0.20		0.05		0.05		0.06	-	0.16	- - -	0.71		0.04
NDT_1		0.44		0.20	+	0.24		0.00	+++	0.76		0.01		0.14	+	0.18		0.08	-	0.19		0.10		0.05
NDT_2		0.44		0.20	-	0.24		0.00	- - -	0.76		0.01		0.14	-	0.18		0.08	+	0.19		0.10		0.05
NDVI	- -	0.71	-	0.43		0.08	+	0.20		0.00	+++	0.43		0.00		0.05		0.12		0.01		0.05	-	0.19
NDVI_SD	++	0.83	+	0.39		0.01	-	0.15		0.06	+	0.23		0.03		0.08		0.08		0.03		0.03		0.10
NDVI_X		0.06		0.14		0.12		0.07		0.11	+++	0.88		0.06	+	0.16		0.01		0.00		0.01	-	0.23
FOR_OLD		0.39		0.16		0.08	-	0.22		0.09		0.09		0.12	+++	0.71		0.01		0.10	+	0.12		0.06
PRIMIT_2		0.10		0.23		0.15	- - -	0.74		0.08		0.13		0.06		0.05		0.02		0.04	++	0.24		0.07
ROADDST	+	0.48	+	0.38	-	0.29	-	0.19	-	0.24		0.04		0.07		0.05		0.11	-	0.18	+	0.13		0.03
ROAD_WT	-	0.46		0.31		0.01	+++	0.75		0.03		0.07		0.02	-	0.20	+	0.13	+	0.13		0.03		0.01
ACCESS		0.44	-	0.41		0.16	++	0.32		0.13	+	0.18		0.01	- - -	0.35		0.01	+	0.13	- - -	0.41		0.01
CFRAG		0.39	- - -	0.89		0.07		0.15		0.00		0.06		0.00		0.04		0.02		0.07		0.05		0.04
ROOTDP		0.39	- - -	0.89		0.07		0.15		0.00		0.06		0.00		0.04		0.02		0.07		0.05		0.04
KIND_IC		0.39	+++	0.89		0.07		0.15		0.00		0.06		0.00		0.04		0.02		0.07		0.05		0.04
KIND_OR		0.39	- - -	0.89		0.07		0.15		0.00		0.06		0.00		0.04		0.02		0.07		0.05		0.04
PARENT_C		0.39	- - -	0.89		0.07		0.15		0.00		0.06		0.00		0.04		0.02		0.07		0.05		0.04
PARENT_U		0.39	+++	0.89		0.07		0.15		0.00		0.06		0.00		0.04		0.02		0.07		0.05		0.04
KIND_R2		0.39	+++	0.89		0.07		0.15		0.00		0.06		0.00		0.04		0.02		0.07		0.05		0.04
KIND_SO		0.39	- - -	0.89		0.07		0.15		0.00		0.06		0.00		0.04		0.02		0.07		0.05		0.04
SLOPE	+	0.68		0.19		0.12	-	0.16		0.10		0.12	- - -	0.45	+	0.13		0.12	- -	0.28	+	0.15		0.01
SOL_DURA		0.40		0.12	+	0.29		0.01		0.12		0.16	+++	0.64	-	0.17	-	0.23		0.00		0.04		0.10
SOL_ENER		0.11		0.02		0.08		0.05		0.05		0.02	+++	0.92		0.05	+	0.22		0.09		0.09		0.07
WETLAND		0.18		0.13		0.15		0.04		0.06		0.11		0.01		0.05		0.08	+++	0.77		0.01		0.04
WVI	- - -	0.85		0.17		0.17		0.12		0.10		0.00		0.14		0.06	- -	0.29		0.06		0.07	+	0.12
WVI_SD	+++	0.86		0.30		0.04		0.10		0.00		0.09		0.12		0.01	+	0.15	-	0.17	+	0.16		0.03
WVI_X	++	0.81		0.33		0.11		0.06		0.03		0.11		0.08		0.08		0.07	-	0.21	+	0.20		0.08
SOL_DURA		0.40		0.12	+	0.29		0.01		0.12		0.16	+++	0.64	-	0.17	-	0.23		0.00		0.04		0.10

