ECOLOGY, GENETICS AND CONSERVATION OF

Himalayan Brown Bears

Muhammad Ali Nawaz

PhD Thesis 2008-9

ISBN: 978-82-575-0806-7
ISSN: 1503-1667

Ås, 2008

Department of Ecology and Natural Resource Management
Norwegian University of Life Sciences

ABSTRACT

Asian bears are greatly threatened due to the impact of human activities, yet there is a critical lack of knowledge about their status and requirements for survival, which complicates conservation efforts. This study documents ecological requirements, genetic structure and life history of Himalayan brown bears (*Ursus arctos*), which have fragmented and mostly declining populations in South and Central Asia.

Presently, brown bears in Pakistan are distributed over three main mountain ranges (Himalaya, Karakoram, and Hindu Kush), probably in seven populations. All of these populations are small and declining. Deosai National Park (DNP) supports the largest and most likely the only growing population (5% annual growth, based on the 14-years census). The genetic and field methods provided a population estimate of 40-50 individuals in DNP. The fecal DNA analysis revealed that the level of nuclear genetic diversity of the Deosai population was globally lower than brown bear populations that are considered to have a good conservation status, such as in Scandinavia or North America. However, in spite of the presence of a bottleneck genetic signature, the Deosai population has a moderate level of genetic diversity and is not at immediate risk of inbreeding depression. The DNP population has an exchange of individuals with neighboring populations in Pakistan and India, which is maintaining its genetic health.

The analysis of the diet of brown bears in DNP, combing classical and molecular genetic techniques, indicated a great diversity in food species. They consumed over 50 plant species, invertebrates, ungulates, and several rodents. Eight plant families; Poaceae, Polygonaceae, Cyperaceae, Apiaceae, Asteraceae, Caryophyllaceae, Lamiaceae, and Rubiaceae were commonly eaten. However, graminoids made up the bulk of the diet. Golden marmots (*Marmota caudata*) comprised the major mammalian biomass in the park, and were also the main meat source for bears. Animal matter, comprising 36% of the dietary content, contributed half of the digestible energy, due to its higher nutritious value. Male brown bears were more carnivorous than females, probably because of their larger size, which requires higher energy and also makes them more efficient in capturing marmots. The habitat analysis (by Ecological Niche Factor Analysis) revealed that bears avoided higher elevations and steeper slopes, and showed a higher preference for more productive parts of the park (marshy, grassy, and stony vegetation types). The marshy vegetation was the most preferred habitat, probably due to its highest forage production and highest density of golden marmots. Brown bears tolerated human structures, such as roads and camps, but strongly avoided grazing areas with higher livestock density.

We followed recognizable individuals from 1993 through 2006, and documented an extremely low reproductive rate in the Deosai population, due to late age of first reproduction (8.25 years), a long reproductive interval (5.7 years), and a small litter size (1.33). The family association (4.2 years) is the longest ever reported for brown bears and might have contributed to relatively higher survival of young. The reproductive rate of the Deosai population was the lowest yet documented for any brown bear population.

The estimated digestible energy available to brown bears in Deosai National Park was also the lowest yet documented for any brown bear population, due to the lack of fruits and relatively lower meat content in the diet. The poor quality of the diet and high cost of metabolism in a high altitude environment probably explain the very low reproductive potential of this population. The combination of poor intrinsic growth potential and exchange of individuals suggest that the observed population growth was a product of both reproduction and immigration.

The recovery of the brown bear population in Deosai is significant, because the species is declining throughout most of its range in South Asia. However, considering that the population is still small, has poor growth potential, and a relatively low genetic diversity, it requires a continuous field and genetic monitoring. Maintaining and improving the connectivity with adjacent populations in Pakistan and India will be of paramount importance for its long-term survival. Managing human resource use without adversely affecting the brown bear population has been a major management challenge in DNP, and seems to have been achieved. We recommend monitoring the numbers and distribution of livestock and conducting a detailed inventory of the rangeland to maintain sustainable stocking rates in future. Brown bear conservation efforts in South Asia must target reducing human-caused mortalities, particularly of adult females. Involvement of people can increase efficiency in conservation, in addition to reducing cost and conflicts. Environmental education is an important instrument to change perceptions and attitudes, and is vital to achieving synergy in conservation efforts.

SAMMENDRAG

Asiatiske bjørner er svært truet av menneskelig aktivitet, og bevaringen er vanskelig fordi det er for liten kunnskap om deres status og overlevelseskrav. Dette studiet dokumenterer de økologiske kravene, den genetiske strukturen og livshistorien til den himalayiske brunbjørnen (*Ursus arctos*), som i dag består av fragmenterte og stort sett minkende populasjoner i Sør- og Sentral-Asia.

Brunbjørnen i Pakistan har tilhold i tre hovedfjellkjeder (Himalya, Karakoram og Hindu Kush), og er antageligvis fordelt på syv populasjoner. Alle disse populasjonene er små og minkende. Den største og eneste økende populasjonen (5 % årlig vekst basert på tellinger over 14 år) er i Deosai Nasjonal Park (DNP). Basert på genetikk- og feltmetoder er populasjonen estimert til 40-50 individer i DNP. DNA-analyser fra bjørneekskrementer avdekket at den genetiske diversiteten var lavere hos Deosaipopulasjonen enn i bjørnepopulasjoner som er kjent for å ha en god bevaringsstatus, som i Skandinavia og Nord-Amerika. Til tross for tilstedeværelsen av en genetisk flaskehals, har Deosaipopulasjonen en moderat genetisk diversitet og er ikke utsatt for umiddelbar innavl. DNP-populasjonen utveksler individer med nabopopulasjoner i Pakistan og India, som opprettholder dens genetiske sunnhet.

Analyser av brunbjørnens diett i DNP ved bruk av klassiske og molekylære genetiske teknikker i kombinasjon, indikerer en stor diversitet i bjørnens føde. De konsumerte over 50 plantearter, invertebrater, hovdyr og flere gnagere. Åtte plantefamilier; Poaceae, Polygonaceae, Cyperaceae, Apiaceae, Asteraceae, Caryophyllaceae, Lamiaceae og Rubiaceae var vanlige i dietten. Graminoidene utgjorde likevel hoveddelen av dietten. Murmeldyr (*Marmota caudata*) utgjorde den største pattedyrbiomassen i nasjonalparken, og var også bjørnenes hovedkilde til kjøtt. Dyr inngikk i 36 % av diettinnholdet, og på grunn av deres høye næringsverdi, bidro de til halvparten av den fordøyelige energien. Hanner var mer kjøttetende enn binner, antageligvis på grunn av en større kropp, som krever mer energi, men som også gjør de mer effektive til å fange murmeldyr. Habitat analysene (økologisk nisjefaktoranalyse) viste at bjørner unngikk høyereliggende områder og bratte skråninger, og viste en høyere preferanse for mer produktive deler av parken (sump, gresseng og steinete vegetasjonstyper). Myrvegetasjonen var den mest foretrukne habitattypen, antageligvis på grunn av høy fórproduksjon og mange murmeldyr. Brunbjørner tolererte menneskelige strukturer som veier og leirplasser, men unngikk spesielt beiteområder med høy tetthet av husdyr.

Vi fulgte identifiserbare individer fra 1993 til og med 2006 og dokumentert en ekstremt liten reproduktiv rate i Deosaipopulasjonen, hvilket skyldtes sen alder for første reproduksjon (8.25 år), lange intervall mellom hver reproduksjon (5.7 år) og små kullstørrelser (1.33). Familietilknytningen (4.2 år) er den lengste som er beskrevet for brunbjørnen og kan ha bidratt til høyere overlevelse for bjørnungene. Deosaipopulasjonens reproduktive rate var den laveste som er beskrevet for alle brunbjørnpopulasjoner. Den estimerte fordøyelige energien som var til rådighet for

brunbjørnen i Deosai nasjonalpark var den laveste som er beskrevet for brunbjørnpopulasjoner, noe som skyldtes mangel på frukter og et relativt lite innslag av kjøtt i dietten. En diett med lavt næringsinnhold og den høye metabolske kostnaden i høyalpine miljøer, forklarer antagelig det lave reproduktive potensialet for populasjonen. Den lave iboende potensielle populasjonsveksten og utveksling av individer, indikerer at den beskrevne populasjonens vekst var et resultat av både reproduksjon og immigrasjon.

Fordi forekomsten av brunbjørn er avtagende i nesten hele Sør-Asia, er økningen i brunbjørnpopulasjonen i Deosai av stor betydning. Liten populasjonsstørrelse, lavt vekstpotensiale og lav genetisk diversitet krever imidlertid kontinuerlig oppfølging i felt og overvåking av den genetiske utviklingen i populasjonen. Opprettholdelse og forbedring av forbindelsen med tilstøtende populasjoner i Pakistan og India kommer til å ha stor betydning for overlevelsen på lang sikt. Forvaltning av menneskelig ressursbruk uten å påvirke brunbjørnpopulasjonen har vært en betydelig forvaltningsutfordring i Deosai nasjonalpark og ser ut til å ha vært vellykket. Vi anbefaler å overvåke antall husdyr og fordelingen av disse gjennom detaljerte inventeringer av beiteområdene slik at en i fremtiden kan opprettholde et bærekraftige beitetrykk. Bevaring av brunbjørn i Sør-Asia må fokusere på å redusere menneskeskapt mortalitet, særlig for binner. Involvering av befolkningen kan øke effekten av bevaringsarbeidet, i tillegg til å redusere utgifter og å dempe konflikter. Utdanning i natur- og miljøvern er en viktig faktor for å endre holdninger og oppfatninger, og vil være av grunnleggende betydning for å oppnå synergieffekter av bevaringsinnsatsen.

KHULASA
خلاصہ

ایشیاء میں ریچھوں کی بقاء انسانی آبادی اور طرز زندگی کی وجہ سے خطرات سے دوچار ہے۔ مزید براں انکی زندگی کی ضروریات کا علم انتہائی محدود ہے جو ان کی بقا کی کوششوں میں حائل ہے۔ ہم نے ہمالیائی بھورے ریچھ کی زندگی کی ضروریات، Genetics اور Life History کا مطالعہ کیا ہے۔ ہمالیائی بھورا ریچھ جنوبی اور وسطی ایشیاء کا باشندہ ہے لیکن اسکی تعداد بہت کم، بٹی ہوئی اور زوال پذیر ہے۔

پاکستان میں بھورے ریچھ کی تقریباً 7 آبادیاں ہمالیہ، قراقرم اور ہندوکش کے پہاڑی سلسلوں میں موجود ہیں۔ تاہم دیوسائی نیشنل پارک کے علاوہ تمام آبادیاں بہت چھوٹی اور سکڑ رہی ہیں۔ دیوسائی میں ان کی آبادی کا تخمینہ 50-40 جانوروں کا ہے۔ فضلہ کے جینیاتی (Genetic) تجزیہ سے پتہ چلا ہے، کہ ان کا جینیاتی تنوع باقی بھورے ریچھوں سے کافی کم ہے۔ تاہم bottleneck کے آثار کے باوجود ان کا جینیاتی تنوع درمیانے درجے کا ہے۔ بھورے ریچھوں کی آمدورفت دیوسائی نیشنل پارک اور قریبی پاکستانی اور بھارتی علاقوں کے درمیان موجود ہے۔ جس کی وجہ سے ان کی جینیاتی صحت برقرار ہے۔

دیوسائی میں بھورے ریچھوں کی خوراک بہت سی اقسام پر مشتمل ہے۔ وہ پچاس سے زیادہ قسم کے نباتات، غیر فقری جانور، چوپائے اور متعدد قسم کے چوہے کھاتے ہیں۔ پودوں کے آٹھ خاندان (Poaceae, Polygonaceae, Cyperaceae, Apiaceae, Asteraceae, Caryophyllaceae, Lamiaceae, Rubiaceae) عموماً ان کی خوراک کا حصہ ہوتے ہیں۔ تاہم خوراک کا بیشتر حصہ گھاس پھونس پر مشتمل ہے۔ سنہرے چوہے دیوسائی میں کثیر تعداد میں دستیاب ہیں اور ریچھوں کیلئے گوشت کا اہم ذریعہ ہیں۔ اگرچہ خوراک کا صرف 36% حصہ حیوانات پر مشتمل ہے لیکن ریچھوں کو نصف توانائی ان سے میسر ہے۔ نر ریچھ زیادہ گوشت خور ہیں جسکی وجہ ان کا نسبتاً بڑا جسم ہوسکتا ہے۔ کیونکہ بڑے جسم کیلئے زیادہ توانائی درکار ہوتی ہے اور وہ چوہوں کی کھدائی کیلئے زیادہ موثر ہوتے ہیں۔ دیوسائی میں ریچھوں کے مسکن کے تجزیے سے پتا چلا ہے کہ وہ زیادہ بلندیوں اور ترچھی ڈھلانوں سے اجتناب کرتے ہیں۔ نباتاتی طور پر زرخیز علاقے ان کے پسندیدہ مسکن ہیں۔ جوہڑ نما گھاس کے میدان (Marshy Habitat) سب سے زیادہ پسندیدہ ہیں۔ کیونکہ ان میدانوں کی نباتاتی پیداوار سب سے زیادہ ہے اور وہاں پر سنہری چوہوں کی تعداد بھی نسبتاً زیادہ ہے۔ ریچھ سڑکوں اور خیموں سے مانوس نظر آتے ہیں لیکن یہ مویشیوں کے چرنے والے علاقوں سے گریز کرتے ہیں۔

ہم نے چودہ سال (2006-1993) تک ریچھوں کا انفرادی طور پر مشاہدہ کیا ہے۔ جس سے پتہ چلا کہ ان کی تولیدی پیداوار انتہائی محدود ہے۔ وہ اوسطاً 8 سال کی عمر میں پہلا بچہ پیدا کرتے ہیں۔ بچوں کا درمیانی وقفہ 5.7 سال ہے اور پیدائش کے وقت اوسطاً 1.33 بچے پیدا ہوتے ہیں۔ ماں اپنے بچوں کو اوسطاً 4.2 سال تک ساتھ رکھتی ہے۔ اتنی لمبی رفاقت ریچھوں میں کہیں اور نہیں دیکھی گئی اور شاید یہ بچوں کی کم شرح اموات کا سبب بھی ہے۔ قدرتی طور پر بڑھوتری کی صلاحیت دیوسائی کے ریچھوں میں دنیا بھر کے بھورے ریچھوں کی نسبت انتہائی کم ہے۔ خوراک سے حاصل کردہ توانائی بھی دوسرے ریچھوں کی نسبت بہت کم ہے جس کی وجہ خوراک میں پھلوں کا فقدان اور گوشت کی کمی ہے۔ ہمارے خیال میں خوراک کی پست غذائیت اور انتہائی بلندی پر رہنے کی وجہ سے زیادہ توانائی کی ضرورت بھورے ریچھوں میں سست افزائش نسل کے اسباب ہیں۔ دیوسائی میں ان کی تعداد میں سالانہ 5% اضافہ ہو رہا ہے۔ جس کی وجہ افزائش نسل کے علاوہ دوسرے علاقوں سے ریچھوں کی آمد ہے۔

