Home Range, Movements and Habitat Use of Snow Leopard (*Uncia Uncia*) In Nepal

Rodney M. Jackson

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1984 - Female snow leopard photographed using a remotely-triggered camera

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Note: The original thesis contained no photographs. I have added a few photos illustrating the study area and focal species for the reader's convenience. The suggested citation is:

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HOME RANGE, MOVEMENTS AND HABITAT USE
OF SNOW LEOPARD (*Uncia uncia*)
IN NEPAL

by

Rodney Malcolm Jackson

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ABSTRACT

Home ranges for five radio-tagged snow leopards (*Uncia uncia*) inhabiting prime habitat in the Nepal Himalaya varied in size from 11-37 km^2. These solitary felids were crepuscular in activity, and although highly mobile, nearly 90% percent of all consecutive day movements involved a straight-line distance of 2 km or less. No seasonal difference in daily movement or home range boundary was detected. While home ranges overlapped substantially, use of common core spaces was temporally separated, with tagged animals being located 1.9 km or more apart during the same day. Spatial analysis indicated that 47-55% of use occurred within only 6-15% of the total home area. These snow leopards shared a common core-use area, which was located at a major stream confluence in an area where topography, habitat and prey abundance appeared to be more favorable. A young female used her core area least, a female with two cubs to the greatest extent. The core area was marked significantly more with scrapes, faeces and other sign than non-core sites, suggesting that social marking plays an important role in spacing individuals.

Snow leopards showed a strong preference for bedding in steep, rocky or broken terrain, on or close to a natural vegetation or landform edge. Linear landform features, such as a cliff or major ridgeline, were preferred for travelling and day-time resting. This behaviour would tend to place a snow leopard close to its preferred prey, blue sheep (*Pseudois nayaur*), which use the same habitat at night. Marking was concentrated along commonly travelled routes, particularly river bluffs, cliff ledges and well defined ridgelines bordering stream confluences -- features that were most abundant within the core area. Such marking may facilitate mutual avoidance, help maintain the species' solitary social structure, and also enable a relatively high density of snow leopard, especially within high-quality habitat.

ACKNOWLEDGEMENTS

The 1981 Rolex Award for Enterprise enabled this study in the first place, and I extend my deep appreciation to Mr. Andre J. Heiniger, Chairman of the Rolex Watch Company, Geneva. Grants were also provided by the National Geographic Society, International Snow Leopard Trust, Wildlife Conservation International (a division of the New York Zoological Society), the World Wildlife Fund - US, and the International Trust for Nature Conservation. The California Institute of Environmental Studies, The Mountain Institute, International Snow Leopard Trust, National Wildlife Federation, Mill Pond Press, Robert Bateman, and Yvon Chouinard helped cover the cost of data analysis and write-up. His Majesty's Government of Nepal authorized the project through the Department of National Parks and Wildlife Conservation (DNPWC) and the King Mahendra Trust for Nature Conservation (KMTNC). I am particularly indebted to His Majesty's Government to work in a remote part of the Shey-Phoksundo National Park. Special thanks are due Mr. Biswa N. Upreti, former Director General DNPWC and Dr. Hemanta R. Mishra, former Member Secretary, KMTNC. Administrative support was offered by Mr. Lhapka Sherpa, then Warden of Lake Rara National Park.

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I am indebted to my parents for enabling me to realize my dream to become a wildlife biologist. My deepest love and appreciation lies with Darla, my partner, who was part of the project from its inception. Darla wrote a well-received popular account of our adventures; with a minimum of prior camping experience, she quickly adapted to the remote Langu Valley and its spartan diet, with mail from the real world that came only once every three months. Her faith and never-ending support enabled me to persevere in the face of severe roadblocks and obstacles from bureaucrats. The lowest point came when high government officials refused permission for Gary to travel to Nepal to join the project so that the movements of the widely-roaming snow leopards could be effectively monitored; they seemed intent on terminating the research program just as I proved it was possible to radio-tag such an elusive creature. These, and porter strikes on high passes were no obstacle to Darla's ever-present smile, her ability to win over friends and her constant words of encouragement.

Finally, I am grateful to the many individuals and corporations who donated equipment, fed us meals after a particularly arduous field session or otherwise made sure that we were properly taken care. Rather than repeating their names, I refer the reader to Darla's book on the project titled, *Vanishing Tracks: four years among the snow leopards of Nepal*, published by William Morrow in 1989.

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Gary Ahlborn mapping terrain and habitat types of the Langu Valley

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PART 1 - INTRODUCTION AND METHODS

CHAPTER 1 INTRODUCTION

1.1 Introduction

The snow leopard (*Uncia uncia*, formerly *Panthera uncia*[1]) inhabits the high, remote mountains of Central Asia, and has been listed in the Red Data Book as an endangered species throughout its range since 1972 (Goodwin and Holloway 1972). The snow leopard meets criteria for endangered status under newly proposed criteria (IUCN 1994). It is widely, but sparsely distributed through the mountain ranges of Tibet and adjoining parts of China, the Himalaya of Nepal, India, Bhutan and Sikkim, the Karakorum Mountains along the Indo-Pakistan border, the Hindu Kush Range of Pakistan and Afghanistan, the Pamirs along the Tajikistan - Afghanistan border, the Tien Shan of Kyrgyzstan, Kazakhstan and China, and the Altai Range of Mongolia and Russia, among other mountain complexes (Schaller 1977).

Snow leopards are closely associated with arid and semi-arid shrubland, grassland or barren habitats. In the Sayan Mountains of Russia and parts of the Tien Shan Range, they inhabit open coniferous forest, although generally avoiding dense forest cover (Heptner and Sludskii 1992). The snow leopard is primarily an inhabitant of the alpine and subalpine zone, from elevations of 900 m to 5,500 m or more, but usually between 3,000 and 4,500 m (except in the northern range limits where snow leopards occur between 900 and 2,500 m) (Heptner and Sludskii 1992; Schaller et al. 1994). In Pakistan, Russia and parts of India they are reported to migrate to lower elevations during winter, following prey (Roberts 1977; Dang 1967).

Despite a vast geographic range of about 2.3 million square kilometers (Fox 1994), it is among the least known of the world's large cats. Until recently, virtually all knowledge

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[1] Nomenclature according to Wozencraft 1993, based upon recent genetic and systematic research. European investigators have long argued that snow leopards merit a separate genus based on morphological and behavioural differences from other members of the genus *Panthera*.

concerning snow leopard in the wild accrued from anecdotal observations, often made by big game hunters roaming remote areas in search of wild sheep and goat trophies (Hemmer 1972; Guggisberg 1975; Roberts 1977; Schaller 1977). For example, Schaller summarized what little natural history information was available on this solitary felid in his book, *Mountain Monarchs*. After intensively searching different parts of the Himalaya for pugmarks and other sign, Schaller (1977:155) surmised that snow leopard must travel far in search of food and that "the size of its home range is unknown, but judging by the long intervals between an animal's visits to certain valleys it must be quite large". While pugmarks indicated that snow leopards travelled alone most of the time, no data existed to determine whether they conformed with the basic pattern of solitary felid social organization -- namely one in which males occupy larger, exclusive ranges which encompass several female ranges (Sunquist and Sunquist 1989). Little or no information was available on habitat preferences, although Schaller noted that snow leopards tended to travel along the base of cliffs leaving abundant sign in the form of scrapes and feces. More data have become available on the snow leopard's diet from different areas, but the accompanying information precludes an examination of basic predator-prey and habitat relationships. See Fox (1989) for a more recent summary of snow leopard status and ecology, but this literature review predated the few telemetry studies that have been undertaken to date (see below). Jackson (1979a) reported on the status and conservation of snow leopards in Nepal.