APPENDIX 7-1

SPECIFIC LABORATORY METHODS FOR STABLE ISOTOPE ANALYSES

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Carbon & Nitrogen

Method

Samples for sulphur isotopic analyses were combusted with an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA); these two gases were separated with a 3m GC column and analyzed with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen) (Brenna et al. 1997, Qi et al. 2003). Isotopic reference materials were interspersed with samples for calibration. Contribution of 17O is corrected by the IRMS software using the Santrock correction (Santrock et al. 1985).

Reporting of Carbon Isotope Ratios

Carbon isotopic ratios were reported in per mill relative to VPDB (Vienna Peedee belemnite) by assigning a value of +1.95 per mill to NBS 19 CaCO3 (Coplen 1994). Current NIST calibration of VPDB uses NBS19 and L-SVEC as anchor points. The carbon isotopic compositions of internationally distributed isotopic reference materials, had the laboratory analyzed them with the samples, are (Coplen et al. 2006):

NBS 19	CaCO3	+1.95 (exactly)
NBS 18	CaCO3	-5.01
IAEA-CO-1	CaCO3	+2.49
L-SVEC	Li2CO3	-46.6
RM 8542	Sucrose	-10.45
USGS24	graphite	-16.05
NBS 22	oil	-30.03
USGS40	glutamic acid	-26.39
USGS41	glutamic acid	+37.63
IAEA-CO-9	BaCO3	-47.32 (exactly)

The 2-sigma uncertainty of carbon isotopic results is 0.5 per mill unless otherwise indicated. This means that if the same sample were resubmitted for isotopic analysis, the newly measured value would lay wihtin the uncertainty bounds 95% of the time. The samples wer normalized using two internal running standards. Running standards were previously calibrated to NBS 19, RM 8542, and IAEA-CO-9 as defined above. The precision (1 sigma) of standards used and associated normalization coefficients are provided with the raw results file.

Sulphur

Method

Samples for sulphur isotopic analyses were combusted with an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA). SO2 gases were separated with a 0.8m GC column (105ºC) and analyzed with a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen) (Brenna et al. 1997). Final determination of 34S was based on collection of ions 64 and 66. The laboratory used a dual reactor configuration (Fry et al. 2002) which uses vanadium pentoxide added to each sample (~5 mg) and a full reactor of quartz chips to buffer 18O contribution to the SO2. No correction for oxygen isotope contribution was made. At least three primary isotopic reference materials were interspersed with samples for calibration.

Reporting of Isotope Ratios

Sulphur isotopic ratios were reported in per mill relative to VCDT (Vienna Canon Diablo Triolite) by assigning a value of -0.3 per mill to IAEA S-1 silver sulfide (Coplen & Krouse 1998). The sulphur isotopic compositions of internationally distributed isotopic reference materials, had the laboratory analyzed them with the samples are as follows (see Coplen et al. 2002 or http://www.ciaaw.org/Sulfur.htm):

IAEA-S-1	Silver sulfide	-0.3 (exactly)
IAEA-S-2	Silver sulfide	+22.67
IAEA-S-3	Silver sulfide	-32.55
IAEA-SO5	Barium Sulfate	+0.49
IAEA-SO6	Barium Sulfate	-34.05
NBS127	Barium Sulfate	+21.1

The 2-sigma uncertainty of carbon isotopic results is 0.5 per mill unless otherwise indicated. This means that if the same sample were resubmitted for isotopic analysis, the newly measured value would lay wihtin the uncertainty bounds 95% of the time. The precision (1 sigma) of standards used and associated normalization coefficients are provided with the raw results file.