دیوسائی میں بھورے ریچھ کی آبادی میں اضافہ نہایت اہمیت کا حامل ہے کیونکہ حیوانات کی یہ نوع پورے جنوبی ایشیاء میں زوال پذیر ہے۔ انکی کم تعداد، قدرتی بڑھوتری کی مختصر صلاحیت اور نسبتاً کم جینیاتی تنوع جیسے عوامل کا تقاضہ ہے کہ اس نادر جانور کی نگرانی اور حفاظت جاری رکھی جائے۔ دیوسائی سے ملحقہ علاقوں میں ان کی آمدورفت کو برقرار رکھنا بلکہ بہتر بنانا ان کے مستقبل کی بقا کیلئے بہت ضروری ہے۔ دیوسائی میں مویشیوں کی تعداد کی نگرانی ہونی چاہئے اور خیال رکھا جائے کہ ان کی تعداد علاقے کی پیداواری صلاحیت سے تجاوز نہ کرے۔

جنوبی ایشیاء میں بھورے ریچھ کو معدومیت سے بچانے کے لیے ان کے شکار کو سختی سے روکا جائے۔ ان کی بقاء کی کاوشوں کو مقامی لوگوں کے اشتراک سے مزید موثر بنایا جاسکتا ہے۔

CONTENTS

LIST OF PAPERS

This thesis is based on following articles, which are referred to in the text by their Roman numerals:

Paper I:	Nawaz, M. A. 2007. Status of the brown bear in Pakistan, Ursus 18:89-100.
Paper II:	Bellemain, E., M. A. Nawaz, A. Valentini, J. E. Swenson, and P. Taberlet. 2007. Genetic tracking of the brown bear in northern Pakistan and implications for conservation, Biological Conservation 134:537-547.
Paper III:	Nawaz, M. A., J. E. Swenson, and V. Zakaria. An increasing low-productive, high-altitude brown bear population in South Asia; a successful case of national park management. – Submitted.
Paper IV:	Valentini, A., C. Miquel, M. A. Nawaz, E. Bellemain, E. Coissac, F. Pompanon, L. Gielly, C. Cruaud, G. Nascetti, P. Winker, J. E. Swenson, P. Taberlet. New perspectives in diet analysis based on DNA barcoding and parallel pyrosequencing: the *trn*L approach. – Molecular Ecology Resources (in press).
Paper V:	Nawaz, M. A., A. Valentini, N. K. Khan, C. Miquel, P. Taberlet, J. E. Swenson. Diet of the brown bear in Himalaya: combining classical and molecular genetic techniques. – Manuscript.
Paper VI:	Nawaz, M. A., and J. E. Swenson. Habitat selection by brown bears in Deosai National Park, Pakistan and implications for park management. – Submitted.

1. INTRODUCTION

There is general agreement that biodiversity is under assault globally due to population growth and an ever-increasing use of natural resources (Lewton and May 1995; Whittaker et al. 2005). The species extinction rate has increased greatly in recent times, and mammals are the most vulnerable (Primack 2002). By adopting the Convention on Biological Diversity, many governments have acknowledged biodiversity conservation as a global concern and an integral part of the development process. However, achieving such a goal in developing parts of the world, like South Asia, is particularly challenging, due to large-scale poverty, an enormous population, and greater dependence on natural resources. In the Himalayan region of the South Asia, rangelands and livestock are dominant sources of subsistence and are the major cause of conflicts with the conservation of mammals (Mishra 2001). Consequently all large mammals are threatened with extinction in Himalaya. Carnivores are particularly vulnerable, because they 1) naturally exist in small populations, and population size is one of the best predictors of extinction (Pimm et al. 1988), 2) they have large spatial requirements and an adequate prey base, and 3) they are poorly accepted by the public, as they pose a threat to livestock. One such carnivore species is the brown bear (*Ursus arctos*), which has declined in numbers and distribution by more than 50% in Asia during the past century (Servheen 1990).

Among the eight species of bears, the brown bear has the most widespread distribution (Servheen 1990; Schwartz et al. 2003). They are found throughout most of the northern hemisphere, including the Palearctic and Nearctic. The brown bears' status throughout the world varies from threatened to common; hence they are categorized as LR (lc) in the 2004 IUCN Red List and placed in Appendix II of the Convention on International Trade in Endangered Species (CITES). The species is most endangered in Asia, where small isolated populations exist mostly in remote mountainous areas (Servheen et al. 1999). The Himalayan brown bear (*U. a. isabellinus*), a subspecies that represents an ancient lineage of the brown bear (Galbreath et al. 2007), is distributed over the Great Himalaya region. Brown bears are generally well studied in North America and Europe. However there is a critical lack of information about their status and requirements for survival in Asia (Servheen et al. 1999), which hinders conservation efforts.

The Deosai Plateau in northern Pakistan has long been recognized as the main stronghold of brown bears in the country (Schaller 1977; Rasool 1991; Roberts 1997; Nawaz 2007). Population surveys in 1993 revealed that there were not more than 20 individuals in Deosai (Paper III), which raised concerns for their survival and lead to the declaration of area as a national park. A conservation program was initiated by the Himalayan Wildlife Foundation in collaboration with the Northern Areas Forest and Wildlife Department to protect the population and its habitat in order to allow the population to recover. Small population size is a great concern in conservation biology, because such populations may go extinct, even while protected, due to their intrinsic limitations (Primack 2002). When population size drops below a threshold, populations become susceptible to genetic, demographic and environmental stochasticities (Shaffer 1981). The loss of genetic diversity, due to genetic drift and inbreeding, is a key concern for the viability of small populations. Evolutionary processes, such as mutations, migration, selection, and stochasticity are also fundamentally different from those in large populations. In small populations, the role of stochasticity increases and the impact of selection is limited (Frankham et al. 2002). Due to demographic stochasticity, variations in birth and death rates cause the population size to fluctuate randomly, and may reduce it further. Species with low reproductive rates, like brown bears (Bunnell and Tait 1981), are particularly susceptible to demographic stochasticity, because they require a longer time to recover (Primack 2002). Random variation in the biological and physical environment causes temporal clustering of birth and death rates, which would increase uncertainty in population size (Lacy 2000).

Unfortunately, these three stochastic factors act simultaneously and often drive the size of populations downward, which ultimately leads to extinction. Such populations would only recover if a careful program is implemented. Understanding the ecological requirements, life history, population size, and dynamic processes that affect the population is vital for formulating an effective recovery and management plan of small populations (Primack 2002). These considerations provided the motivation for this study.

1.1 Aims of the Study

1.1.1 Status and Distribution

Documenting the status and distribution of Asian bears has been identified as a priority action for conservation by the IUCN/SSC Bear Specialist Group (Servheen et al. 1999). We combined field surveys, interviews and non-invasive genetic techniques to answer following questions: *i*) What is current status and distribution of brown bears in Pakistan, and specifically the population size in Deosai National Park (DNP)?, *ii*) Are the Pakistani populations of brown bears isolated genetically and geographically?, *iii*) Is the population in DNP increasing?

1.1.2 Genetic Diversity

Bear numbers in DNP declined drastically to as low as 19 in 1993 (Paper III). Although the population in Deosai has been recovering gradually, due to strict protection and conservation efforts, the decline could have reduced the genetic variability considerably. As a consequence, this population might suffer from inbreeding, and its survival might be compromised. We used the increasingly popular non-invasive genetic technique (Taberlet et al. 1996; Taberlet et al. 1999), and aimed to answer the following questions: *i*) What is the level of genetic diversity in the Deosai population?, *ii*) Did the population suffer from a bottleneck at the genetic level and how long ago did it begin to decline?, *iii*) Are Deosai bears at risk of inbreeding depression?

1.1.3 Diet Selection and Methodological Developments

Knowledge of diet and foraging behavior is important in the understanding of animal ecology and evolution (Sih 1993). Diet studies help identify key environmental resources required by a species, and thus enhance the understanding of habitat preferences and provide a knowledge base for successful management and conservation of wildlife populations. Resource selection is related to reproductive success in animals (McLoughlin et al. 2006), therefore an analysis of diet and habitat help understand the life history of a species.

Several methods, from field observations to microscopic and chemical analysis of feces have been developed to evaluate the composition of animal diets. All of these methods have limitations, and their results are generally not comparable (Shrestha and Wegge 2006). Some methods provide description of food items (e.g, Microhistological analysis, Sparks and Malechek 1968) but are tedious and still identify only part of the diet. Other methods (e.g; Stable-isotope analysis, Hilderbrand et al. 1996; Near Infrared Reflectance Spectroscopy, Foley et al. 1998) provide only an estimation of the nutritional components, and therefore may not be helpful in resource management, because actual food sources remain unidentified. Studying food habits in herbivores is particularly challenging, because of the limited reliability and practicality of the available methods (Barker 1986). In this study we aimed to develop a DNA-based universal method, which could give a reliable and precise description of herbivore's diet. We then combined this new technique with available classical methods to precisely document the diet of the brown bear in DNP in relation to its availability and contribution to energy assimilation.

1.1.4 Habitat Selection

One of the major reasons DNP was created was to protect a declining population of brown bears. Since the livelihoods of local communities were dependent on park resources, a zoning plan was introduced (Paper III). The zoning plan allowed the distribution of park resources among various competing interests, such as human uses and wildlife, in order to meet management goals. The ecological needs of brown bears were not known at that time, therefore the allocation of areas for bears was based on sightings of brown bears and subjective assessments. The brown bear population in the park is growing (Paper III), and at the same time the magnitude of public resource use is increasing. This demands better understanding of the available resources and habitat use by brown bears, for appropriate management in future. We assessed these resources and their spatial distribution, and investigated habitat selection by brown bears.

1.1.5 Life History

The fitness of an organism is influenced by life history traits, which often are flexible and vary with environmental conditions (Dingle 1990; Stearns 1992; Clutton-Brock 1988). Variation in energy and environmental conditions over a geographical range induce variation in life history (Stevans 1989; Rosenzweig and Abramsky 1993; Brown 1995). This geographic pattern of life history variation is not limited to interspecific relationships, as populations may also differ within a species' range (Ferguson and McLoughlin 2000). Habitat stability (i.e., the degree of its seasonality and predictability) and temporal stochasticity are the two environmental factors that have a major impact on life history (Southwood et al. 1974; Clark and Yoshimura 1993). Brown bears are found throughout most of the northern hemisphere and occupy a variety of habitats from tundra to temperate forests (Schwartz et al. 2003; Servheen et al. 1999), consequently their life-history traits are diverse (Dahle and Swenson 2003; Stringham 1990; Zedrosser 2006).

The life history of high-altitude brown bears has never been documented. However, in environmental extremes (high seasonality, low productivity and temporal stochasticity), a less productive life-history is expected (Ferguson and McLoughlin 2000; Boyce et al. 2002; den Boer 1968). The assessment of reproductive performance and survival of individuals is important, because these factors limit population growth (Schwartz et al. 2006). Therefore we estimated demographic parameters and factors affecting the viability of high-elevation brown bears. We are the first to have done this.

2. STUDY AREA

Although we surveyed other parts of Northern Pakistan to determine the status of brown bears in the country, DNP was the main focus during this study (Fig. 1). DNP (75° 27' N, 35° 00' E) is an alpine plateau of about 1800 km^2 east of Nanga Parbat Peak, Northern Areas, Pakistan. The central part of DNP is relatively flat (0-10° slope) at elevations between 3400-4000 m, whereas the peripheral areas are steeper (up to 50° slope), with elevations up to 5300 m. Mean daily temperatures range from –20°C to 12 °C. The annual precipitation is 510 mm to 750 mm, and falls mostly as snow (HWF, 1999). The vegetation is predominately herbaceous perennials, grasses and sedges. There are four kinds of habitats represented in the park; marshy, grassy, stony and rocky (Paper VI). Marshy habitat is dominated by *Poa* and *Carex* spp., with some herbaceous plants. Grassy habitat is dominated by the Poaceace family, and stony habitat has a great variety of herbaceous flowering plants. Rocky habitat is generally devoid of vegetation. Marshy habitats contribute most to the forage production, followed by grassy and stony vegetation habitats, whereas rocky areas are unproductive. The surrounding valleys have habitats distinct from the park (coniferous forest, shrubs, rocky and grassy slopes).

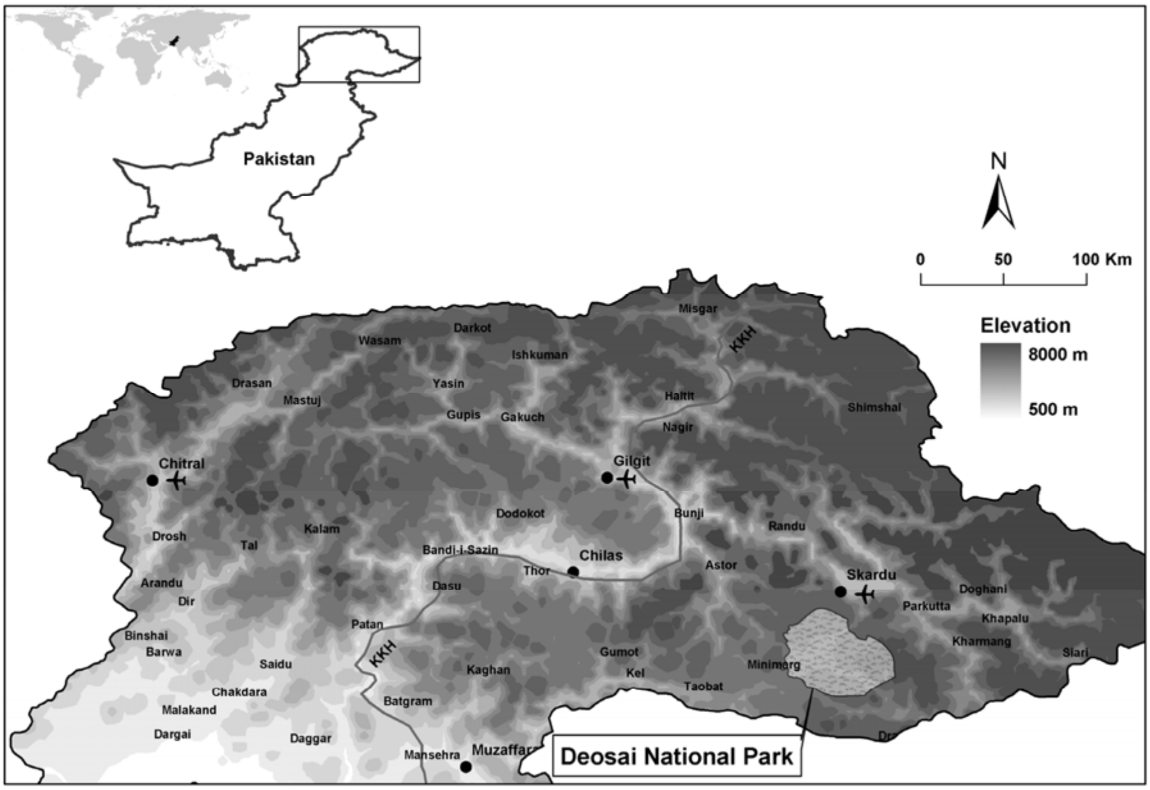

Figure 1: Location of Deosai National Park, Northern Areas, Pakistan.

The brown bear is the flagship species of the park; other mammals include Tibetan wolf (*Canis lupus chanco*), Himalayan ibex (*Capra ibex sibrica*), Tibetan red fox (*Vulpus vulpus montana*), golden marmot (*Marmota caudata*) and 17 other small mammal species (Nawaz et al. 2006). DNP is a typical highlands ecosystem, which is characterized by low atmospheric pressure, cold, aridity, low oxygen and carbon dioxide levels, intense isolation, rapid radiation, and high ultraviolet radiation (Mani 1990; Mani and Giddings 1980). The area has been dynamic climatically and geologically during the late Holocene (Kuhle 1997; Meiners 1997). The park is covered by snow most of the year (October-May, depending on weather). Therefore brown bears, which usually den in the surrounding valleys, come to DNP in June and leave in early October, when the snow returns.