The paucity of behavioral and ecological information can be largely attributed to the species' secretive habits, its low density, sparse distribution and the hostile or inaccessible habitat in which it is found. Investigators who relied upon incidental sightings or sign as a source of data found themselves returning with little substantive information to show for the significant effort they had expended simply to visit remote field sites. As a secretive, shy and extremely well-camouflaged carnivore, the snow leopard is clearly an ideal candidate for the use of radio-telemetry as an investigative tool. The first attempt in 1972 at intensive study was undertaken in Pakistan, but failed because the study population was essentially decimated while researchers attempted to live-trap animals for instrumentation (Schaller pers. comm.). Similar obstacles have discouraged detailed investigations of the sympatric prey species of the snow leopard, such as bharal or blue sheep (*Pseudois nayaur*), Himalayan tahr (*Hemitragus jemlahicus*) and Asiatic ibex (*Capra ibex sibirica*).

This study is the first successful, in-depth attempt at investigating snow leopard ecology using radio-telemetry. Given their almost legendary secretiveness and camouflage, radio-telemetry offers the only realistic option for gathering information on snow leopard movements, home range, patterns of habitat utilization, social organization and activity, among other topics. In late 1981 His Majesty's Government of Nepal (HMG) approved my application to study snow leopards in the Langu Valley of western Nepal under a joint agreement between the California Institute for Environmental Studies and the Department of National Parks and Wildlife Conservation (DNPWC). Field work was undertaken between January 1982 and June 1985, generating detailed information on snow leopard ecology, including home range, movements, activity, marking behavior, and habitat preferences (Jackson and Ahlborn 1988a, 1988b, 1989; Ahlborn and Jackson 1988).

More recently, snow leopards have been radio-tagged in other parts of Nepal (Oli 1994), India (Chundawat 1989, 1990, 1992), and Mongolia (Schaller et al. 1994), but resulting information has been severely limited by a small sample size (1-3 individuals) or short periods of monitoring (all less than 3 months). Our understanding of distribution, habitat use, food habits and marking behaviour has grown, as evidenced by the interest shown in the five international symposia held to date and centered around snow leopard. Driven by concern for its future, researchers have tended to focus upon determining snow leopard status and distribution, identifying conservation actions, and addressing issues related to the depredation of livestock (for example, Buzurukov and Muratov 1994; Fox and Chundawat 1988; Fox 1994; Jackson et al. 1994a; Koshkarev 1984; Mallon 1984a & b; Oli, 1994; Schaller et al. 1987, 1988a and b, 1994). However, conservation will only be effective if protection programs and specific initiatives are based upon a thorough understanding of how snow leopards utilize, share and compete for available habitat and other resources. Ideally, such research should be followed by range-wide surveys to identify habitat distribution, availability and quality at the landscape level (Maehr and Cox 1995; Villarrubia and Jackson 1994).

1.2 Study Objectives

The Langu Valley study area supports good populations of snow leopard and two of its key prey species, blue sheep and Himalayan tahr. It offered an excellent opportunity to examine snow leopard ecology in high or very high quality habitat, without interference from livestock grazing and with minimal human disturbance. Overall study objectives were to examine, to the extent possible in 3.5 years, snow leopard activity and movement patterns, home range size and configuration, habitat utilization and predator-prey relationships (food habits and basic ungulate prey population dynamics). I sought to gather as much data on a diverse topics as time and resources permitted. Although I attempted to gather data both incidentally and systematically, using direct and indirect methods of study, difficult logistics, the exceedingly remote study site and its rugged terrain greatly hampered efforts at intensively radio-tracking snow leopards. This dissertation focusses on the following specific questions:

(1) How closely does the snow leopard's home-range pattern and social system resemble that shown in other large solitary cats, such as puma (also known the cougar or mountain lion) (*Felis concolor*, considered *Puma concolor* by Wozencraft 1993), common or forest leopard (*Panthera pardus*), jaguar (*P. onca*), or the tiger (*Panthera tigris*)?

(2) What are its daily movement and activity patterns, and how do snow leopards space themselves both temporally and spatially within an area of prime habitat?

(3) What habitat preferences are shown by snow leopard, and how is home range size, configuration and spatial utilization influenced by such preferences?

(4) What lessons can this study offer for conserving snow leopards, their prey and the associated high-altitude ecosystem, in order for the snow leopard to be justifiably removed from the endangered species list?

Unless otherwise specifically noted, I was responsible for designing, directing and undertaking all work presented in this dissertation. From June, 1983 until the end of the study, Gary. G. Ahlborn, a trained wildlife biologist joined me to assist in radio-tracking, habitat mapping and characterization, along with one or two Nepalese field assistants. Mr. Ahlborn was primarily responsible for designing and conducting the study of marking behavior in the snow leopard, findings of which are reported in Ahlborn and Jackson (1988). Mr. Karan B. Shah, the Nepalese counterpart assigned to the project by the Government of Nepal, undertook concurrent research on blue sheep and Himalayan tahr, focussing upon their status, distribution, herd dynamics, activity pattern, and habitat use. Mr. Shah is submitting his work to Tribhuvan University, Kathmandu (Nepal) as part of his Ph.D. program there.

Full-time data analysis was curtailed six months after completing the field work in 1985 due to lack of funding, but research findings on capture and immobilization techniques, home range, movement patterns and marking behavior were reported in a series of published papers over the following years (Jackson and Ahlborn 1984, 1988a, 1988b, 1989, 1990; Jackson et al. 1990). I prepared and wrote all papers except for the one on marking behavior mentioned above. In March 1994, I applied for readmittance to the doctoral program and completed an in-depth analysis of habitat utilization by snow leopards, using the data-set gathered earlier and employing the emerging technology of Geographic Information System (GIS) software. This thesis focusses upon that work.

The Study Area in the Langu Gorge of Western Nepal showing Tillisha Cave (4,300 m)
- the highest camp used to track radio-collared snow leopards

CHAPTER 2 THE STUDY AREA

2.1 Location and Topography

The study area (Longitude 82°, 33' to 41' E; Latitude 29°, 30' to 35' N) lies along the middle portion of the Langu River gorge (*Namlang Khola* in Nepalese), to the north of the main Himalayan Range near the border with Tibet in the far western region of Nepal (Figure 1). It encompasses the Dolphu Village Development Council (VDC) administrative unit of Mugu District in the Karnali Zone, Nepal's only major administrative region that is entirely roadless. The core study area is located on the western edge of the Dolpo Plateau in the Shey-Phoksumdo National Park, which was established in 1985 by His Majesty's Government partially on the basis of recommendations from my study. Enclosing a 3,555 km^2 area, it is the largest of Nepal's 8 national parks, and protects Tibetan fauna and flora, as well as culture. The project study area totals some 300 km^2, including an 80 km^2 core zone located immediately north of the Langu Khola, where most field work was undertaken.

The terrain is among the most rugged and forbidding in the Himalaya (Tyson 1969), and the trail along the Langu River into Dolpo can only be negotiated in winter when water-levels and temperatures are low. Elevations range from 2,700 m along the Langu River to over 6,800 m in the Kanjiroba *Himal* or mountain range which forms the study area's southern boundary. The Langu River, which drains nearly all of the Dolpo Plateau, runs almost east - west, joining the Mugu Karnali River about 25 miles downstream of the study site. The river has eroded a deep gorge, bounded by cliffs and steep, rocky slopes in excess of 35 degrees. Tributary streams like Dhukyel and Tillisha are also deeply incised and are bordered by banded rock buttresses which are virtually impenetrable to humans on foot. Prolonged water erosion has created a series of large, somewhat isolated mountain massifs.

Due to high solar radiation and evaporation, very little of the study area has permanent snow or ice cover, and only land over 5,400 m in elevation supports remnant ice-fields and glaciers. Thus, the only glacier of any consequence in the core study area is that associated

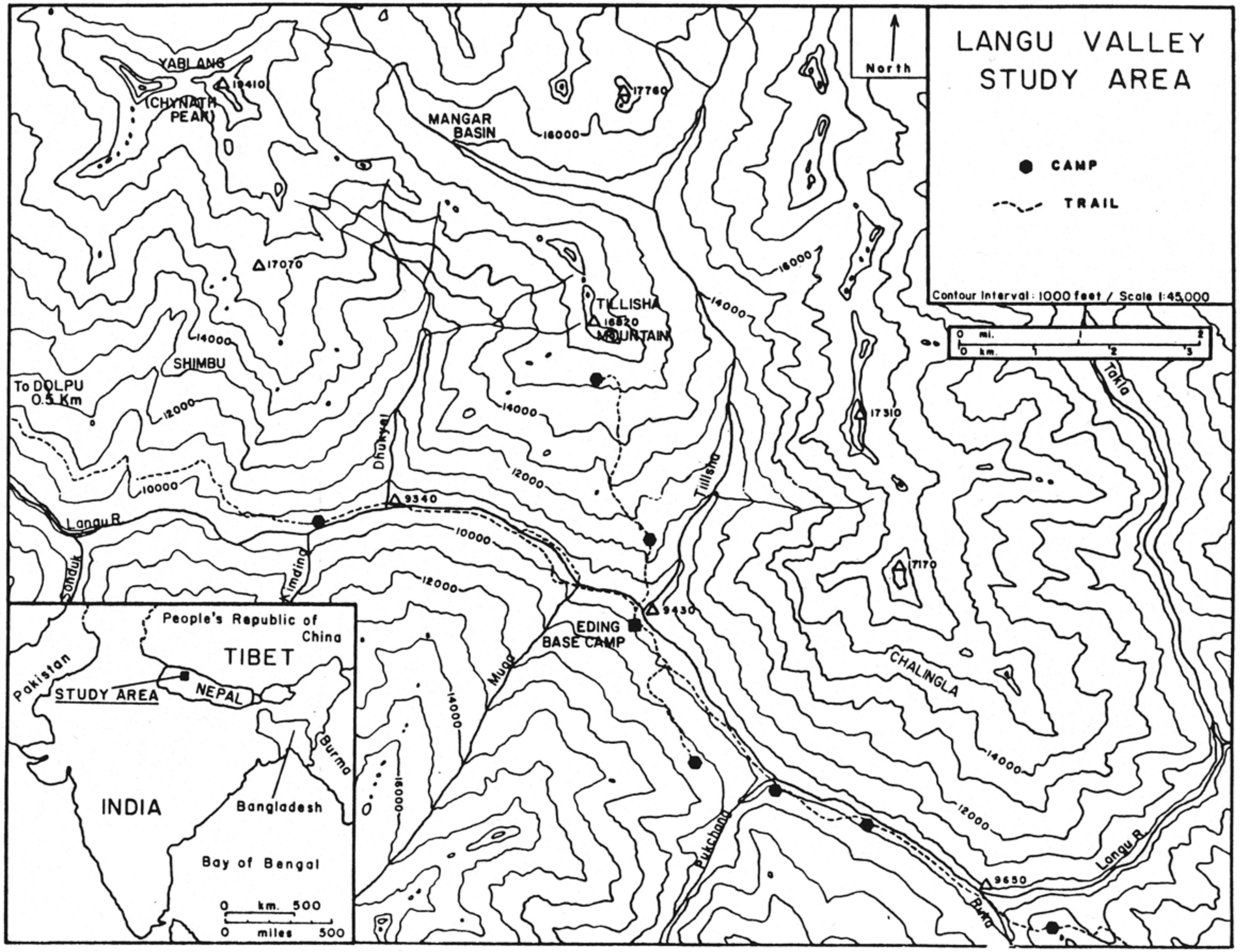


Figure 1: Langu Valley Study Area

with the north-eastern buttress of Mt Chynnath (5,918 m); by contrast most peaks to the south of the Langu River, along the Kanjiroba and Sisne *Himal*, support permanent glaciers, although these appear to be receding. Incised river and stream erosion has resulted in drainages with well-defined V-shaped valley profiles, with only one U-shaped valley remaining within the core area. Past deposition of river silt, sand and gravel have created small, discontinuous alluvial terraces near most stream confluences with the Langu river, although many of these are now 100 - 150 m above the present river-bed, indicative of rapid down-cutting. Such terraces are extensively used by snow leopard for social marking.

Landforms in the study area fall into four distinct types in terms of land-surface ruggedness (Figure 2), with each type exhibiting different geomorphic or topographic features: (1) *Broken Terrain* consists of areas slightly to moderately broken by rocky outcrops, drainages (primarily dry gullies) and ridges, occupying 13.1 percent of the immediate study area; (2) *Very Broken Terrain* represents areas which are highly broken in all dimensions (such as strongly fractured cliffs and ridges), and comprise 12 percent of the area; (3) *Smooth Terrain* is dominated by relatively evenly-surfaced slopes and gently rolling terrain with few rock outcrops (totalling 40.3 percent of the area); and (4) *Cliffs*, defined as land with slopes in excess of 50°, comprise 34.6 percent of the study area. See Section 3.6 for additional information on the terrain types.

2.2 Geology and Soils

Very little is known about the area's geology, and to my knowledge the only reports available are those which address western Nepal's geology at a gross regional scale. Most rock strata have been heavily-folded and consist primarily of gneiss, belonging to Tibetan Tethys sediments of Jurassic to Proterozoic ages, with intrusive Tertiary tourmaline granites (Karmacharya 1989; Ohta and Akiba 1973). The light-grey gneiss of the Ghilang Formation are medium to fine grained in texture, containing black tourmaline, although augens may or may not be present. Bands of gneiss and schist alternate, interspersed with a few layers of highly micaceous quartzite containing a few pink and light brown garnets. Other rock formations include limestone along the southern flanks of the Langu River, while granitic outcrops dominate the peaks to the north. Granite probably belongs to the Mugu Formation, a Tertiary leucocratic granite rich in quartz and feldspar that has been