DNP is a relatively flat area between narrow valleys and steep mountains, close to the Line of Control with India. Although there is no permanent habitation, because of the high altitude and extreme climate, there are many settlements along the periphery of DNP. They are located in numerous valleys and have various stakes in Deosai, especially traditional grazing rights. All but four peripheral communities utilize DNP's outer slopes and peripheral valleys for grazing. Four communities, Sadpara, Shilla, Dhappa and Karabosh, claim traditional grazing rights within the boundaries of DNP and their livestock occupy the eastern part of DNP during summer. In addition to these sedentary communities, there are nomad groups (*Bakarwals* or *Gujjars*), which come from the lowlands and compete for grazing resources. Approximately 9,000 livestock (belonging to resident and nomad communities), mainly goats and sheep, grazed within DNP in 2004.

3. MATERIALS AND METHODS

3.1 Methodological Advances

Working with a small population of a large carnivore in Himalaya required special considerations regarding methodology. We refined existing techniques, developed new methods, and used multiple approaches for each component of the study to ensure robust results (Fig. 2). For example we evaluated field-based population size estimates with a genetic method (Paper II), and combined classical scat analysis, molecular genetic technique, and stable-isotope analysis for understanding nutritional ecology. For genotyping of feces, we adopted a protocol developed for the Scandinavian brown bears (Bellemain and Taberlet 2004). The fecal samples from Himalaya were more degraded and less polymorphic, due to small population size (e.g., Mu10 and G10L were represented by only one or two alleles). Therefore we further developed that protocol by designating two new microsatellite primer pairs, namely G10J and G10H (Paper II). We ensured a high reliability of the genetic data by repeating amplifications (multi-tubes approach) and selecting samples with high quality-indices.

Two life forms of plants, graminoids and herbs, dominate in DNP, and in the bears' diet. Therefore differentiating diet components in scats on the basis of morphology was difficult. To overcome this limitation, we developed a new molecular technique (the *trn*L approach, Paper IV) to identify diet components to a finer detail. The *trn*L approach combines the plant barcoding concept (Chase *et al.* 2005, 2007) with the new highly parallel sequencing systems (Margulies *et al.* 2005). This method amplifes the P6 loop of the chloroplast *trnL* (UAA) intron (Taberlet et al. 2007) via the polymerase chain reaction (PCR; Mullis and Faloona 1987) and by subsequently sequencing individual molecules of this PCR product on the 454 automated sequencer (Roche Diagnostic, Basel, Switzerland). This method is very robust, fast, simple to implement, and broadly applicable to potentially all herbivorous species eating angiosperms and gymnosperms, from mammals to insects, birds and mollusks. The *trn*L approach represents a significant breakthrough in plant identification when using fecal material. We also introduced an approach to link DNA-based individual identification, the trnL approach, scat analysis and stable-isotope analysis for investigating the diet of an omnivorous species

3.2 Sample Collection

Three components of the study; genotyping, diet, and habitat use, were based on scat samples (Fig. 2), which were collected between 2003-2007. We divided the study area into five blocks, and searched each block for bear scats in order to cover most of the park. Transects were placed in each block, and walked by a team of 2-3 people. Apart from this planned collection, the field staff of DNP also collected samples during their normal patrolling in the park. For most of samples, the date and location (Geographic latitude/longitude) were recorded using a Global Positioning System (GPS) receiver (Garmin 12XL). Scats were air dried and stored in polythene bags for analysis in the lab.

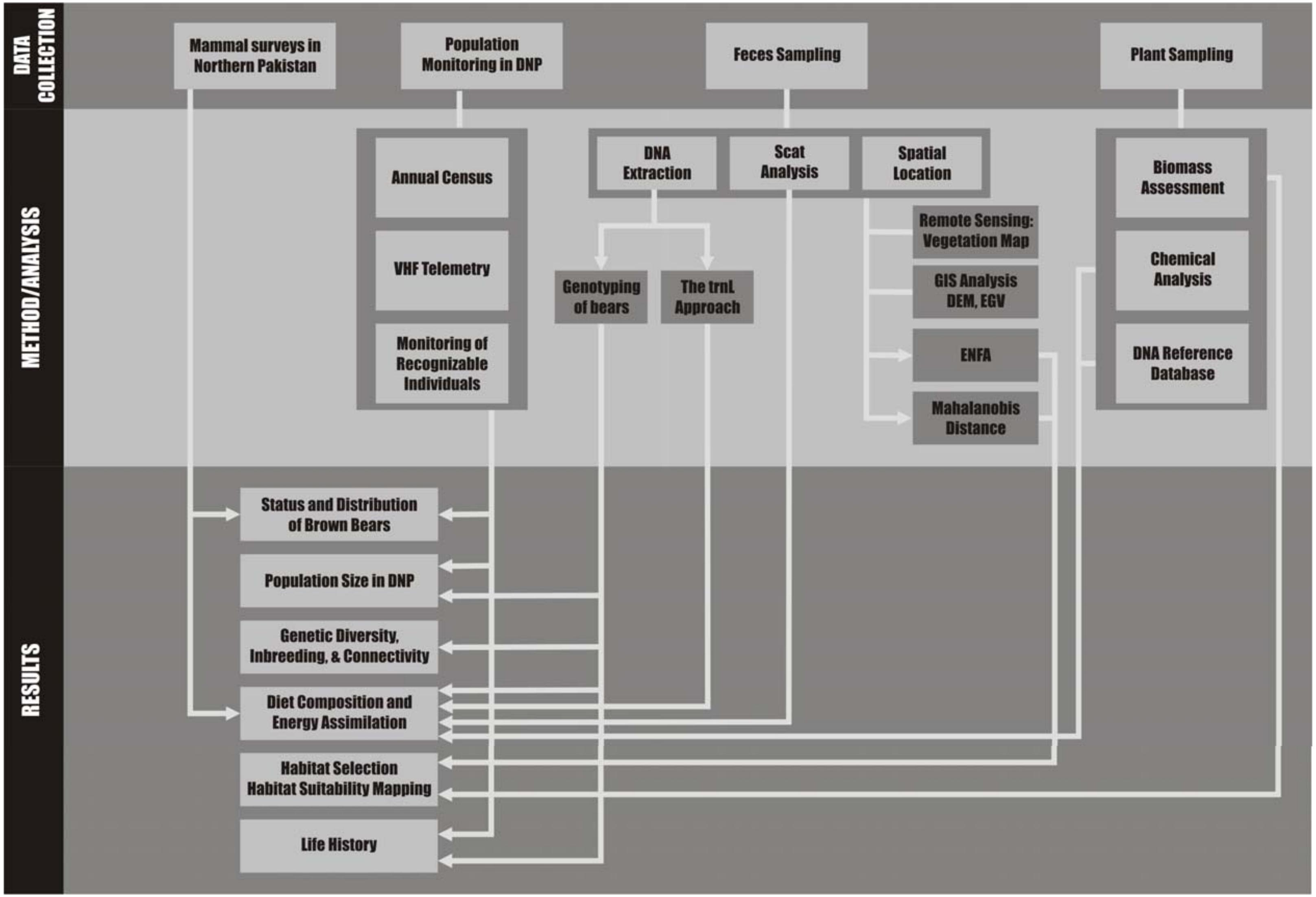

Figure 2: Methodological framework of the study

Samples for genetic analysis (1 cm^3) were collected in 20-ml plastic bottles with a stick of wood. Bottles were then filled with 95% alcohol to preserve the samples until DNA extraction. We used 136 scat samples in genetic analyses, 334 scats in diet analyses, and locations of 450 scats in habitat analyses. We also collected 112 plant specimens (Appendix A) from Deosai for developing a reference database to be used in the *trn*L approach for the diet study (see details below). These plants were identified by taxonomists from the University of Karachi, Karachi, Pakistan Museum of Natural History, Islamabad, and Quaid-i-Azam University, Islamabad.

3.3 Status and Distribution

We conducted field surveys, interviews and consulted published and unpublished literature. Field surveys were conducted in Neelam and Gurez valleys of Azad Jammu and Kashmir, in the Northern Areas of Pakistan, and eastern part of the NWFP Province. We interviewed people in local communities, mountain nomads (*gujjars*), field staff of wildlife or forest departments, tourist operators (particularly for glacier areas), wildlife biologists, and relevant institutions and organizations.

DNP was surveyed every year (1993-2006) during 10-15 days in late September or early October to obtain a population census. The recognizable bears monitored during the summer season (see details below) helped us avoid double counting and increased the reliability of the census. We also estimated population size from the genetic data (see below) by rarefaction indices, using equations developed by Kohn et al. (1999) and Eggert et al. (2003). These methods calculate the population size as the asymptote of the relationship between the cumulative number of unique genotypes and the number of samples typed.

We estimated the finite rate of increase (λ) from annual censuses of the Deosai population, with λ as the ratio of numbers in two successive years (Caughley 1977). The λ was calculated by the exponential rate of increase, β, which was estimated by regressing population size (ln N) on year.

3.4 Genetic Diversity

DNA extractions were performed using the Qiamp DNA Stool Kit (Qiagen, Netherlands). For individual identification, the extracted DNA was amplified using the six microsatellite primers; Mu23, Mu50, Mu51, Mu59, G10J and G10H. For sex identification, we used the sex-primers described in Bellemain and Taberlet (2004). To estimate population genetics parameters and relatedness, we amplified the following 12 additional microsatellites: G1A, G1D, G10B, G10C, G10L, G10P, G10X, G10O (Paetkau et al. 1995; Paetkau and Strobeck 1994) and Mu05, Mu10, Mu15, Mu61 (Taberlet et al. 1997), using a modified protocol from Waits et al. (2000). A quality index (Miquel et al. 2006) was calculated for each sample and locus. The loci G10P, Mu05, and Mu61 were discarded from the analysis because of their low quality-indices (below 0.6). Finally, genotypes were obtained based on 15 loci. The multilocus gentotypes allowed us to determine the gene flow between the brown bear population in DNP and neighboring areas.

Using the software GIMLET version 1.3.1 (Valière 2002), we computed the probability of identity. We used a Bayesian approach to detect and date a potential bottleneck in the Deosai bear population. This method is implemented in the MSVAR program (Beaumont 1999), available at http://www.rubic.rdg.ac.uk/~mab.

Based on the 15 loci genotypes, we ran population genetic analyses using the softwares GENEPOP version 3.4 (Raymond and Rousset 1995) and GENETIX version 4.02 (Belkhir et al. 1996-2004). Nuclear genetic diversity was measured as the number of alleles per locus (A), the observed heterozygosity (Ho), as well as Nei's unbiased expected heterozygosity (He) (Nei 1978). Deviations from Hardy-Weinberg equilibrium were tested using an exact test. We calculated pairwise genetic relatedness between pairs of individuals using Wang's estimator (Wang 2002) and the software SPAGeDi version 1.0 (Hardy and Vekemans 2002).

3.5 Diet Composition and Energy Contribution

We surveyed the park area and surrounding valleys in order to estimate the biomass of ungulates and golden marmots available to brown bears. The composition of the brown bear diet was investigated by combining three methods; scat analysis, *trn*L approach, and stable-isotope analysis.

Scat analysis: Scats were soaked and washed through a 0.8-mm mesh. We selected three sub-samples from this homogenized mixture, and sorted diet components into nine categories; 1) rodents, 2) ungulates, 3) invertebrates, 4) graminoids, 5) forbs, 6) shrubs, 7) roots, 8) seeds, and 9) crops. To adjust for differential digestibility of diet items, we applied Correction Factors (CF) proposed by Hewitt and Robbins (1996). We estimated the energy contribution of each component of diet, by multiplying adjusted volumes by their respective estimated digestible energy values. For animal matter we used digestible energy values reported in Pritchard and Robbins (1990). For plants we collected fresh samples of 20 plant species (9 graminoid, 10 forbs and 1 shrub) during early August 2006. These plants were weighted when fresh, air dried, and stored in paper envelopes. The chemical analysis was conducted at the Animal Science Institute, National Agricultural Research Council, Islamabad. The following parameters were determined using methods described in AOAC (1984): dry matter (DM), crude protein (CP), crude fiber (CF), ether extract (EE), nitrogen free extract (NFE), and total digestible nutrients (TDN). The digestible energy (DE) was calculated as: DE (Mcal/kg) = 0.0365 x TDN%+0.172 (Fonnesbeck et al. 1967; Fonnesbeck 1968).

Genetic analysis (the *trn*L approach): The genetic analysis was carried out in four main steps (Paper IV and V); 1) total DNA was extracted from about 10 mg of a feces sample with the DNeasy Tissue Kit (Qiagen GmbH, Hilden, Germany). 2) Each sample was amplified with primers *g* and *h* (Taberlet et al. 2007), modified by the addition of a specific tag on the 5' end in order to allow the recognition of the sequences after the pyrosequencing, where all the PCR products from the different samples are mixed together.. 3) Large-scale pyrosequencing was carried out on the 454 sequencing system (Roche, Basel, Switzerland) following the manufacturer's instructions, and using the GS 20. 4) To determine bear diet, the sequences were first compared to the reference database (developed from DNP plants, Appendix A) and then, if no match was found, to public databases using the MEGABLAST algorithm (Zhang et al. 2000). We plotted the frequencies of identified families and classified them as regular (≥10% occurrence) and occasional diet items (<10% occurrence) for brown bears. Families with >50% frequency were considered as preferred plant food for bears.

Stable-isotope analysis: The fundamental concept in stable-isotope analysis is that the stable-isotope ratios in a consumer's tissues are related to its diet (Hobson et al. 2000), therefore measurement of animal tissue reveals its ingested diet. Hair samples from six radio-collared brown bears (Paper III) were analyzed for ^{15}N and ^{13}C by G.V. Hilderbrand, Washington State University, USA by the method described in Hilderbrand et al. (1996). The interpretation of stable isotope values in terms of meat content in the diet requires knowledge of stable-isotope values in the food items (plants and animals). As we do not have such values for DNP, we used isotope measurements of food items reported by Hobson et al. (2000) from British Columbia, Canada ($\delta^{15}N$ -2.1 and 3.3 for plant and animal food respectively), and calculated dietary meat of the brown bear population using equation no. 5 in Hobson et al. (2000).

3.6 Habitat Selection

We used the 28 July 1998 LANDSAT Thematic Mapper (TM) satellite image to classify DNP into six vegetation based habitat classes; marshy, grassy, stony, rocky, water and snow (Fig 3). A habitat-specific index of forage production was obtained by sampling standing crop (Soest 1994; Vallentine 1990). A digital elevation model of DNP was prepared using elevation data from the Shuttle Radar Topography Mission (SRTM) (http://www2.jpl.nasa.gov/srtm/) and topographical sheets of the Survey of Pakistan (Fig. 4). Streams were digitized from the 30 September 2001 LANDSAT image, and roads were digitized from topographical maps of the Survey of Pakistan. Locations of camps belonging to nomad and local livestock herders and seasonal hotels were recorded with a GPS receiver. An index of grazing impact was obtained from the proportion of plants grazed in quadrats.