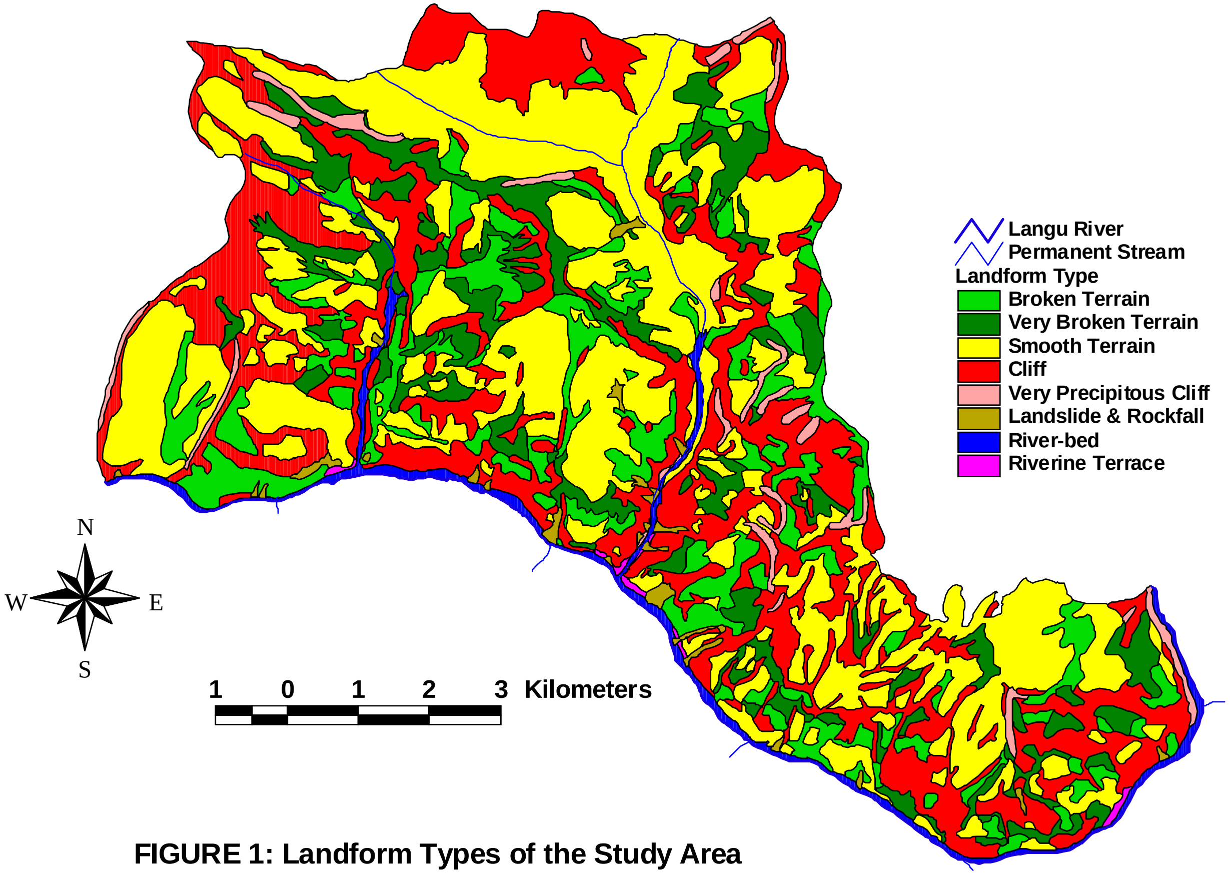


FIGURE 1: Landform Types of the Study Area

intruded into Precambrian crystalline schists, but remains relatively unweathered. Deposits of copper-bearing ore are found in the Sangduk Khola, south of Dolphu village. Heavy faulting, folding and jointing occurs throughout the area, with a dominant NNE strike and a dip averaging 50-60° (Karmacharya, 1989).

Soil texture and structure varies widely, although most soils are shallow and poorly developed, with substantial expanse of exposed bedrock. Since there is no cultivation or settlement in the core study area, all soils are subject only to natural weathering.

2.3 Climate

The study area is situated in the "Inner Valley" semi-arid vegetation zone described by Stainton (1972) and Schweinfurth (1957). This climatic regime results from the rain-shadow effect due to the nearby Kanjiroba Himal which captures most of the moisture, as well as orographically-induced diurnal wind circulation in the Mugu-Karnali river system (Bishop 1990). Other factors contributing to the semiarid conditions include low winter temperatures, high evaporation, and a swift spring snow-melt and runoff. Climate of the study area is best characterized as being temperate, with relatively little snowfall, most of which occurs from late December into early March. Total annual precipitation is estimated at 500-1,000 mm, with more than half occurring as rain during the monsoon period (July - September). Data from Mugu, the nearest weather station to the study area (located about 18 km to the northwest), indicate that 71 percent of the precipitation occurs during the summer monsoon (Bishop 1990:37). Annual precipitation is extremely variable, ranging from less than 500 mm to about 1,500 mm during exceptionally wet years (Dobremez 1976: 75, Figure 64).

Weather data gathered during this study at Eding Base Camp (located on the Langu River at an elevation of 2,950 m) are summarized in Table 1. The coldest and driest months are January and November/December, while the warmest and wettest months are May and July-August, respectively. Average daily temperatures over the three-year period 1982 - 1985 at Base Camp were 1° Celsius in January and 17.5° in June. Diurnal temperature ranges of more than 25° are not uncommon, especially in late winter and spring; the hottest period is generally late May through mid-June, immediately before the cooling influence of the monsoon. Snowfall rarely remained on the ground for more than a few days on

Table 1: Temperature and precipitation measurements taken at Base Camp (1982 - 1985)

	Daily Temperature (degrees Celsius)[1]					Precipitation[2]	
		Minimum		Maximum			
Month	N[3]	Avg	Range	Avg	Range	Snow	Rain
January	87	-5.0	-14.0 to 0.0	7.1	-6.0 to 20.0	1.49	0.00
February	78	-4.8	-13.0 to 5.0	9.8	0.0 to 20.0	0.79	0.00
March	84	-0.1	-15.0 to 8.0	15.2	0.0 to 25.0	1.51	0.02
April	97	3.4	-5.0 to 17.0	17.2	-0.5 to 25.0	0.21	0.10
May	104	7.4	-1.0 to 15.5	21.3	12.0 to 31.5	0.00	0.12
June	88	11.4	5.0 to 19.0	23.7	16.0 to 31.0	0.00	0.17
July	28	14.0	12.0 to 16.0	24.9	19.0 to 29.0	0.00	0.14
August	31	13.9	8.0 to 18.0	24.0	17.0 to 29.0	0.00	0.26
September	13	11.0	8.0 to 14.0	20.3	13.0 to 25.0	0.00	0.33
October				No data			
November	17	-0.2	-6.0 to 4.0	11.2	6.0 to 17.0	0.01	0.00
December	78	-2.7	-11.5 to 4.0	10.4	0.5 to 18.5	0.27	0.00

Notes:

[1] Temperature = degrees (Celsius), as measured in the shade at Eding Base Camp (2,875 m)
[2] Precipitation = mean daily precipitation (centimeters)
[3] N = number of days sampled

south-facing slopes, in contrast to northerly slopes which retain their winter snow cover for up to several months. Periods of greatest soil-water deficiency are the months of May and June, prior to the monsoon, and then again from October into December preceding winter snowfall.

The monsoon usually reaches the study area in late June or early July, and lasts until the end of September. July and August tend to be the wettest months, but precipitation varies widely from year to year. During these periods rainfall generally occurs on a near daily basis under cloudy skies. Compared to the southern slopes just a few miles away, there is significantly less rainfall, less mist and better visibility, with higher incidence of sunshine. For the purposes of this study, the seasons were defined as winter (December to mid-March); spring (mid-March to May); summer (June to September); and fall/autumn (October to November).

2.4 Vegetation

Three brief floral surveys have been undertaken in or near the study area (Grey-Wilson 1974; Shrestha 1982; and Williams 1953). Collections made during the course of this study are housed with Dr. H. Tabata at the Laboratory for Plant Ecology, Kyoto University, Kyoto, Japan. Polunin and Stainton (1984) was used to identify flowering plants collected while in the field, with final identifications accruing from taxonomic examination of specimens provided to Dr. Tabata. The vegetation types described here are adapted from Dobremez (1976), Stainton (1972), Shrestha (1982) and Schweinfurth (1957).

A review of the literature indicates vegetation of the study area contains elements typical of those forest and shrub types found in comparable parts of the Jumla-Humla region, as well as the neighboring but noticeably drier Dolpo region (Stainton 1972). The Langu Valley encompasses the Upper Temperate and Alpine Zones delineated by Dobremez (1976). West Himalayan floral elements are well represented, indicating a closer affinity with flora from Kashmir or the Gharwal region of India than with the eastern Himalayan elements dominating the flora of Sikkim or Bhutan (Dobremez 1976; Stainton 1972). However, its geographic location north of the main Himalayan Range (and subsequent protection from the full effect of the monsoon) ensures the presence of plant species more commonly associated with Tibet's xeric flora (Chang 1981).

Based primarily upon temperature and rainfall regimes, Dobremez and Shrestha (1980) developed a 1:250,000 scale map of potential vegetation types for the Jumla - Saipal region, including the Langu Valley study area. However, this model failed to fully incorporate the pervasive effect aspect has on community structure and composition. Thus, it failed to predict the occurrence of coniferous forest along the south side (but north-facing) slopes of the Langu River, although it more accurately depicted the north bank vegetation as a *Caragana, Lonicera* and *Artemisia* dominated steppe.

Seven vegetation types were recognized (Figure 3). The steppe shrub community which dominates the northern side of the Langu Gorge between elevations of 2,800 m and about 3,900 m is comparable to Dobremez's(1976) *Tree and Shrub Steppe* types and Stainton's (1972) *Dry Alpine Scrub* category. Dominant shrubs include black juniper (*Juniperus indicus*), *Caragana gerardiana, Lonicera* spp., *Abelia triflora, Rabdosia pharica, Cotoneaster* spp., and sagebush (*Artemisia* spp.). *Rosa* - *Berberis* - *Ribes* - *Jasminium* occupy rocky sites, while *Prunus mira* occurs in gully bottoms and some talus slopes. This community was subdivided into two vegetation types, Mixed Shrubland and Subalpine Shrubland as noted below.

Barren areas (less than 10 percent ground cover) occupy about 53 percent of the north Langu slopes, with alpine grassland covering about 16 percent, and shrubland the remaining 26 percent. Small isolated stands of blue pine (*Pinus wallichiana*) occur in most large tributaries, with birch (*Betula utilis*) on some higher, moist north-facing ledges and slopes. Alpine grassland (dominated by the sedge *Kobresia*) occurs on the more evenly sloping and less rocky mountain slopes above about 3,900 m, as well as narrow glacial bowls and high cliff ledges. The upper limit of grassland is about 4,800 m. A few hardy succulents grow on screes as high as 5,200 m.

In contrast to the semi-arid conditions found north of the Langu River, the cooler, moister north-facing slopes to the south support expansive, rather open blue pine forests, interspersed with a few Himalayan silver fir (*Abies spectabilis*) and West Himalayan spruce (*Picea smithiana*). Above the discontinuous forest belt, at about 3,500 m there is a dense zone of birch forest and shrubland. Much of the forest has been destroyed by fire, so that dense successional stands of *Cotoneaster, Caragana* and rose shrubland occur. Sage dominates in lower, more open areas.

These communities are described in more detail below, ordered according to the two major elevational and climatic zones present:

TEMPERATE AND SUBALPINE ZONE (< 3,300 - 4,200 m)

Riparian Woodland: This community occurs below 3,000 m along permanent water-courses like the Langu River, and Tillisha or Dhukyell streams. It consists of narrow and highly

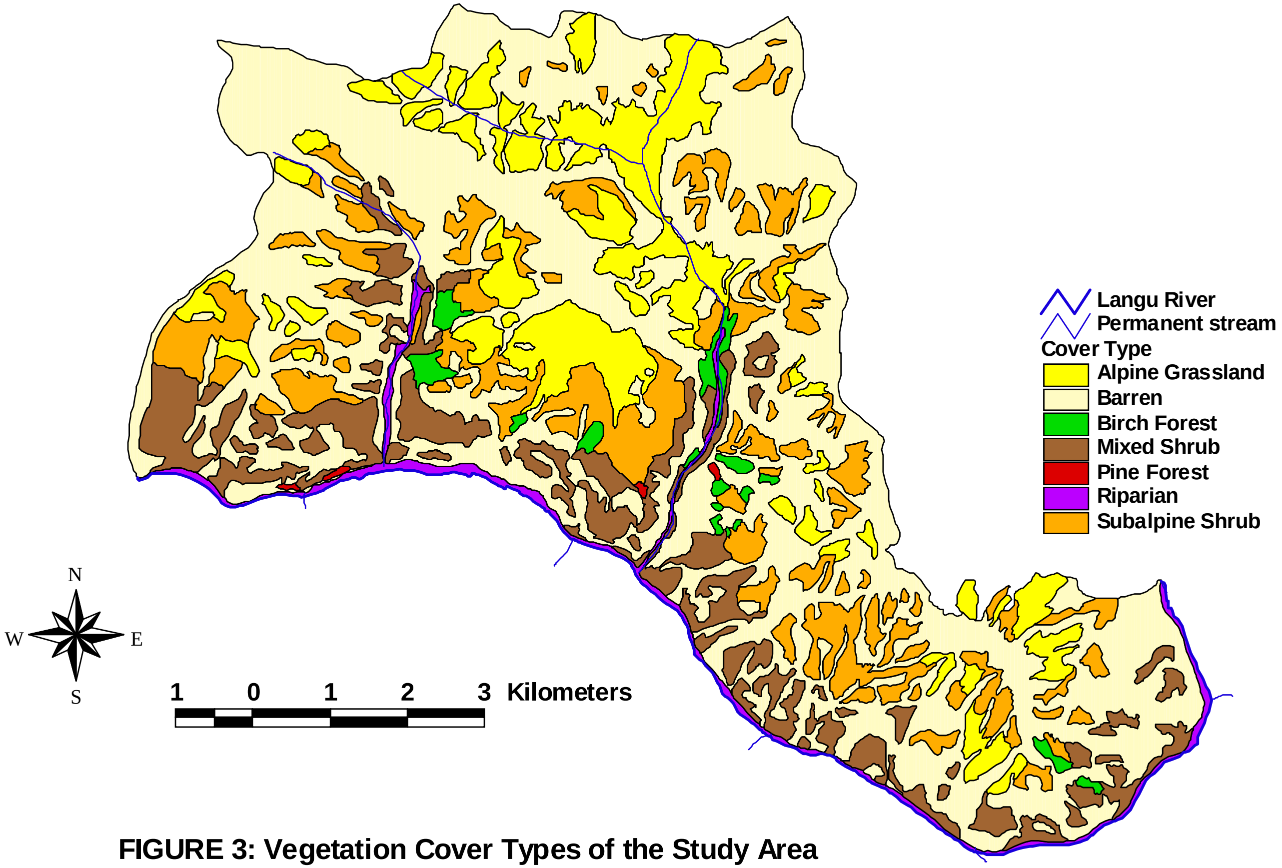


FIGURE 3: Vegetation Cover Types of the Study Area

discontinuous stands of Himalayan poplar (*Populus ciliata*), willow (*Salix spp*) and *Abelia triflora, Sambucus* or jasmine (*Jasminium humile*), interspersed with other vegetation types. Stainton (1972) recognized poplar woodlands as a distinctive forest type, although it is usually a component of *Aesculus - Juglans - Acer* forests which are found along major river courses in western Nepal between 2,300 - 3,200 m elevations. Dobremez (1976) described this as a subtype of silver fir forests. Riparian woodland is poorly developed in the study area, probably as a result of poor soil, aridity, unstable slopes and erosive flooding.

Shaded sites with deep soils along the Langu River supported *Desmodium elegans* and *Butea minor*, two tree species which are common below elevations of 2,900 m. Buckthorn (*Hippophae* spp) and *Myricaria* scrub, characteristic of streambeds in Dolpo and Tibet, are absent from the study area.

Mixed Shrubland: This widespread vegetation type is found between elevations of 2,700 - 3,800 m, occupying about 11 percent of the core study area. It is a diverse shrub community containing up to 6 common shrubs, including black juniper (*Juniperus indica*), a tree or shrub that is especially abundant on south-facing slopes. The understory usually contains many herbs, grasses or forbs. Shrubs stand between 0.3 - 1.5 m in height and usually 1 - 3 species dominate a particular site. Ground cover is extremely variable depending upon slope steepness, moisture, aspect and soil development, but averages 24 percent. Individual woody plants are widely spaced, although this pattern varies widely, with the greatest cover and densest spacing in sites supporting deep soils. Shrub composition varies between 15 and 100 percent, averaging 76 percent.

The most widespread shrub species are caragana (*Caragana gerardiana*), *Lonicera* spp., *Spirea arcuata*, shrubby cinquefoil (*Potentilla fructicosa*), *Rhododendron lepidotum, Berberis* spp. and *Cotoneaster* spp. On the drier more southwesterly slopes *Rabdosia pharica*, wild peach (*Prunus mira*), and *Ephredra gerardiana* are also present and tend toward dominance, while the more mesic north-facing slopes are dominated by *Abelia triflora, Lonicera hypoleuca* and *Viburnum* spp. Dry north-facing sites support *Artemisia* spp. with shrubby cinquefoil, wild asparagus (*Asparagus filicinus*) and *Allium*, a strong-smelling chive. Rocky sites tend to be dominated by stands of *Rosa, Berberis, Ribes Incarvillea arguta, I. mairei* and jasmine. Wild peach is especially well represented in rocky gullies.

The mixed shrub type appears to be similar to Stainton's Dry Alpine Scrub, but since species typical of the dry Dolpo-Mustang area are absent, I have not used his nomenclature. Examples of species that are absent include *Hippophae, Sophora morecroftiana* and *Ceratostigma ulicinum*. In other respects, species composition is very similar. Mixed shrub is comparable to Dobremez's *Steppe Caragana* subtype. Stainton (1972) recognized a forest type dominated by black juniper from Nepal's "Inner Valleys" or areas sequestered from the full-effect of the monsoon like the Langu Valley. However, this juniper rarely forms dense stands that could qualify as "forest", perhaps because of soil conditions or past burning by people hunting in the area. In the Langu, *J. indicus* tends to grow as a low tree or shrub less than 3 m tall.