We used the Ecological Niche Factor Analysis (ENFA) (Hirzel et al. 2002) to investigate habitat preferences of the brown bear. Eleven ecogeographical variables (described above, details in Paper VI) were used as explanatory variables in ENFA and locations of brown bear feces were used as indicators of areas used by bears. The ENFA extracts one axis of marginality and several axes of specialization. The marginality axis measures the difference between the conditions used on average by the species and the mean available habitat, whereas the specialization measures the width of the niche within available habitat. The Mahalanobis distance statistic (Clark et al. 1993) was used to compute a habitat suitability map. In order to evaluate validity of the habitat suitability map, we computed a curve of the ratio of expected-to-predicted frequencies of evaluations points (Hirzel et al. 2006).

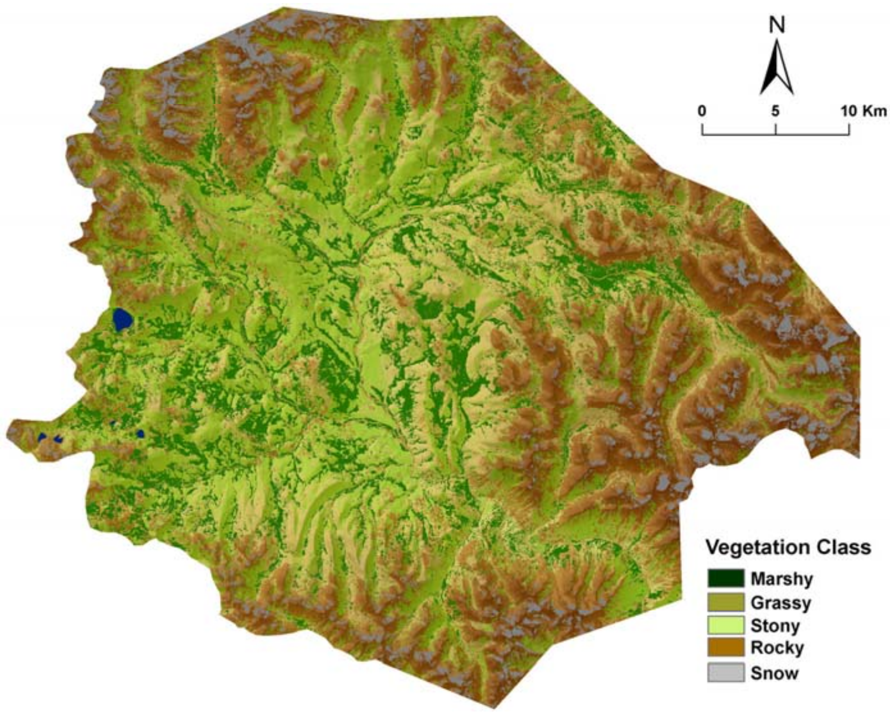

Figure 3: Vegetation map of Deosai National Park, Pakistan, based on LANDSAT Thematic Mapper

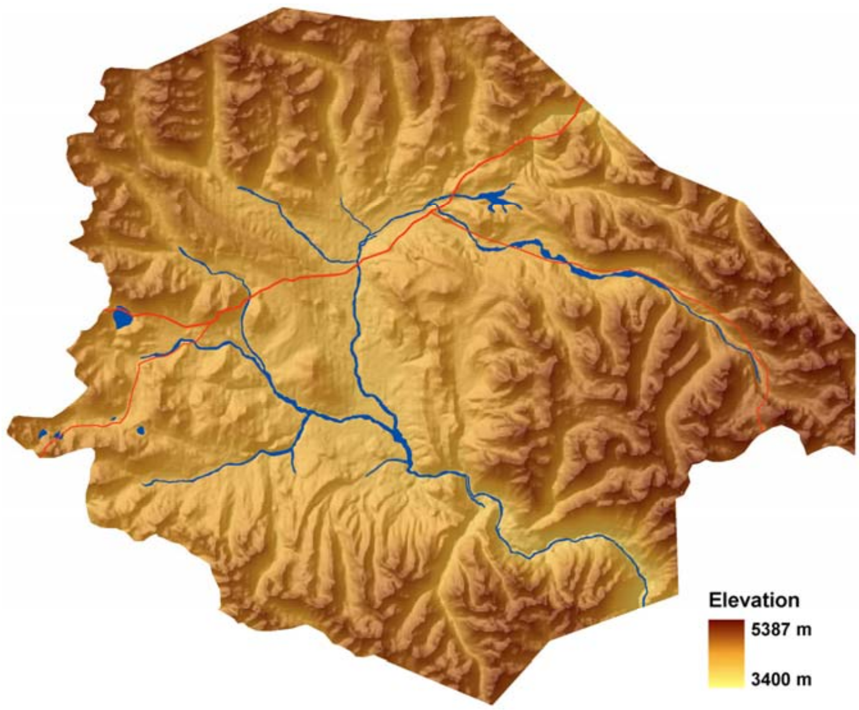

Figure 4: A Digital Elevation Model of Deosai National Park, Pakistan, developed from the SRTM Data

3.7 Life History

The park staff of the Himalayan Wildlife Foundation (HWF) operated a summer field camp in DNP from 1993-2006. The staff observed individual bears regularly and documented their movements and behavior. The following factors helped in individual recognition: 1) Color variation; in DNP four pelage colors were identifiable; blonde, silvertip, light brown and dark brown (Fig. 5). 2) White patches; many individuals had characteristic white patches, which differed in size and shape. 3) Size; brown bears are sexually size dimorphic (Schwartz et al. 2003), adult females in Deosai have a mass of 60-80 kg and adult males 120-150 kg. 4) Radiotelemetry; the 7 radio-collared adults comprised about 40% of the adult population at that time. This increased the reliability of the observational study. 5) Genetic analysis; a genetic analysis of the population (Paper II) gave a population estimate similar to the results of the field census, verified maternal relationships among individuals that were assumed from field observations, and also verified patterns of individuals' distributions as observed in the field.

This study particularly targeted females with young, which allowed documentation of the females' reproductive activity and survival of young. We used method of Garshelis et al. (1998) to calculate age of first reproduction, and extended this method to estimate litter interval and length of family association. We calculated mean litter size using all litters observed after den emergence. We used two methods to calculate reproductive rate (young born/ year/ reproducing adult female): 1) by dividing the mean litter size by the mean litter interval, and 2) from the reproductive history of 6 females that provided 11 complete birth intervals.

We estimated the minimum mortality rate by dividing the recorded deaths by the number of bears observed. Some females and associated young disappeared from the study area during the winter, and we were not sure about the fate of the associated young. We therefore reported mortality in a range of minimum (based on known mortalities) and maximum (by including undocumented loss). We calculated intrinsic growth (based on reproduction) for the best and worse case scenarios, using minimum and maximum mortality rates, respectively, using the deterministic Leslie matrix (Leslie 1945, 1948) and the Vortex Program (Lacy et al. 2006).

Figure 5: Photographs of brown bears from Deosai National Park, Pakistan, showing pelage color variation among individuals.

4. RESULTS

4.1 Status and Distribution (Papers I, II, III)

Today approximately 150–200 bears may survive in seven populations in northern Pakistan. All of these populations are probably declining, except for the population in DNP. In DNP we counted 19 individuals during 1993, which increased to 43 individuals towards end of the study. Averaged over the study period, there were 41% adults, 8% subadults and 18% young (up to 4 years of age) in the population. The adult sex ratio remained quite equal, except for recent years when it became male biased. Among the 11 cubs that successfully grew to adults during the study period, the female-to-male ratio was 6:5.

From the genetic analysis of fecal samples in 2004, 28 individual genotypes were obtained (16 males, 10 females and 2 individuals of unknown sex). The probability of identity for unrelated individuals was 1.881e-05 and 1.206e-02 for related individuals (siblings), thus we could identify each individual reliably. The Kohn's estimate yielded a population size of 47 bears (95% CI: 33-102), whereas the Eggert's estimate gave an estimate of 32 bears (95% CI: 28-58). The finite growth (λ) of the population in DNP was estimated from the annual censuses at 1.05 (95%CI: 1.03, 1.07).

4.2 Genetic Diversity (Paper II)

The number of alleles per locus among the 28 individual genotypes ranged from 2 to 7, with an average of 3.87 ± 1.36 (Appendix B provides consensus genotypes). The mean observed heterozygosity was 0.557, a value not significantly different from the unbiased expected heterozygosity (0.548). Global tests showed that the population is at Hardy-Weinberg equilibrium, although three loci (G10L, G10O, Mu10) had a significant deficiency in heterozygocity at the $p<0.05$ level. The overall multilocus Fis value was -0.016. The average pairwise relatedness in the Deosai bear population was 0.0265 ± 0.292 (SE), which was not significantly different from that for the Scandinavian populations.

4.3 Diet Composition (Papers IV, V)

About 70% of the scats were composed of only plant residues. Graminoids (grasses and sedges) had the highest frequency (93%), and constituted the bulk (85%) of the volume of the scat residues. The diet category with the second highest frequency was forbs, at 52% (presence verified by stems and inflorescences only). The volume of animal residues was only 4%, with rodents constituting most (88%) of it. With the *trn*L approach, we found a total of 57 plant taxa in the bear feces, belonging to 50 genera and 29 families. The regular plant diet (≥ 10% occurrence) of brown bears was comprised of only 8 families; Poaceae, Polygonaceae, Cyperaceae, Apiaceae, Asteraceae, Caryophyllaceae, Lamiaceae, and Rubiaceae. The first four families constituted the preferred diet, with more than 50% occurrence (Fig. 6).

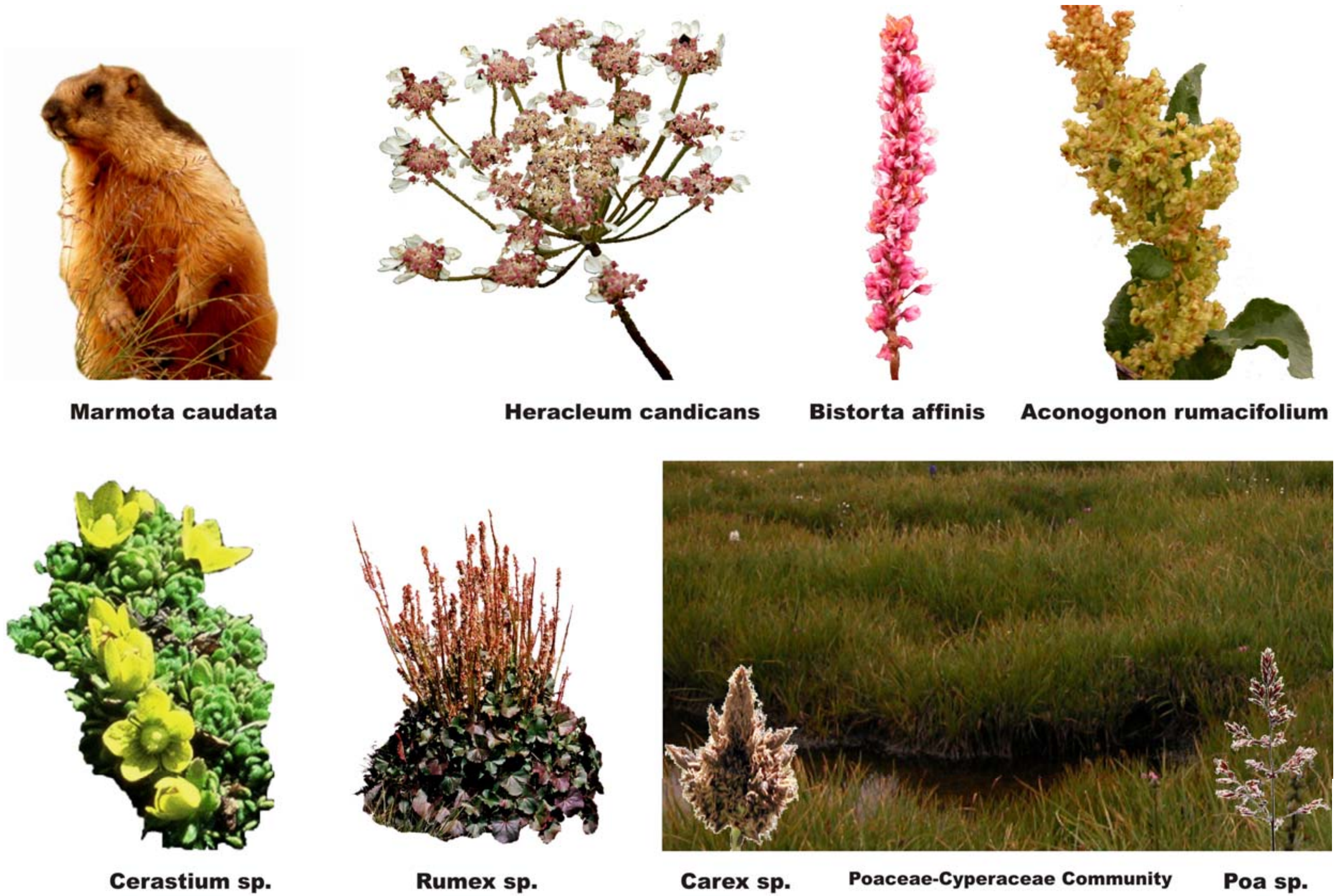

Figure 6: Common food species of brown bears in Deosai National Park, Pakistan.

The average values of stable-isotope from hair samples were 3.23 (SD: 1.127) and -23.6 (SD: 0.303) for $\delta^{15}N$ and $\delta^{13}C$, respectively (Appendix C). Assuming similar levels of isotopic values of plant and animal food in DNP as that reported by Hobson et al. (2000), the average contribution of animal matter in diet of brown bears was estimated at 9.5%, ranging from 0-27% in individuals. One subadult male was probably not consuming animal food at all. Excluding this individual gave an average meat consumption of 18.5% for the remaining of five individuals. The amount of dietary animal matter was positively related to the body mass of individuals (r= 0.59).

The average values of crude protein, crude fat and nitrogen free extract (carbohydrates) for nine graminoids were 11.6 (SD: 3.01), 3.8 (SD: 2.46) and 50.5% (SD: 4.27) dry matter, respectively (Appendix D). For forbs, the average values of these parameters were 12.7 (SD: 3.62), 3.3 (1.35) and 48.0% (SD: 9.29). The digestible energy (kj/g) was estimated at 11.8 for graminoids, 11.2 for forbs, and 12.2 for shrubs. In the diet of brown bears, the relative contribution to the energy assimilation was almost equal for animal (54%) and plant (46%) components of the diet. Rodents (48%) and graminoids (33%) were the main sources of energy. Ungulates (7.7%) and roots (7%) were second, and other components were not important. The energy gained by brown bears per gram of ingested food was estimated at 14.8 kj.

Males were more carnivorous than females, and they also ate higher proportions of three plant species; *Bistorta affinis*, *Carex diluta*, and *Carex* sp. Four habitats of DNP were homogenous with respect to the diet of brown bears, but diet differed significantly between the park and the surrounding valleys. In the valleys, the diet consisted predominantly of graminoids and crops, whereas the park provided more nutritious and diverse food.

4.4 Habitat Selection (Paper VI)

Bear habitat use differed significantly from random (Fig. 7), as indicated by randomization tests carried out on marginality and the first axis of specialization ($P < 0.001$, for both tests). Bears strongly avoided higher elevations and steeper slopes, and showed a higher preference for more productive parts of the park (marshy, grassy, and stony vegetation types). Brown bears tolerated human structures, such as roads and camps, but strongly avoided grazing areas with high livestock density. DNP had a range of poor to excellent habitat for brown bears. About 49% of the area was classified as poor habitat, 39% was suitable, and 12% of the area constituted high quality habitat. The habitat suitability map generally followed the biomass productivity patterns of the park. It identified the central part as suitable, and classified half of the park, mainly peripheral areas, as not suitable for brown bears. A validity test indicated good predictive power for the suitability map (Boyce Index; r: 0.98, $P < 0.01$).