Subalpine Shrubland: Found between elevations of 3,700 and about 4,300 m, this vegetation type is best described as a low dwarf-shrub community dominated by *Caragana versicolor, Potentilla fructicosa* or *P. cuneata* with isolated pure stands of prostrate juniper (*J. squamata*). Numerous herbaceous plants are also present including *Thermopsis barbata, Arnebia benthami, Euphorbia wallichii, Stellaria chamaejasme, Morina polyphylla*, and *Astragulus* spp. At lower elevations, dense stands of *Caragana nepalensis* and *Spirea arcuata* are evident where this cover type gradually intergrades into mixed shrubland. Therefore, the ecotone between subalpine and mixed shrubland is poorly defined, and boundary mapping is somewhat subjective.

Subalpine shrubland is best developed on the rolling hillslopes of Tillisha Mountain and those slopes within the eastern section of the study area. However, it also occurs in steep, highly broken terrain, covering about 16 percent of the study area. Shrub composition ranges from 45 to 100 percent, averaging 35. Few shrubs grow higher than 0.75 m, and canopy coverage averages 26 percent.

Coniferous Forest: Study area forests are dominated by Himalayan blue pine (*Pinus wallichiana*) with Himalayan silver fir (*Abies spectabilis*) and some West Himalayan spruce (*Picea smithiana*). This vegetation type is equivalent to the *Temperate Blue Pine Forest* types of Dobremez (1976) and Stainton (1972).

There is a well developed shrub understory beneath the 10 - 15 m high canopy. Generally, the study area is too sheltered, dry or high for oak forests, although isolated stands of *Quercus semecarpifolia* occur in a few sunny sites. Associated species are black juniper, birch, and *Rhododendron arboreum*. Understory shrubs are represented by *R. lepidotum, Lonicera* spp., *Rosa macrophylla, R. sericea, Caragana nepalensis, Ribes glaciale, Virburnum* spp, jasmine, and *Cotoneaster* spp. Herbaceous plants include various species of *Anenome, Gaultheria, Trillium, Fragaria, Anaphalis, Tanacetum, Saussurea, Senecio, Aster, Polygonum* and *Nepeta*, as well as geraniums (*Geranium* spp.), violets (*Viola* spp.) and *Stellaria chamaejasme*, characteristic of sandy soils. Due to differences in soil type, exposure and human modification (primarily burning), the coniferous forests tend to be well interspersed with successional shrub types, dominated by species like sage, wild peach, *Potentilla fructicosa, Lonicera hypoleuca, Cotoneaster*, and black juniper.

Birch Forest: Small patches of birch (*Betula utilis*) forest occur along the upper parts of the subalpine zone. South of the Langu River this vegetation type forms a more or less continuous band above the blue pine forest belt, but below alpine grassland (i.e., between elevations of 3,500 and 4,100 m). Birch forest also tends to dominate sites prone to avalanches and related disturbances (Oliver and Larson 1990). North of the Langu, birch forest occurs only as very small, fragmented patches found on the most protected ledges or slopes with a distinct northern aspect. This distribution pattern within the core area reflects the species' ability to tolerate winter snow accumulation, its preference for mesic soils, and the short growing season. The understory supports several species of rhododendron and honeysuckle (*Lonicera*), *Sorbus* spp., as well as rose and several herbs. Pine, fir and spruce are also present.

ALPINE ZONE (above 4,200 - 5,000 m):

Alpine Grassland: This vegetation type occurs between elevations of 3,900 m and over 4,700 m. While the dominant plants are sedges (*Kobresia nepalensis* and *K. pygmae*), these were interspersed with grasses like *Calamagrostis, Stipa, Poa* and *Danthonia,* as well as herbs and forbs which are especially prolific in sites with well-developed soils or areas heavily grazed by wild ungulates. Common species include *Saxifraga, Lagotis, Chesneya nubigena, Primula, Aconitum, Saussurea, Gentiana, Anenome, Bistorta,* and *Euphorbia wallichii*. Drier, rocky sites tend to support *Astragulus candolleanus, Aster, Arenaria, Dicranostigma lactucoides* and isolated patches of prostrate juniper.

The ecotonal division between alpine grassland and subalpine shrubland is poorly defined in most places, but the coverage of shrubs is always low in the grassland type. Typically, the terrain is rolling, with a smooth surface and moderate or gentle slope steepness. Alpine grassland occupies about 16 percent of the inner study area. Grasses and forbs comprise about 85 percent of the species present by life-form, with the remainder being low-growing shrubs. Ground cover averages 42 percent. No grasses were found above about 4,800 m. Pincushion plants increase in abundance and dominance with increased elevation, but their coverage is typically less than 1 - 5 percent. Such sites are characterized by rock, scree and talus (fell-fields), a very short growing season and deep snows which remain until late June in protected places. They were mapped as the barren cover type.

Barren: This vegetation cover type may occur at any elevation; it is defined as having less than 10 percent plant canopy coverage and being dominated by exposed bedrock or talus. It is most commonly associated with glacial moraine, cliffs, landslides, rockfalls, river gravels, river bluffs and other sites bare of plant growth. More than 53 percent of the area north of the Langu River consists of this type. As mentioned earlier, barren sites include areas supporting a sparse cover of alpine pincushion and rock plants, such as *Arenaria bryophylla, Androsace, Saxifraga, Saussurea* and *Crassulaceace* spp.

2.5 Fauna

Faunal composition reflects the area's intermediate geographic position between the Palaearctic region to the north (Tibet) and the Indo-Himalayan elements which penetrate from the south (Corbett 1978; Schaller 1977). Little is known about geographic or habitat distribution and the status of Nepal's rich bird fauna, especially in remote or poorly sampled areas like the Langu valley (Inskipp and Inskipp 1985). Avifaunal species diversity was not high, as evidenced by the low number of bird species (N = 63) recorded during the study. However, most observations were made in barren, shrubland and other species-poor habitat, with little time being spent in conifer or birch forest, or in successional forest types where species diversity is known to be higher. Similarly, sampling is biased against breeding birds, with relatively little field work being undertaken during the monsoon period.

There are no detailed investigations of the mammalian fauna of Nepal. The only ungulates within the core area are blue sheep (*Pseudois nayaur*), Himalayan tahr (*Hemitragus* *jelamhicus*) and musk deer (*Moschus chrysogaster*). Goral (*Nemorhaedus goral*) and serow (*Capricornis sumatraensis*) occur downstream of Dolphu, as do wild pig (*Sus scrofa*). According to Karan B. Shah (pers. comm.), local people report that a few Himalayan black bears (*Ursus thibetanus*) occasionally penetrate the gorge as far upstream as Eding; however, I found no sign during the time I spent in the area, and cannot corroborate this observation. It may have been possible for the occasional bear to visit the study area during the summer (a season when little field work was undertaken), without my detecting sign later in the fall. The primary large carnivores are snow leopard and common or forest leopard (*Panthera pardus*). No evidence was ever found to suggest that forest leopard presently occur on the northern side of the Langu Valley beyond Dolphu or the summer livestock herding *gott* (camp) at Shimbu, several kilometers upstream. Therefore, snow leopard and common leopard are only sympatric on the southern side of the Langu River within the core study area. The forest leopard is, however, common in forests downstream of Dolphu and Wangri, according to reports of villagers. For these reasons, I concentrated my efforts on the north side of the Langu River, in areas supporting only snow leopard.

Smaller mammalian predators include the yellow-throated marten (*Martes flavigula*), stone marten (*M. foina*), the Himalayan least weasel (*Mustela nivalis*), the red fox (*Vulpes vulpes*), and possibly the jungle cat (*Felis chaus*) or less likely the leopard cat (*F. bengalensis*). Small felid tracks were regularly observed south of the Langu Khola, but no animals were ever seen. To my knowledge, lynx (*Lynx lynx*) and Pallas' cat (*F. manul*) are absent from the study area or its immediate surroundings. According to local people, Asiatic jackals (*Canis aureus*) regularly prey upon domestic sheep and goat near the village. In December 1976, I observed a lone dhole (*Cuon alpinus*) above Dolphu, but the excessively broken terrain of the study area probably provides marginal habitat for this species. Similarly, the terrain is too rough, steep or heavily dissected to offer suitable habitat for wolf (*Canis lupus*), although they may occasionally visit its fringes.

Other mammals include small insectivores, rodents or hares, including the Royle's or large-eared pika (*Ochotona roylei*; synm. *O. macrotis*), voles (Royle's mountain vole *Alticola roylei*, and possibly the Stoliczka'a mountain vole, *A. stoliczka*), rat (*Rattus rattus*), house mouse (*Mus musculus*), field mouse (*Apodemus sylvaticus*), water shrews (*Chimarogalle* spp. or Tibetan water shrew *Nectogale elegans*), and possibly the black-naped hare (*Lepus nigricollis*). Although no hares were sighted, the remains of one was found. There are no marmots (*Marmota himalayana*) in the core study site, although they occur in nearby mountains.

Few reptiles or amphibians inhabit the study area. The Kashmir agamid (*Agama tuberculata*) was the most commonly seen reptile, along with the Himalayan pit viper (*Ancistrodon himalayanus*). Japura (*Japura*) lizards occurred at higher elevations, while skinks were present in the lower regions.

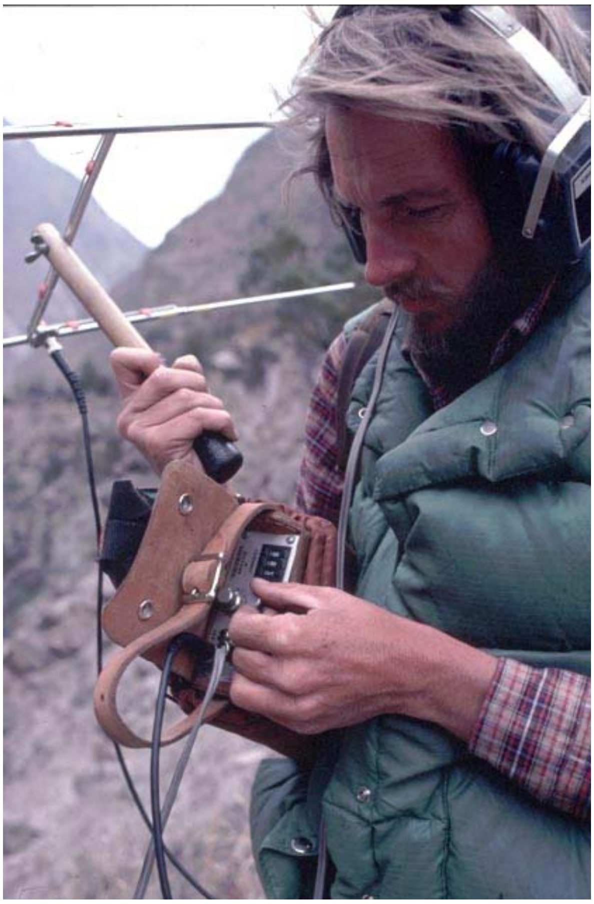
2.6 Human Activities

The local people are Tibetans or *Bhotias*, whose existence in the harsh environment depends upon a complex system of trade and barter to supplement marginal agricultural activities (Bishop 1990; Clarke 1977; Jest 1975; Von Furer-Haimendorf 1975). Herds of yak are maintained by Dolphu residents to provide milk, butter and meat, or serve as transport animals for sustaining a remarkably complex trade system linking distant settlements in the Karnali Zone with temporary encampments along the Tibetan border. Bishop (1990) provides a detailed account of traditional grain-salt trading between the villages of Nepal's Middle Hill and Tibet, conducted by the *Bhotias* living along the northern border. Due to the influx of cheaper salt from the India borderlands, the construction of roads and alternative transport facilities, an ever-increasing cash-driven economy, and other socio-economic factors, this trade pattern is rapidly dying out from large parts of western Nepal (Valle and Summers 1993).

The villages closest to the study area are Dolphu and the neighboring settlement of Wangri. Located at 3,350 m immediately downstream of the study area, Dolphu has some 50 families for a total population of 210. There are no permanent human habitations within the core study area, and furthermore, livestock are unable to penetrate the gorge above Shimbu (some 4 km upstream of the village) because of precipitous topography and lack of suitable trails. Therefore, the only ungulates utilizing pasturages within the study site are blue sheep, Himalayan tahr, and musk deer. Villagers periodically enter the gorge to hunt wildlife, collect *jimbu* (*Allium* a wild garlic), the kernel of wild peach (used as cooking oil), and *marang*, a highly resinous form of pine wood used for lighting the interiors of homes

or as torches to move about the village after dark. Otherwise, all fodder, fuelwood and timber for house construction are obtained from pastures and forests situated close to the village.

In past years, hunting of snow leopard and musk deer has been pervasive (Jackson 1979b), but such activity was largely curtailed during my study, because the villagers feared we would report them to the police. Previously, Dolphu and Wangri residents mined nearby copper-bearing ores until prohibited from doing so by government decree in the fifties, on the grounds that fuelwood smelting damaged the area's forests (Barry Bishop, pers. comm.). In response to the loss of this mineral resource and the imposition of Chinese restrictions on trading along the Tibetan border, there may have been increased incentive for these villagers to undertake commercial hunting of wildlife, despite the fact that, as Buddhists, they have strong sanctions against killing animals (Bishop 1990; Jackson 1979b). Under a system of well-organized communal hunts conducted during winter (when it is too cold to practice agriculture), villagers expend considerable effort to hunt musk deer for its highly prized "musk pod", which are carried only by males. With musk being literally as valuable as gold, a single pod could provide a significant portion of a family's annual cash requirements (Jackson 1979b).



The author radio-tracking

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Plotting movements of a tagged snow leopards on a topographic map

© Darla Hillard

CHAPTER 3 STUDY METHODS

3.1 Introduction

Field assistance was provided by Mr. Karan B. Shah, a Nepalese counterpart assigned to the project by the Government of Nepal, and by Mr. Gary Ahlborn, an experienced biologist. Mr. Ahlborn was employed by the project from the second year of study when it became evident that several skilled persons were needed to locate radio-tagged snow leopards on a daily basis; also, the study called for simultaneous radio-locating from different parts of the study area. Local Tibetans were hired to carry food and equipment and to service the six tracking camps.

Self sufficiency in terms of food (except for potatoes and other staple items) and field equipment required that all items be purchased abroad or in Kathmandu and then flown by a chartered STOL aircraft to the nearest airfield, located in Jumla to the south of the study area. It was then portered by human and draft animal (primarily yak) for 10 or more days over 60 km of difficult trails to Dolphu village. Porters carried the supplies the remaining 19 km to the project's base camp at Eding, a journey that usually required another two days of hard travel.

Field Studies: Twenty-six months were devoted to research in the core study area during the 4-year period 1982 - 1985 (Table 2). Field work was not undertaken during the monsoon or post-monsoon period (July through October), except for the first year of study. Another 162 days (5.4 months) were needed to travel between base camp and Kathmandu (Nepal's capital city), while project administration duties required me to spend over 7 months in Kathmandu during the course of the study. The remainder of my time was spent in the United States developing grant applications and fund-raising to cover the annual project cost of approximately $ 45,000.

Except for the first visit, 6 to 17 days were usually required to reach my project's base camp, depending upon the availability of charter flights and porters. The initial journey to the study area took 31 days, and involved an overland jeep drive (via the East-West

Highway) to the Indian border at Nepalganj and onto Chinsu, from which a three-week trek was required to reach Dolphu.