4.5 Life History (Paper III)

We calculated the mean age of reproduction as 8.25 years (range: 7-10), and the mean litter interval as 5.7 years (range: 4-8). Litters consisted of 1 or 2 cubs, and averaged 1.33. The proportion of two-cub litters was 0.3. Both methods produced similar estimates of reproductive rate (natality), at 0.23 (SD: 0.066) cubs per adult reproducing female per year.

The survival estimates for the cubs-of-the-year (0.800-0.965), yearling (0.848-1.00), and ≥ 2 age group (0.923-0.976) were all within ranges, without point estimates, because we could not resolve undocumented loss in the population. The estimates of intrinsic growth (based on reproduction) by the Leslie matrix and Vortex methods were similar but lower than the observed growth. The intrinsic population growth rates estimated under best- and worst-case scenarios considering survival rates were 0.965 and 1.030, respectively, indicating uncertainty in the intrinsic population growth. However the population would be intrinsically stable only if at least half of the undocumented loss actually survived (λ: 0.997 at 50% survival of undocumented loss).

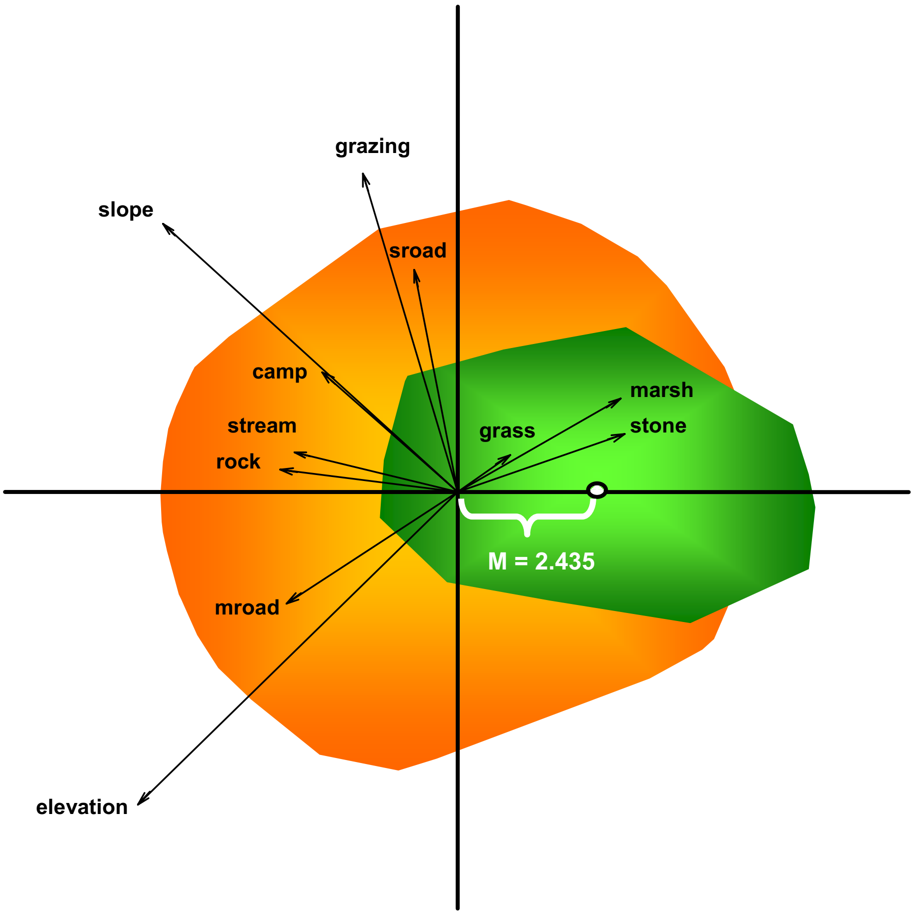

Figure 7: Biplot of the Ecological Niche Factor Analysis of brown bear habitat in Deosai National Park, Northern Areas, Pakistan. The brown area represents the available habitat and the green area corresponds to the ecological niche of the brown bear (used area). The plane consists of marginality on the X axis and the first specialization on the Y axis. Ecogeographical variables are projected by arrows. The marginality (M) factor measures the difference between the conditions used on average by the species and the mean available habitat.

5. DISCUSSION

5.1 Status and Distribution of Brown Bears in Pakistan

The Himalayan brown bear historically occupied the western Himalayas, the Karakoram, the Hindu Kush, the Pamir, the western Kunlun Shan, and the Tian Shan ranges in southern Asia. In Pakistan the subspecies ranged over approximately 150,000 km^2 in the northern part of the country. However it has been extirpated from the southern part of its historical range in Pakistan, and remaining population are no longer contagious (Fig. 8). The brown bears' range in Pakistan falls under three administrative divisions (Azad Jammu and Kashmir, Northern Areas of Pakistan, North West Frontier Province), and, as the wildlife management is a provincial subject in Pakistan, these administrative divisions have three different governing legislations. Bears are legally protected, however, and recently designated as critically endangered in IUCN's Red List of Mammals of Pakistan.

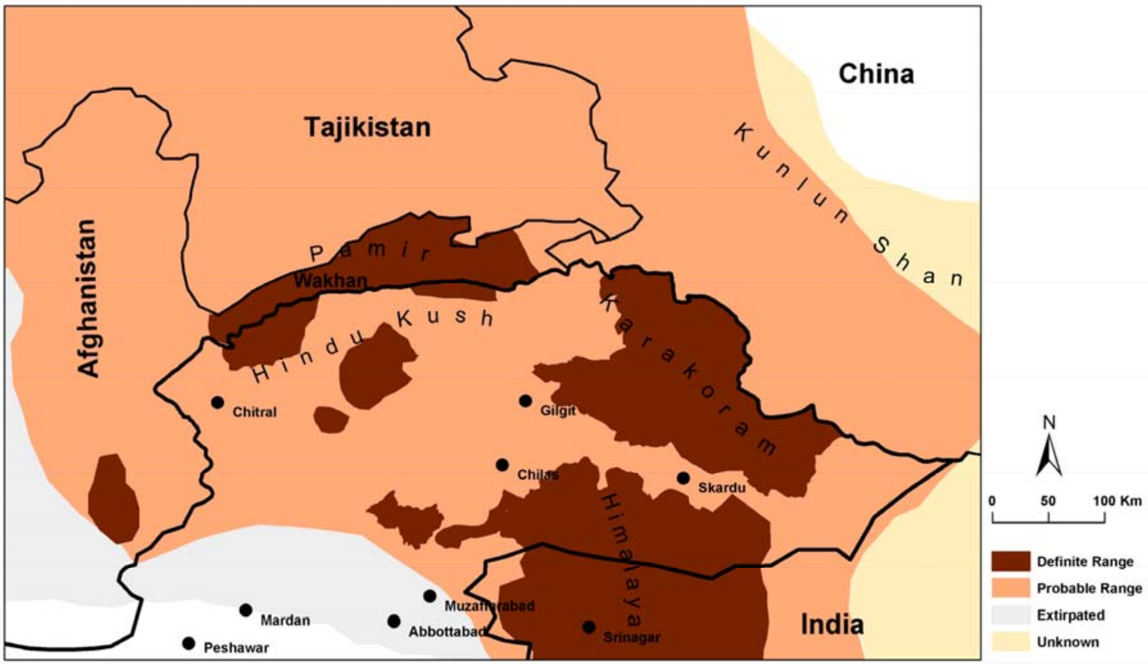

Figure 8: Present distribution of brown bears in Pakistan and neighboring countries. (Prepared in collaboration with IUCN SSC Bear Specialist Group)

In Deosai National Park, the population size estimates provided by the two rarefaction indices were in the same order of magnitude as the numbers derived from the field censuses, which gives us confidence that those results are realistic. The Eggert method seemed to underestimate the population size, whereas Kohn's method seemed to be more realistic, although the upper limit of the confidence intervals (102) seemed to be an overestimate. We conclude that approximately 40-50 bears were present in the park in 2004. Four individuals in our genetic dataset showed private alleles at two different loci, suggesting that they could be migrants (or descendants from migrants) from outside of the study area. Field observations support this hypothesis (Paper I). Brown bears also exist in the Minimerg and Astore valleys, which are adjacent to Deosai National Park. Movements of bears have been observed between these areas during recent surveys, and the Deosai population may have interchange not only with bears in these valleys, but also with the bear populations in the Neelam Valley and in Indian Kashmir through these valleys.

Considering the geomorphology of the area, evidence collected during field surveys, and genetic results, we conclude that the Pakistani populations of brown bears exhibit regional connectivity primarily through three corridors: the Himalayan population is connected to the populations in Zanskar and Ladakh ranges in India, the Hindu Kush population is connected to bears in the Tian Shan Range through the Pamir population in the Wakhan Corridor (Afghanistan) and Central Asia, and the Karakoram population may have connectivity with the Kunlun Shan in China (Fig 8, Paper I).

5.2 Genetic Diversity

The population genetics analyses revealed that the level of nuclear genetic diversity of the Deosai population was globally lower than brown bear populations that are considered to have a good conservation status, such as in Scandinavia or North America (Paper II). However, the population is in Hardy-Weinberg equilibrium and its level of relatedness was similar to that in the Scandinavian brown bear population. Therefore, the Deosai bear population does not appear to be at immediate risk of inbreeding depression. Its level of genetic diversity is comparable to the brown bear population in the Yellowstone area, USA. Lacy (1987) suggested that even a low frequency of migration between populations minimizes loss of genetic diversity associated with small population size. We believe that the moderate level of genetic diversity observed in DNP has been maintained by gene flow with adjacent populations in Pakistan and India.

We found a genetic signature of the population bottleneck. The results from the population analysis using the program MSVAR suggested that a decline in the Deosai population occurred approximately 80-100 generations ago. The ancestral population (before the decline; N1) was estimated at 10,000-12,500 individuals. This estimate seems realistic considering an approximate area of 200,000 km² of bear distribution range in northern Pakistan and Kashmir, which gives a density of about 55 bears per 1000 km². The historic phase of glaciations in High Asia (Kuhle 1997; Meiners 1997) may have acted as a proximal cause of this decline, destroying part of the population and fragmenting the rest. The influence of a growing human population, political unrest due to presence of the Tibetan army in the area and its clashes with local people and China (Sheikh, 1998; Rashid S, personal communication), and the spread of firearms in the late 19th century probably contributed further to the population decline and did not allow bears to disperse in a natural way.

5.3 Resource Selection

The *trn*L approach, stable isotope analysis, and classical scat analysis are complementary techniques, and together can provide a comprehensive understanding of feeding ecology of an omnivore species like brown bear. The *trn*L approach provided a more accurate description of plant diversity in the diet and its frequency. The scat analysis helped ascertain relative volumes of major diet groups, particularly the animal prey, which could not be determined by the *trn*L approach. The stable-isotope analysis does not provide details on composition of the diet, but is useful in determining amount of the animal matter in the diet.

The brown bear diet was quite diverse in DNP, represented by 57 plant species, insects, ungulates and several rodent species. However the adjusted diet content indicated that only graminoids (represented by sedges and grasses) and golden marmots comprised the bulk of the diet, and provided 81% digestible energy (Paper V). Looking at plant and animal resources separately, we found consumption in accordance with availability. Graminoids are the most abundant, concentrated and consistent source of forage in DNP, and they were the dominant component of bear diet. Likewise golden marmots comprised the major mammalian biomass in the park, and were also the main protein source for bears. The stable-isotope analysis also agreed with the results of scat analysis, but indicated a lower amount of animal matter, which could be due to; 1) small sample size, particularly large males, which are more carnivorous (Paper V), were not represented in isotope samples, 2) calculations were based on isotope values of food plant and animal matter from another geographical location, and isotope signatures vary geographically (Chamberlain et al. 1996; Garten 1993). Soil ^{15}N is known to become depleted with altitude (Mariotti et al. 1980) which can be reflected in local food webs (Gröcke et al. 1997). Isotopic measurements from vegetation and animal prey from DNP, and also from more individuals, would be required to appropriately interpret the results of the stable isotope analysis.

Multivariate methods, such as ENFA or Mahalanobis distances, allow the inclusion of several variables (elevation, slope, human disturbance, vegetation types) simultaneously in analyses and therefore allow a more comprehensive understanding of habitat selection. In contrast to the diet, habitat selection by brown bears differed significantly from the mean of available conditions (Fig. 7). Habitat selection by brown bears in DNP was related primarily to biomass production, and marshy vegetation was the most selected habitat, which is consistent with the finding of diet analysis (because graminoids dominate the plant community in marshy habitats, Paper VI). Moreover, the abundance of golden marmots, which is the main protein source for brown bears, was also highest in marshy areas (1.4 times higher density than in grassy and stony vegetation, Paper V). Both diet and habitat analyses highlighted the importance of marshy areas for bears. These habitats cover only 15% of the park area, but produce half of the park's vegetation biomass. Vegetation in marshy habitats remains physiologically active, and thus nutritious, even during the late growing season, due to the availability of water (Graham 1978; Hamer and Herrero 1987). The marshy habitat, which provide a continuous, nutritious, abundant and concentrated source of forage, is therefore the key factor explaining habitat selection by brown bears.

5.4 Life History

Brown bears occupy a wide geographical range (Servheen et al. 1999), and variation in its life-history traits has been documented earlier in North American populations

(Bunnell and Tait 1981). European studies widened this spectrum further by documenting the life history of Scandinavian populations, which are the most productive in the world (Sæther et al. 1998). The reproductive parameters of 35 North American and European brown bear populations range between mean ages of first reproduction of 3-9.6 years, mean litter sizes of 1.4-2.5 cubs, mean reproductive intervals 2.4-5.8 years, and mean reproductive rates of 0.36-0.96 cubs/year/adult female (Paper III). High-latitude brown bear populations are reported to be less productive than other terrestrial and coastal brown bear populations (Ferguson and McLoughlin 2000). However we documented that the reproductive parameters of the high-elevation brown bear populations are even lower than those of the high-latitude populations. The population in the Eastern Brooks Range, Alaska, is the least productive in North America (Paper III), but is 1.8 times more productive than the Deosai population. At the other end of the spectrum, the Scandinavian population has a reproductive rate that is 4.2 times higher than the Deosai population (Paper III). Thus, by documenting the life history of high-elevation brown bears in Asia, this study has increased the known range of life-history traits in brown bears considerably. Consistent with our findings, Blumstein and Arnold (1998) reported delayed ages of reproduction and infrequent reproduction in golden marmots living in high elevations of Himalaya.

The energy allocation theory assumes that reproductive strategies are the result of an optimal allocation of surplus power (the part of the acquired energy left after satisfying metabolism) to growth and reproduction (Demetrius 1975; Ware 1980). The quantity of the surplus power depends on the available energy and the cost of maintenance in an environment (Stearns 1992). The brown bear is an opportunistic, omnivorous species, and consumes a large variety of food according to local conditions. Meat is the most nutritious food, and has a positive influence on reproductive performance in brown bears (Bunnell and Tait 1981; Reynolds and Garner 1987; Hilderbrand et al. 1999). Fruits are the second most important source of energy (Pritchard and Robbins 1990), however a mixed diet (meat and fruits) is most desirable for growth of brown bears (Robbins et al. 2007). Energy assimilation from food in 22 brown bear populations averaged 22.5 kj per gram of ingested food (Paper V). The Deosai population lacked fruits in its diet and had relatively little meat, consequently it assimilated the lowest amount of energy from its food of all brown bear populations with comparable data (35% less than the average for 22 other populations). Our results also showed that the food energy was even lower for the female brown bears, because they had relatively lower amounts of meat in their diet than males (Paper V). The very low amount of food energy and higher cost of metabolism at high altitudes (Mani 1990; Westerterp and Kayser 2006), probably contributed to the very low reproductive rates of the brown bear population in DNP. This conservative life-history strategy, however, may have selective advantages in high-altitude environments, because low fecundity increases the population's ability to persist in stochastic environments (Demetrius 1975; Murdoch 1966).

6. IMPLICATIONS FOR MANAGEMENT

It was interesting to learn that brown bears with such a low productivity still could maintain their existence in such environmental extremes, while obtaining most of their diet from grasses. However our results show that population is highly sensitive to harvesting, because of their limited intrinsic growth potential. Hunting has been a traditional practice in northern Pakistan, and is also the key threat to Himalayan brown bear populations in other parts of their range (Servheen et al. 1999). Increasing accessibility to bear habitat has increased hunting in recent decades. Bears have been hunted for sport, persecuted by villagers who feel their livestock is threatened, and also killed for commercial purposes. Hence poor growth potential makes their conservation highly challenging. Nevertheless, our study documents that these low-productive bears can be conserved by reducing human-caused mortalities, particularly of adult females.

Deosai National Park supports a growing population and the highest density of brown bears yet documented in High Asia. It should remain the focus of conservation efforts, because the future of the brown bear in Pakistan, and perhaps in the region, largely will depend on stability in this park. Current protection and monitoring must be maintained, and connectivity with neighboring populations should be improved. Managing human resource use without affecting the brown bear population has been a major management challenge in the park, and seems to have been achieved. However a large influx of livestock by nomad grazers in recent years needs urgent attention, if the brown bear population is to continue to recover. We recommend monitoring the numbers and distribution of livestock and conducting a detailed inventory of the rangeland to understand grazing dynamics in the park and to maintain sustainable stocking rates.

We documented movement of brown bears between Deosai and adjoining areas, which has important implications for conservation, through maintaining gene flow and influencing demographic processes. Because some individuals apparently have home ranges larger than the park, we recommend that protection be extended to the adjacent valleys, while allowing communities to sustain their livelihoods. We also documented that the Pakistani populations are connected to other regional populations through three corridors (Fig. 8). These movement corridors, particularly the Neelam Valley and the Pamir Range, provide ideal venues for management of brown bears on broader landscape through cross-border cooperation. A peace park around the Pamir Knot (involving Afghanistan, Tajikistan, China and Pakistan) is already under consideration, and the Neelam Valley along the Line of Control with India provides another opportunity. Such initiatives would benefit many other threatened large mammals as well, including the Asiatic black bear (*Ursus thibetanus*), common leopard (*Panthera pardus*), snow leopard (*Panthera uncia*), musk deer (*Moschus moschiferus*), Himalayan ibex, and Marco Polo sheep (*Ovis ammon polii*).

The presence of humans in occupied brown bear habitat is a reality, and the livelihood of local people is linked with it. Conservation planning based on the exclusion of people and implemented with force therefore has a very poor chance to succeed. DNP was managed on the participatory approach and the observed growth of brown bear population suggests that the park has been successful in achieving its major goal. This success adds to the growing recognition that the local communities should be integrated in planning and management of protected areas (PAs) (Dearden et al. 2005; Hiwasaki 2005). Changes to the legislative and regulatory framework of the PAs that would recognize the rights of communities and provide the framework for community participation and benefit sharing would promote the involvement of the local people. Participation of local communities in the management process not only minimizes conflicts, but also leads to efficient conservation planning.

PAs cover most of the brown bear range in Northern Pakistan. However, most of these are poorly managed, due to limited financial resources and lack of training of the management staff. Strengthening the PA system and improving its efficiency in Pakistan can prevent many endangered mammals from declining further. Carnivores as a whole are considered odious and it is usually difficult to generate support by local communities for their conservation. People always question such efforts because, unlike ungulates, carnivores do not have any meat value and pose a threat to humans and livestock. Environmental education is an important instrument to change perceptions and attitudes. Launching education and awareness initiatives that cater to local communities, staff of the PAs, visitors, and the general public can bridge the knowledge gap and be vital to achieving synergy in conservation efforts.

7. RESEARCH PERSPECTIVES

This study documents, for the first time, the ecological requirements, life history and genetic structure of the Himalayan brown bear. Therefore it provides the basic information required for the population and habit management of brown bears in Himalaya. There are, however, several questions to answer that are beyond the limits of our data or have arisen based on our results. We list here some of the questions that need to be pursued during future research.

We documented that the population growth in DNP was the product of reproduction and immigration (Paper III). We estimated reproductive parameters and survival from observations of recognizable individuals. Some individuals were lost from contact, due to either death, emigration, or large-scale movement, but we could not resolve their fate. In order to account for this undocumented loss to the population, we reported survival and consequently intrinsic growth rate in a range. These estimates did not allow us to adequately interpret the contribution of reproduction to the observed population growth. The visual monitoring was useful as long as the bears remained in the open plateau of the study area. To monitor individuals over larger distances in the highly rugged terrain of Himalaya and resolve such questions as long-term movements and monitoring, an advance technique such as GPS telemetry would be required. With the use of GPS telemetry, or combining it with conservation genetics techniques, we could answer many important questions, for example; 1) Determine age-specific estimates of survival and the nature and magnitude of threats to bears beyond the boundary of the national park. 2) Patterns of bear movements in the broader landscape, particularly to answer whether individuals are emigrating/immigrating or whether they just have large-scale movements. 3) Complete home ranges and resource selection within home ranges. Habitat and diet analysis during present study was limited to the park area. Many individuals had home ranges larger than the park, and it is therefore important to understand which resources they utilize over the course of the year. 4) Subadult bears comprised a substantial part of the undocumented loss of the population (Paper III), which might be due to dispersal. We should investigate dispersal and other aspects of social organization.

The distribution range of the Himalayan brown bear encompasses diverse habitats, from scrub land to coniferous forests and alpine meadows. We documented their habitat selection in DNP, which is an alpine habitat. Alpine meadows, particularly marshy areas, should therefore be recognized as their preferred habitat throughout their range. However their habitat requirements in other landscapes (e.g., forested areas) are likely to be different, and need to be investigated. We recommend surveys and sample collection from the rest of their range in Pakistan, and preferably throughout their range in High Asia through collaborative arrangements. This will give a comprehensive understanding of resource selection, and also allow the computing of habitat suitability maps for their entire range, which would serve as an effective management tool on regional scale. Genetic samples from the entire range of Himalayan brown bears would allow delineating populations and investigating patterns of gene flow.

In Deosai National Park, the park staff provided a cost-effective and efficient means of primary data collection. They should continue monitoring the population and habitat of the brown bears. The most important activities are annual censuses of the brown bear population, documentation of natural and human-caused mortalities, livestock numbers, and tourism activity. Following recognizable individuals has been an important component of the monitoring in the park, which contributed to reliable estimates of the population size every year. The HWF staff remained associated with the brown bear monitoring for a long time, and their experiences and ability to recognize individuals enhanced the quality of the data. Recently the HWF handed over most of the park responsibilities, including monitoring, to the Northern Areas Forest and Wildlife Department (NAWD). Most of the NAWD staff is new and inexperienced. Brown bear numbers have also increased; therefore following unmarked individuals visually will be increasingly difficult in the future. Instead we recommend counting females with cubs-of-the year for estimating population size and monitoring change in the population (Knight et al. 1995; Keating et al. 2002; Harris et al. 2007; Ordiz et al. 2007). This method would allow the park staff to evaluate their annual counts of bears in the park. The field estimates should also be evaluated with a periodic DNA-based census (e.g., every 10 years) of the populations using fecal samples. From the amplification success of this study, we recommend that fecal samples older than one week not be collected, in order to optimize the cost and benefit of the genetic analyses. Increasing the size and range of fecal sampling would not only allow a more precise estimate of the population size, but also give a better estimate of gene flow.

8. ACKNOWLEDGEMENTS

My interest with brown bears started in early 1998, when Vaqar Zakaria invited me to take a volunteer research position in the Deosai Brown Bear Project. He started this project with Anis ur Rahman in 1993 for the conservation of brown bears in Northern Pakistan. There are not many projects in the history of Pakistan that have had the impact on the landscape that this project has had. This dissertation also makes this project the most documented one in Pakistan. I commend their efforts for conserving this charismatic species, and also appreciate them for involving me in their efforts.

The journey of my PhD project started when the International Bear Association accepted my very late submitted abstract for the 14th International Conference in Steinkjer, Norway in 2002. Prof. Jon Swenson invited me for a preconference expedition to the study area of the Scandinavian Brown Bear Research Project (SBBRP) in Sweden, and received me at the Gardermoen Airport. I enjoyed that expedition even more than the conference. This was my first visit to Europe and I found Jon to be the most friendly person in that crowd. This encouraged me to discuss my research interests during a lunch break. He was brave enough, I think, to accept a student from Pakistan, knowing that I may cost him lot more in terms of energy and resources than usual European students. It is difficult to put in words the excellent supervision he provided me. Apart from his great contribution in developing my research skills, he has been a good friend and made my time enjoyable in Norway.

I am thankful to Pierre Taberlet, my second supervisor, for inviting me to Grenoble. I had a wonderful time at his lab (LECA), where he introduced me to conservation genetics. I am sorry for destroying some expensive chemicals! I appreciate Eva Bellemain’s patience during this training and answering all of my questions. Thanks to Christian Miquel and other colleagues at LECA for their help. My association with Alice has been beneficial for me. She did great job of completing genotyping and the diet work, and has been explaining new genetic techniques to me from time to time.

Though I was not much aware of the SBBRP when I came to Norway, I am now confident that this was the best opportunity in the world! Thanks to Jon again for steering such a wonderful group of people and making me part of it. Everybody in the project has been extremely cooperative and friendly to me. Thanks for amazing social and scientific gatherings. Thanks to Sven and Lena for hospitality at the field station, and arranging moose meat especially for me. Andreas has always been accessible, and provided guidance whenever required. Ole-Gunnar, Andrés, Richard, Jonas, Jonna provided constructive criticism and helped many times. Bjørn guided in scat analysis. Jodie taught me multivariate techniques of habitat analysis. Thanks to Åsa and Prof Jon Arnemo for entertaining questions during capturing and sedation of brown bears.

Many teachers at UMB provided excellent training in statistics, ecology, genetics, GIS and remote sensing. I am particularly thankful to Øystein Dick, Owe Løfman, Ellen

Sandberg, Gary Fry, Solve Sæbø, and Manfred Heun for wonderful teaching and helping me whenever needed. Ole Wiggo Røstad, Mette Solsvik, Anne Ombustvedt at INA were always helpful in administrative and IT related issues. 'Brakka' is the best place at UMB, I agree with all PhD folks there. I cherish memories of working with a multinational group of PhD colleagues and look forward to build up these relations in future. Panadda, Daniel, Zerihun, Rinjan, Narendra, Chhatra provided good company. Anne-Line, Eivind Meen and Lisbet Bach did Norwegian translation of the abstract as a "communal work", thanks. Prof. Per Wegge was also our neighbor at Barakka. He was very friendly and highly knowledgeable about conservation issues in South Asia, so he kept me educating in corridor discussions.

Field data collection was the most important component of the study, and would not have been possible without the support of the staff of the Himalayan Wildlife Foundation and the Northern Areas Forest and Wildlife Department. I am especially thankful to my following colleagues for their enormous help in field and sharing their observations on brown bears and other park related issues: Noor Kamal Khan, Rafiq Rajput, Ghulam Murtaza, Muhammad Yunus, and Ghulam Mehdi. While working with a "Spang Drenmo" (vegetarian bear), understanding the vegetation was important. I am thankful to Dr Muhammad Qaiser and Jan Alam (University of Karachi, Karachi), Dr. Muqarrab Shah (Pakistan Museum of Natural History, Islamabad), and Dr. Mir Ajab Khan (Quaid-e-Azam University, Islamabad) for identification of food plant species. Dr Sarwat Mirza (University of Arid Agriculture, Rawalpindi) helped with vegetation biomass assessment, and Dr. Abdul Ghaffar Khan and Dr. Atiya Azim (Animal Science Institute, PARC, Islamabad) conducted nutritional analysis of plants. Sadar Nawaz designed the title cover and formatted the thesis, and Usman Ghani shared nice photographs of the brown bear.

Thanks to the Norwegian people and government for supporting my living in Norway. The Pakistani community of Norway is particularly acknowledged for giving us a feeling of home. The International Bear Association (John Sheldon Bevins Memorial Foundation) provided financial support for the genetic research, and also paid my trips to Italy and Japan for attending IBA meetings. The Deosai Brown Bear Project received financial assistance from the UNDP/GEF Small Grants Programme, US Fish and Wildlife Service, the South African National Parks Board, and the Norwegian Agency for Development Cooperation (NORAD).

Finally thanks to Zaib for her support and patience during last four years, to Abdullah and Omair for keeping life in balance, to my parents for love and always high ambitions for me, and to my parents in law for being always supportive.

REFERENCES

A.O.A.C. 1984. Official methods of analysis, Arlington, Virginia, 22209, USA.

Baker R.D. 1986. An investigation into the accuracy of herbivore diet analysis. Australian Wildlife Research 13: 559-568.

Beaumont M. 1999. Detecting population expansion and decline using microsatellites. Genetics 153: 2013-2029.

Belkhir K., Borsa P., Chikhi L., Raufaste N. and Bonhomme. F. 1996-2004. GENETIX 4.05, logiciel sous Windows TM pour la génétique des populations. Laboratoire Génome, Populations, Interactions, CNRS UMR 5000, Université de Montpellier II, Montpellier (France).

Bellemain E. and Taberlet P. 2004. Improved noninvasive genotyping method: application to brown bear (Ursus arctos) faeces. Molecular Ecology Notes 4: 519-522.

Blumstein D.T. and Arnold W. 1998. Ecology and social behavior of golden marmots (*Marmota caudata aurea*). Journal of Mammalogy 79: 873-886.

Boyce M.S., Kirsch E.M. and Servheen C. 2002. Bet-hedging applications for conservation. Journal of Biosciences 27: 385-392.

Brown J.H. 1995. Macroecology. University of Chicago Press.

Bunnell F.L. and Tait D.E.N. 1981. Population dynamics of bears — implications. *In* Fowler C. W. and Smith T. D. (eds.), Dynamics of large mammal populations, pp. 75-98. John Wiley and Sons, New York.

Caughley G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York.

Chamberlain C.P., Blum J.D., Holmes R.T., Feng X., Sherry T.W. and Graves G.R. 1996. The use of isotope tracers for identifying populations of migratory birds. Oecologia 109: 132-141.

Chase M.W., Cowan R.S., Hollingsworth P.M., van den Berg C., Madri, N S., Petersen G., Seberg O., rgsensen T., Cameron K.M., Carine M., Pedersen N., Hedderson T.A.J., Conrad F., Salazar G.A., Richardson J.E., Hollingsworth M.L., Barraclough T.G., Kelly L. and Wilkinson M. 2007. A proposal for a standardised protocol to barcode all land plants. Taxon 56: 295-299.

Chase M.W., Salamin N., Wilkinson M., Dunwell J.M., Kesanakurthi R.P., Haidar N. and Savolainen V. 2005. Land plants and DNA barcodes: short-term and long-term goals. Philosophical Transactions of the Royal Society B: Biological Sciences 360: 1889-1895.

Clark C.W. and Yoshimura J. 1993. Behavioral responses to variations in population: A stochastic evolutionary game. Behavioral Ecology 4: 282-288.

Clark J.D., Dunn J.E. and Smith K.G. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management 57: 519-526.

Clutton-Brock T.H. 1988. Reproductive success. University of Chicago Press, Chicago.

Dahle B. and Swenson J.E. 2003. Factors influencing length of maternal care in brown bears (*Ursus arctos*) and its effect on offspring. Behavioral Ecology and Sociobiology 54: 352-358.

Dearden P., Bennett M. and Johnston J. 2005. Trends in global protected area governance, 1992–2002. Environmental Management 36: 89-100.

Demetrius L. 1975. Reproductive strategies and natural selection. The American Naturalist 109: 243-249.

den Boer P.J. 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18: 165-194.

Dingle H. 1990. The evolution of life histories. *In* Wohrmann K. and Jain S. K. (eds.), Population Biology, pp. 267-289. Springer-Verlag, Berlin.

Eggert L.S., Eggert J.A. and Woodruff D.S. 2003. Estimating population sizes for elusive animals: the forest elephants of Kalum National Park, Guana. Molecular Ecology 12: 1389-1402.

Ferguson S.H. and McLoughlin P.D. 2000. Effect of energy availability, seasonality, and geographic range on brown bear life history. Ecography 23: 193-200.

Fonnesbeck P.V. 1968. Digestion of soluble and fibrous carbohydrate of forage by horses. Journal of Animal Sciences 27: 1336-1344.

Fonnesbeck P.V., Lydman R.K., Vander Noot G.W. and Symons L.D. 1967. Digestibility of the proximate nutrients of forage by horses. Journal of Animal Sciences 26: 1039-1045.

Foley W.J., McIlwee A., Lawler I., Aragones L., Woolnough A.P. and Berding N. 1998. Ecological applications of near infrared reflectance spectroscopy - a tool for rapid, cost-effective prediction of the composition of plant and animal tissues and aspects of animal performance. Oecologia 116: 293-305.

Frankham R., Ballou J.D. and Briscoe D.A. 2002. Introduction to conservation genetics. Cambridge University Press, Cambridge, UK.

Galbreath G.J., Groves C.P. and Waits L.P. 2007. Genetic resolution of composition and phylogenetic placement of the isabelline bear. Ursus 18: 129-131.

Garshelis D.L., Noyce K.V. and Coy P.L. 1998. Calculating average age of first reproduction free of the biases prevalent in bear studies. Ursus 10: 437-447.

Garten C.T. 1993. Variation in foliar ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. pp. 2098-2113.

Graham D.C. 1978. Grizzly bear distribution, use of habitats, food habits and habitat characteristics in Pelican and Hayden valleys, Yellowstone National Park, Montana State University: Bozeman.

Gröcke D.R., Bocherens H. and Mariotti A. 1997. Annual rainfall and nitrogen-isotope correlation in macropod collagen: application as a palaeoprecipitation indicator. Earth and Planetary Science Letters 153: 279-285.

Hamer D. and Herrero S. 1987. Grizzly bear food and habitat in the front ranges of Banff National Park, Alberta. International Conference on Bear Research and Management 7: 199-213.

Hardy O.J. and Vekemans X. 2002. SPAGeDi: a versatil computer program to analyse spatial genetic structure at the individual or population levels. Molecular Ecology Notes 2: 218-620.

Harris R.B., White G.C., Schwartz C.C. and Haroldson M.A. 2007. Population growth of Yellowstone grizzly bears: uncertainty and future monitoring. Ursus 18: 168-178.

Hewitt D.G. and Robbins C.T. 1996. Estimating grizzly bear food habits from fecal analysis. Wildlife Society Bulletin 24: 547-550.

Hilderbrand G.V., Farley S.D., Robbins C.T., Hanley T.A., Titus K. and Servheen C. 1996. Use of stable isotopes to determine diets of living and extinct bears. Canadian Journal of Zoology 74: 2080-2088.

Hilderbrand G.V., Jacoby M.E., Schwartz C.C., Arthur S.M., Robbins C.T., Hanley T.A. and Servheen C. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. Canadian Journal of Zoology 77: 132-138.

Himalayan Wildlife Foundation (HWF). 1999. Management plan for Deosai National Park Northern Areas Pakistan. Islamabad, Pakistan.

Hirzel A.H., Hausser J., Chessel D. and Perrin N. 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83: 2027–2036.

Hirzel A.H., Laya G.e.L., Helfera V.e., Randina C. and Guisana A. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 1999: 142–152.

Hiwasaki L. 2005. Toward sustainable management of national parks in Japan: securing local community and stakeholder. Environmental Management 35: 753–764.

Hobson K.A., McLellan B.N. and Woods J.G. 2000. Using stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes to infer trophic relationships among black and grizzly bears in the upper Columbia River Basin, British Columbia. Canadian Journal of Zoology 78: 1332-1339.

Keating K.A., Schwartz C.C., Haroldson M.A. and Moody D. 2002. Estimating numbers of females with cubs-of-the-year in the Yellowstone Grizzly bear population. Ursus 13: 161-174.

Knight R.R., Blanchard B.M. and Eberhardt L.L. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. Wildlife Society Bulletin 23: 245–248.

Kohn M.H., York E.C., Kamradt D.A., Haught G., Sauvajot R.M. and Wayne R.K. 1999. Estimating population size by genotyping feces. Proceedings of the Royal Society of London B Biological Sciences 266: 657-663.

Kuhle M. 1997. New findings concerning the Ice Age (Last Glacial Maximum) glacier cover of the East-Pamir, of the Nanga Parbat up to the Central Himalaya and of Tibet, as well as the age of the Tibetan Inland Ice. GeoJournal 42: 87-257.

Lacy R.C. 1987. Loss of genetic diversity from managed populations: Interacting effects of drift, mutation, immigration, selection and population subdivision. Conservation Biology 1: 143-158.

Lacy R.C. 2000. Considering threats to the viability of small populations using individual-based models. Ecological Bulletins 48: 39-51.

Lacy R.C., Borbat M. and Pollak J.P. 2006. Vortex: A stochastic simulation of the extinction process. Version 9.61. Chicago Zoological Society, Broodfield, Illinois.

Leslie P.H. 1945. On the use of matrices in certain population mathematics. Biometrika 33: 183-212.

Leslie P.H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika 35: 213-245.

Lewton J.H. and May R.M. (eds.) 1995. Extinction rates. Oxford University Press, Oxford.

Mani M.S. 1990. Fundamentals of high altitude biology. Aspect Publications Ltd., London.

Mani M.S. and Giddings L.E. 1980. Ecology of highlands. Dr. W. Junk bv Publishers, The Hague.

Margulies M., Egholm M., Altman W.E., Attiya S., Bader J.S., Bemben L.A., Berka J., Braverman M.S., Chen Y.-J., Chen Z., Dewell S.B., Du L., Fierro J.M., Gomes X.V., Godwin B.C., He W., Helgesen S., Ho C.H., Irzyk G.P., Jando S.C., Alenquer M.L.I., Jarvie T.P., Jirage K.B., Kim J.-B., Knight J.R., Lanza J.R., Leamon J.H., Lefkowitz S.M., Lei M., Li J., Lohman K.L., Lu H., Makhijani V.B., McDade K.E., McKenna M.P., Myers E.W., Nickerson E., Nobile J.R., Plant R., Puc B.P., Ronan M.T., Roth G.T., Sarkis G.J., Simons J.F., Simpson J.W., Srinivasan M., Tartaro K.R., Tomasz A., Vogt K.A., Volkmer G.A., Wang S.H., Wang Y., Weiner M.P., Yu P., Begley R.F. and Rothberg J.M. 2005. Genome sequencing in microfabricated high-density picolitre reactors. Nature 437: 376-380.

Mariotti A., Pierre D., Vedy J.C., Bruckert S. and Guillemot J. 1980. The abundance of natural nitrogen 15 in the organic matter of soils along an altitudinal gradient (Chablais, Haute Savoie, France). CATENA 7: 293-300.

McLoughlin P.D., Boyce M.S., Coulson T. and Clutton-Brock T. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society B: Biological Sciences 273: 1449-1454.

Meiners S. 1997. Historical to Post Glacial glaciation and their differentiation from the Late Glacial period on examples of the Tian Shan and the N.W. Karakorum. GeoJournal 42: 259-302.

Miquel C., Bellemain E., Poillot C., Bessiere J., Durand A. and Taberlet P. 2006. Quality indexes to assess the reliability of genotypes in studies using noninvasive sampling and multiple-tube approach. Molecular Ecology Notes 6: 985-988.

Mishra C. 2001. High altitude survival: conflicts between pastoralism and wildlife in the Trans-Himalaya, Wageningen University: The Netherlands.

Mullis K.B. and Faloona F. 1987. Specific synthesis of DNA in vitro via a polymerase-catalysed chain reaction. Methods in Enzymology 155: 335-350.

Murdoch W.W. 1966. Population stability and life history phenomenon. The American Naturalist 100: 45-51.

Nawaz M.A. 2007. Status of the brown bear in Pakistan. Ursus 18: 89-100.

Nawaz M.A., Shah M. and Zakaria V. 2006. Environmental baseline of Deosai National Park. Draft Report. Himalayan Wildlife Foundation, Islamabad.

Nei M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590.

Ordiz A., Rodríguez C., Naves J., Fernández A., Huber D., Kaczensky P., Mertens A., Mertzanis Y., Mustoni A., Palazón S., Quenette P.Y., Rauer G. and Swenson J.E. 2007. Distance-based criteria to identify minimum number of brown bear females with cubs in Europe. Ursus 18: 158–167.

Paetkau D. and Strobeck C. 1994. Microsatellite analysis of genetic variation in black bear populations. Molecular Ecology 3: 489-495.

Paetkau D., Calvert W., Stirling I. and Strobeck C. 1995. Microsatellite analysis of population structure in Canadian polar bears. Molecular Ecology 4: 347-354.

Pimm S.L., Jones H.L. and Diamond J. 1988. On the risk of extinction. American Naturalist 132: 757-785.

Primack R.B. 2002. Essentials of conservation biology. Sinauer Associates, Sunderland, Mass.

Pritchard G.T. and Robbins C.T. 1990. Digestive and metabolic efficiencies of grizzly and black bears. Canadian Journal of Zoology 68: 1645-1651.

Rasool G. 1991. Status and conservation needs of bear species in northern areas of Pakistan. Nature Conservation and Environmental Protection, pp. 46-47. Pakistan Wildlife Conservation Foundation, Islamabad.

Raymond M. and Rousset F. 1995. Genepop (version 1.2), population genetics software for exact tests and ecumenicism. Journal of Heredity 86: 248-249.

Reynolds H.V. and Garner G.W. 1987. Patterns of grizzly bear predation on caribou in northern Alaska. International Conference on Bear Research and Management 7: 59-67.

Robbins C.T., Fortin J.K., Rode K.D., Farley S.D., Shipley L.A. and Felicetti L.A. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. Oikos 116: 1675-1682.

Roberts T.J. 1997. The Mammals of Pakistan Oxford University Press, New York.

Rosenzweig M.L. and Abramsky Z. 1993. How are diversity and productivity related? *In* Ricklefs R. E. and Schluter D. (eds.), Species diversity in ecological communities: historical and geographical perspectives, pp. 52-65. University of Chicago Press.

Sæther B.E., Swenson J.E., Engen S., Bakke Ø. and Sandegren F. 1998. Assessing the viability of Scandinavian brown bear, *Ursus arctos*, populations: The effects of uncertain parameter estimates. Oikos 83: 403-416.

Schaller G.B. 1977. Mountain monarchs: Wild sheep and goats of the Himalaya. The University of Chicago Press, Chicago and London.

Schwartz C.C., Haroldson M.A., White G.C., Harris R.B., Cherry S., Keating K.A., Moody D. and Servheen C. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161.

Schwartz C.C., Miller S.D. and Haroldson M.A. 2003. Grizzly bear. *In* Feldamer G. A., Thompson B. C. and Chapman J. A. (eds.), Wild mammals of North America: biology, management, and conservation., pp. 556-586. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Servheen C. 1990. The status and conservation of the bears of the world. International Association for Bear Research and Management Monograph Series No.2.

Servheen C., Herrero S. and Peyton B. (eds.) 1999. Status survey and conservation action plan for bears. IUCN/SSC Bear and Polar Bear Specialist Groups. IUCN, Gland, Switzerland and Cambridge, UK.

Shaffer M.L. 1981. Minimum population sizes for species conservation. BioScience 31: 131-134.

Sheikh A.G. 1998. Ladakh and Baltistan through the Ages. *In* Stellrecht I. (ed.), Karakoram-Hindukush-Himalaya: dynamics of change. Rudiger Koppe Verlag Koln, Germany.

Shrestha R. and Wegge P. 2006. Determining the composition of herbivorediets in the Trans-Himalayan rangelands: a comparison of field methods. Rangeland Ecology and Management 59: 512-518.

Sih A. 1993. Effects of ecological interaction on forager diets: competition, predation risk, parasitism, and prey behavior. *In* Hughes R. H. (ed.), Diet selection an interdisplinary approach to foraging behavior, pp. 182-211. Blackwell Scientific Publications, Oxford.

Soest P.J.V. 1994. Nutritional ecology of the ruminant. Comstock Publishing Associates, London.

Southwood T.R.E., May R.M., Hassell M.P. and Conway G.R. 1974. Ecological strategies and population parameters. The American Naturalist 108: 791-804.

Sparks D.R. and Malechek J.C. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 21: 264-265.

Stearns S.C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Stevans G.C. 1989. The latitudinal gradient in geographical range: how so many species co-exist in the tropics. American Naturalist 133: 240-256.

Stringham S.F. 1990. Grizzly bear reproductive rate relative to body size. International Conference on Bear Research and Management 8: 433-443.

Taberlet P., Camarra J.J., Griffin S., Uhres E., Hanotte O., Waits L.P., Dubois-Paganon C., Burke T. and Bouvet J. 1997. Noninvasive genetic tracking of the endangered Pyrenean brown bear population. Molecular Ecology 6: 869-876.

Taberlet P., Coissac E., Pompanon F., Gielly L., Miquel C., Valentini A., Vermat T., Corthier G., Brochmann C. and Willerslev E. 2007. Power and limitations of the chloroplast trnL (UAA) intron for plant DNA barcoding. pp. e14-.

Taberlet P., Griffin S., Goossens B., Questiau S., Manceau V., Escaravage N., Waits L.P. and Bouvet. J. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. Nucleic Acids Research 24: 3189-3194.

Taberlet P., Waits L.P. and Luikart. G. 1999. Nonivasive genetic sampling: Look before you leap. Trends in Ecology and Evolution 14: 323-327.

Valière N. 2002. Gimlet: a computer program for analyzing genetic individual identification data. Molecular Ecology Notes 2: 377.

Vallentine J.F. 1990. Grazing management. Academic Press, Inc., New York.

Waits L., Taberlet P., Swenson J.E., Sandegren F. and Franzen R. 2000. Nuclear DNA microsatellite analysis of genetic diversity and gene flow in the Scandinavian brown bear (Ursus arctos). Molecular Ecology 9: 421-431.

Wang J. 2002. An estimator for pairwise relatedness using molecular markers. Genetics 160: 1203-1215.

Ware D.M. 1980. Bioenergetics of stock and recruitment. Canadian Journal of Fisheries and Aquatic Sciences 37: 1012-1024.

Westerterp K.R. and Kayser B. 2006. Body mass regulation at altitude. European Journal of Gastroenterology & Hepatology 18: 1-3.

Whittaker R.J., Araújo M.B., Jepson P., Ladle R.J., Watson J.E.M. and Willis K.J. 2005. Conservation biogeography: assessment and prospect. Diversity and Distribution 11: 3-23.

Zedrosser A. 2006. Life-history strategies of brown bears, Norwgian University of Life Sciences: Ås.

Zhang Z., Schwartz S., Wagner L. and Miller W. 2000. A greedy algorithm for aligning DNA sequences. Journal of Computational Biology 7: 203-214.

APPENDIX A REFERENCE DATABASE OF PLANT SPECIES FROM DEOSAI NATIONAL PARK, USED IN GENETIC ANALYSIS OF THE BROWN BEAR DIET

No.	Family Name	Species Name
1	Alliaceae	*Allium carolinianum*
2	Alliaceae	*Allium fedtschenkoanum*
3	Alliaceae	*Allium himalayense*
4	Boraginaceae	*Myosotis alpestris*
5	Boraginaceae	*Myosotis* sp.
6	Brassicaceae	*Brassica* sp.
7	Brassicaceae	*Chorispora sabulosa*
8	Brassicaceae	*Draba oreades*
9	Brassicaceae	*Thlaspi andersonii*
10	Brassicaceae	Unknown Species
11	Caryophyllaceae	*Cerastium cerastoides*
12	Caryophyllaceae	*Cerastium pusillum*
13	Caryophyllaceae	*Holosteum umbellatum*
14	Caryophyllaceae	*Silene tenuis*
15	Compositae	*Anaphalis nepalensis*
16	Compositae	*Aster falconeri*
17	Compositae	*Cremanthodium decaisnei*
18	Compositae	*Cremanthodium ellissi*
19	Compositae	*Hippolytia dolichophylla*
20	Compositae	*Jurania himalaica*
21	Compositae	*Lactuca lessertiana*
22	Compositae	*Leontopodium brachyactis*
23	Compositae	*Saussurea atkinsonii*
24	Compositae	*Saussurea falconeri*
25	Compositae	*Saussurea obvallata*
26	Compositae	*Senecio analogus*
27	Compositae	*Seriphidium leucotrichum*
28	Compositae	*Taraxacum dissectum*
29	Compositae	*Taraxacum officinale*
30	Crassulaceae	*Hylotelephium ewersii*

…Continued, Appendix A

No.	Family Name	Species Name
31	Crassulaceae	*Rhodiola heterodonta*
32	Crassulaceae	*Rosularia alpestris*
33	Crassulaceae	*Rhodiola adriatica*
34	Crassulaceae	*Rhodiola quadrifida*
35	Crassulaceae	*Rhodiola* sp.
36	Cyperaceae	*Carex diluta*
37	Cyperaceae	*Carex orbicularis*
38	Cyperaceae	*Carex* sp.
39	Cyperaceae	*Carex canescens*
40	Cyperaceae	*Carex* sp.
41	Cyperaceae	*Carex dioica*
42	Ephedraceae	*Ephedra gerardiana*
43	Fumariaceae	*Corydalis falconeri*
44	Gentianaceae	*Gentiana* sp.
45	Gentianaceae	*Gentianodes eumarginata*
46	Gentianaceae	*Gentianodes tianschanica*
47	Gentianaceae	*Gentianopsis paludosa*
48	Gentianaceae	*Sewertia* sp.
49	Geraniaceae	*Geranium pratens*
50	Labiatae	*Dracocephalum nutans*
51	Labiatae	*Nepeta linearis*
52	Labiatae	*Thymus linearis*
53	Onagraceae	*Epilobium angustifolium*
54	Onagraceae	*Epilobium latifolium* L. subsp*. latifolium*
55	Papavaraceae	*Papaver nudicaule*
56	Papilionaceae	*Astragalus rhizanthus*
57	Papilionaceae	*Oxytropis cachemiriana*
58	Poaceae	*Agrostis vinealis*
59	Poaceae	*Elymus longi-aristatus*
60	Poaceae	*Elymus nutans*
61	Poaceae	*Koeleria macrantha*
62	Poaceae	*Phleum alpinum*
63	Poaceae	*Piptatherum gracile*
64	Poaceae	*Poa alpina*
65	Poaceae	*Poa annua*
66	Poaceae	*Poa* sp.
67	Poaceae	*Poa supina*

…Continued, Appendix A

No.	Family Name	Species Name
68	Poaceae	*Poa*. sp.
69	Poaceae	Unknown Species
70	Polygonaceae	*Aconogonon rumicifolium*
71	Polygonaceae	*Aconogonon tortuosum*
72	Polygonaceae	*Bistorta affinis*
73	Polygonaceae	*Oxyria digyna*
74	Polygonaceae	*Oxytropis cachemiriana*
75	Polygonaceae	*Polygonum cognatum* subsp. *cognatum*
76	Polygonaceae	*Polygonum paronychioides*
77	Polygonaceae	*Polygonum pyrodiodes*
78	Polygonaceae	*Polygonum* sp.
79	Polygonaceae	*Rumex nepalensis*
80	Primulaceae	*Androsace septentrionalis*
81	Primulaceae	*Primula macrophylla* var. *macrophylla*
82	Primulaceae	*Primula schlagintweitiana*
83	Ranunculaceae	*Pulsatilla wallichiana*
84	Ranunculaceae	*Aconitum heterophyllum*
85	Ranunculaceae	*Aconitum violaceum* var. *violaceum*
86	Ranunculaceae	*Caltha alba*
87	Ranunculaceae	*Ranunculus* sp.
88	Ranunculaceae	*Ranunculus* sp.
89	Rosaceae	*Alchemilla* sp.
90	Rosaceae	*Cotoneaster affinis*
91	Rosaceae	*Potentilla argyrophylla*
92	Rosaceae	*Potentilla gelida*
93	Rubiaceae	*Artemisia dubia*
94	Rubiaceae	*Galium boreale*
95	Rubiaceae	*Galium himalayense*
96	Rubiaceae	*Galium* sp.
97	Salicaceae	*Salix caesia*
98	Salicaceae	*Salix* sp.
99	Saxifragaceae	*Saxifraga flagellaris* subsp. *crassiflagellata*
100	Saxifragaceae	*Saxifraga hirculus*
101	Scrophulariaceae	*Lagotis kunawurensis*
102	Scrophulariaceae	*Pedicularis albida*
103	Scrophulariaceae	*Pedicularis bicornuta*
104	Scrophulariaceae	Pedicularis oederi

…Continued, Appendix A

No.	Family Name	Species Name
105	Scrophulariaceae	*Pedicularis punctata*
106	Scrophulariaceae	*Veronica anagallis* var *aquatica*
107	Umbelliferae	Unknown Species
108	Umbelliferae	*Heracleum candicans*
109	Umbelliferae	*Pleurospermum hookeri* var. *thomsoni*i
110	Umbelliferae	*Pleurospermum hookeri* subsp. *tibetica*
111	Umbelliferae	Pleurospermum sp.
112	Unknown Family	Unknown Species

APPENDIX B MULTILOCUS GENOTYPES OF HIMALAYAN BROWN BEARS FROM DEOSAI NATIONAL PARK, PAKISTAN

		Microsatellites																													
ID	sex	Mu23		Mu50		Mu51		Mu59		G10Jnew		G10Hnew		G1A		G1D		G10B		G10C		G10L		G10O		G10X		Mu10		Mu15	
1	F	140	150	92	92	119	119	109	113	80	86	243	245	189	193	171	177	150	150	104	108	159	159	195	195	142	142	154	154	141	141
2	?	136	140	92	92	119	119	113	117	80	86	245	249	189	193	175	179	150	150	104	108	143	143	195	195	?	?	?	?	141	141
3	F	140	150	92	92	119	119	95	117	80	88	241	245	193	193	171	179	136	136	108	108	155	157	195	195	142	142	152	154	139	141
4	F	136	146	92	92	119	119	95	117	80	84	241	241	189	189	171	179	150	150	104	104	157	159	195	195	142	142	152	152	139	141
5	F	136	136	100	100	119	121	119	119	80	80	241	245	189	?	177	179	136	150	104	108	155	157	195	195	142	?	152	154	139	141
6	F	140	150	92	92	119	119	113	117	84	86	241	?	189	193	177	177	150	150	108	108	157	159	195	195	142	142	154	154	141	141
7	M	140	144	92	94	119	121	95	111	80	86	243	245	189	193	179	179	150	150	108	108	155	159	195	195	142	142	152	154	139	141
8	M	140	150	92	92	119	119	117	117	84	86	241	241	189	189	171	179	150	150	104	108	157	157	195	195	142	142	154	154	141	141
9	M	140	144	92	94	119	121	95	109	86	86	241	245	189	189	171	179	136	136	?	108	?	?	195	195	142	142	152	154	139	141
10	M	136	150	92	100	119	121	95	119	80	88	241	245	189	193	179	179	136	150	104	104	155	157	195	195	142	142	152	152	139	139
11	M	136	150	92	100	119	121	119	119	80	80	241	241	193	193	171	?	150	150	104	104	155	155	195	195	142	142	152	152	139	139
12	M	144	150	92	100	119	119	109	119	80	86	241	241	189	193	179	179	136	150	104	108	?	?	195	195	142	142	152	152	139	139
13	M	140	150	92	100	119	121	95	119	80	88	241	245	193	193	177	179	150	150	104	108	155	157	195	195	142	142	150	154	137	141
14	M	146	150	92	92	119	119	109	117	84	88	241	245	189	189	171	179	136	150	104	108	155	159	195	195	142	142	152	152	139	139
15	M	136	140	92	100	119	119	95	119	88	88	241	245	189	193	177	179	136	150	104	108	143	143	195	195	154	154	142	142	139	139
16	M	140	144	96	100	119	121	95	109	80	88	245	245	189	193	177	179	136	150	108	108	157	159	193	195	142	142	152	154	139	141
17	F	140	144	92	94	119	121	111	115	80	86	243	245	189	189	171	175	136	150	108	108	157	159	195	195	142	142	152	154	139	141
18	F	144	150	92	100	119	127	95	113	80	88	245	245	189	193	171	179	136	150	104	104	155	157	195	195	142	142	152	154	139	141
19	M	140	150	92	92	119	119	109	113	86	88	241	245	189	189	177	179	136	136	104	108	143	143	195	195	154	156	140	140	139	141
20	M	136	140	92	100	119	121	109	119	80	80	241	245	189	189	177	179	136	?	108	108	?	157	195	195	142	142	?	154	139	141
21	M	140	144	92	94	119	121	111	115	80	86	?	?	189	189	?	?	136	150	108	108	?	?	?	?	142	142	152	154	139	141
22	F	140	140	92	94	119	119	95	109	80	86	243	245	189	193	177	177	136	150	104	108	159	163	195	195	142	142	152	152	139	139
23	F	136	144	92	94	119	121	95	109	80	86	241	245	193	193	179	179	136	150	104	108	155	155	195	195	142	142	152	154	139	141
24	M	136	144	94	100	119	119	95	109	80	80	241	243	189	189	177	179	136	150	104	108	157	159	195	195	142	142	154	154	141	141
25	F	140	150	92	92	119	121	109	117	80	80	241	245	189	193	177	179	136	150	108	108	157	159	195	195	142	142	152	154	139	141
26	M	140	146	92	92	119	119	95	117	80	80	241	245	189	193	177	179	150	150	104	108	159	159	195	195	142	142	152	154	139	141
27	M	136	140	92	92	119	121	95	117	80	80	241	245	?	193	177	179	136	150	108	108	143	143	195	195	156	158	140	142	141	141
28	?	136	136	92	96	121	121	117	117	80	84	243	?	189	191	177	179	150	150	104	108	143	143	195	195	156	158	140	140	?	141

APPENDIX C STABLE ISOTOPE VALUES FROM HAIRS OF BROWN BEARS CAPTURED IN DEOSAI NATIONAL PARK, PAKISTAN

Sample	Sex	Weight (kg)	$\delta^{15}N$	$\delta^{13}C$	Estimated Animal Matter (%)
1	Female	68	4.0	-24.0	23.4
2	Male	55	3.5	-23.5	13.2
3	Male	55	1.1	-23.6	0.0
4	Female	79.5	3.4	-23.9	11.2
5	Female	80	4.2	-24.3	27.5
6	Female	65	3.7	-24.1	17.3

APPENDIX D NUTRITIONAL CONTENT OF PLANT SPECIES FROM DEOSAI NATIONAL PARK, PAKISTAN

Species	Forage Type	DM	Proximate composition of %DM					
		%	CP	CF	T. Ash	EE	NFE	TDN
Cyperaceae								
Carex polyphylla	Graminoid	28.9	17.27	21.9	7.76	1.74	51.33	70.83
Carex bulbeosaris	Graminoid	41	11.3	25.74	7.16	6.04	49.76	59.23
Carex alpina	Graminoid	31.9	10.49	24.52	6.23	3.99	54.77	63.15
Poaceae								
Agrostis or poa sp	Graminoid	55.3	9.51	30.19	7.41	2.28	50.61	62.14
Molinia caerulea	Graminoid	63.9	10.95	24.93	7.16	8.36	48.6	54.54
Phalaris arundinacea	Graminoid	40.8	13.12	23.89	11.68	5.98	45.33	57.79
Avena aspera	Graminoid	31	6.31	36.32	6.25	2.21	48.91	58.06
Festuca pratensis	Graminoid	26.6	11.74	21.21	5.58	2.41	59.06	68.19
Aliaceae								
Allium himolyense	Forb	23.1	9.57	20.71	4.47	2.81	62.44	69.77
Apiaceae								
Harcleum candicans	Forb	36	18.24	30.26	9.66	3.92	37.92	63.37
Astraceae								
Anaphalis nepalensis	Forb	30.25	9.27	31.67	7.19	2.74	49.13	60.86
Jurinea halaica	Forb	-	12.08	23.98	15.45	5.21	43.28	55.49
Lactuca sp.	Forb	0.12	13.3	18.27	19.72	5.78	42.93	54.34
Fabaceae								
Oxytropis cachemiriana	Forb	46.2	18.36	22.58	19.35	1.33	38.38	63.18
Polygonaceae								
Aconitum hetrophyllum	Forb	14.7	12.16	21.4	24.42	3.03	38.99	52.64
Primulaceae								
Primulla miscrophylla	Forb	22	13.8	16.56	17.28	2.39	49.97	62.5
Rubiaceae								
Galium himalayense	Forb	26.37	12.77	19.21	10.33	2.41	55.28	66.03
Saxifragaceae								
Saxifraga flagellaris	Forb	33.4	7.09	19.16	8.99	3.11	61.65	62.37
Salicaceae								
Salix caesius	Shrub	36.6	15.97	18.42	5.19	6.27	54.15	66.13

(DM: Dry Matter, CP: Crude Protein, CF: Crude Fiber, EE: Ether Extract, NFE: Nitrogen Free Extract, TDN: Total Digestible Nutrients)