3.2 Live-trapping, Capture and Immobilization

Snow leopards were live-trapped using leg-snare traps (Novak 1980) placed along frequently travelled wildlife trails. Traps were buried and concealed in the ground and a snare cable was attached to a one-meter long metal stake driven into the ground or anchored via cable to rock-bolts drilled into large boulders. Most traps were placed along the edge of a bluff bordering the Langu River that served as a regularly used travel lane for snow leopards visiting the core study area. Two or more "trap sets", each containing one or two traps, were placed within 150 m of each other. Up to four traps were used at some places, of which a few were baited with live goats for short periods. The most effective trapping location consisted of a place where vegetation, boulders and other physical structures constrained the movement of snow leopard to a natural trail less than 0.5 m wide, and where an abundance of fresh snow leopard scrapes and related sign indicated recent visitation and ongoing marking activity. For a detailed description of capture techniques, see Jackson et al. (1990).

Table 2: Schedule of field time spent in the Langu Valley study area (1982 - 1985)

Dates of Field Work	Season	Number of Days in Field
17 January - 14 April 1982	Winter - Spring	88
28 May - 17 September 1982	Summer	109
26 November 1982 - 21 January 1983	Fall - Winter	71
26 March - 1 July 1983	Spring - Summer	98
27 November 1983 - 1 July 1984	Winter - Summer	217
31 November 1984 - 19 June 1985	Winter - Summer	202
	Total Number of Days	785

Only a few sites were baited with live goats; most trap sites were scented with attractants like wildcat urine (Stanley Hawbaker, Fort Loudon, Pennsylvania), FAS (a fatty acid scent used on carnivore scent-station transects, Roughton and Sweeney 1982), catnip (*Valeriana officinalis*), and freeze-dried urine from a captive snow leopard that was in oestrus at the time. A pair of domestic chicken wings were hung from branches within "flag sets" in an attempt to attract the attention of any leopard passing nearby.

Trapping was undertaken primarily in winter and early spring, between December and late April. Traps were checked at least twice daily, at dawn and then again at dusk. Trap-site disturbance and human scent was minimized by using spotting scopes or powerful binoculars to search each location, although periodic visits were needed to reset accidentally tripped traps or to feed bait animals. Most of the snow leopards captured during this study spent 12 hours or less entrapped, judging by the amount of site disturbance.

All captured snow leopards were immobilized with ketamine hydrochloride (*Ketaset*, Bristol Laboratory, Syracuse, New York) administered by intramuscular injection in the rear hip. Drug delivery was accomplished using (i) a 1.25 meter long, rigid jabstick with 3.0 or 6.0 ml syringes and 16 or 18 gauge needles, (ii) by darts projected from a 1 meter x 10 mm blowpipe (Telinject, Encino, California), or (iii) by a combination (Jackson et al. 1990). Darts were propelled by a Vario air-pistol or lung-power. Each animal was given a dosage of approximately 6.6 mg/kg and administered with 3.5 ml of penicillin (*Flocillin*); gum lacerations were treated with an anti-bacterial furacin (*Nitrofurazone*), while a topical biotic ointment (*Panalog*) was used to treat skin abrasions and other wounds.

Anaesthetized animals were shaded or swabbed with water to prevent hyperthermia. Each animal's head was covered with a cloth to prevent damage to its dilated pupils and to minimize stress related to human presence. Prior to recovery, all leopards were moved away from the river bluff and left beneath a shady tree or bush. The animal's activity was observed from across the 25 m wide Langu River with a spotting scope.

Each immobilized animal was weighed, measured, tattooed in the inside of one ear with an identifying number, and fitted with a radio-collar. The following measurements were taken: tip of nose to base of tail; tail length; front shoulder height; front and hind paw width; weight; canine length. Facial and dorsal spotting patterns were photographed and subsequently sketched for positive identification with or without the attached radio-collar (Blomqvist and Nystrom 1980). Animals were sexed and classified according to three age-classes: (1) Cubs: <12 months of age; (2) Subadults: > 12 - < 36 months old; and (3) Adults: > 36 months old. Criteria used to establish age-class included size, weight, estimated birth date, reproductive condition, canine size and wear, general dentition, and subsequent behaviour as determined by radio-tracking. Females were examined for evidence of recent lactation, as indicated by large pigmented nipples. Trapped snow leopards were assigned to 1 of 4 classes categorizing any trap-related wounds (Jackson et al. 1990, as adapted from Van Ballenberghe 1984).

3.3 Telemetry Equipment and Radio-tracking Procedures

The radio-telemetry equipment used was supplied by Telonics, Inc. of Mesa, Arizona. Each transmitter operated in the 149 MHz frequency band and was fitted with a fast (± 80 pulses per minute) - slow (± 65 ppm) mortality mercury ball tip switch or motion sensor, set to a delay time of 3 minutes; thus, the transmitter reverts to slow transmission following 3 minutes without any head or neck movement. Each collar weighed about 450 g. Radio signals were monitored using a Telonics TR-2 receiver (recharged with a solar panel) and a hand-held 2-element Adcock or "H" receiving antenna.

Radio-location was undertaken on foot, since aerial tracking would have been too costly and difficult to arrange. Daily attempts were made to contact and then locate the position of each radio-tagged snow leopard using triangulation by two or more observers and homing techniques (Cochran, 1980; Samuel and Fuller 1994). Each observer would search for signals from a prominent ridge or from the opposite slope of the valley; when contact was made with a radio-tagged snow leopard, the observer moved closer for more accurate compass bearings and locations based upon null rather than signal peaks (Samuel and Fuller 1994). The most likely of two resulting 180 degree nulls was determined by observing radio-wave reception in relation to "blocking" landforms and different locations. Directional bearings were taken using a sighting compass and plotted on a 1:24,000 scale topographic map (contour interval 100 feet) of the study area to provide a probable location and associated areal polygon. Three to five bearings were taken at each location and whenever possible animals were located while stationary or at rest.

Error in locating the source of signals resulted from variation in signal propagation due to animal movement, transmitter pulse rate, other aspects of equipment operation and performance, and from mapping imprecision or compass sighting error (Samuel and Fuller 1994). The mountainous, rocky terrain strongly affected radio-wave propagation and reception range, due primarily to radio-wave attenuation, signal bounce and deflection (Amlaner and MacDonald 1980). Distinguishing between direct ("line-of-sight") and reflected signals proved to be extremely time-consuming, and was often not possible. However, observer skill and success were enhanced by practicing with radio-transmitters carried by moving humans or placed (without the observer's knowledge) in different parts of the study area and thus subject to varying signal propagation interference. The use of two tracking teams facilitated triangulation by permitting synchronous or nearly synchronous locations from different parts of the study area. For a review of problems and procedures associated with radio-telemetry, see Harris et al. (1990), Kenward (1987) and White and Garrott (1990).

Samuel and Fuller (1994) report that a 1° error in compass bearing to a true location results in 17.5 m of linear error per kilometer from the receiving site. In addition, signal deflection and absorption due to the rugged terrain introduced bias that was both irregular and geographically difficult to predict. However, it was usually possible to detect signal reflection by moving a few meters and then observing signal response. For these reasons we utilized bearings made closest to the source (but without moving too close as to disturb the animal in question) and those least affected by deflection. In addition, efforts were made to avoid the use of bearings that intersected close to baseline sites, or those with intersection angles of < 20° or >160°, since these usually result in relatively large error polygons. Except for locations with visual confirmation, the minimum triangulated area was about 3.2 ha (180 m^2). This grid size was chosen because most locations were made from a distance of 2 km or less, and tests in the field indicated that the average linear error (difference between radio-location and true location) at this distance was on the order of 100 - 150 m or 7.5°. These locational distances were feasible even when animals were being tracked from the opposite side of the Langu River valley, a procedure that greatly enhanced the possibility for obtaining unreflected radio signals.

Locations were not finalized until all information was in hand. Based upon the quality of the null and variability in signal strength and reflectivity, each bearing was assigned to one of 4 relative classes, indicative of overall signal reliability (see below). Two or more resulting bearings were then plotted on a 1:24,000 topographic map, and the boundaries of the error polygon adjusted in light of ridgelines or other "signal-blocking" terrain features. The geographical center of each error polygon was used as the actual location, which was then transformed into grid coordinates. Each locational polygon was classified according into one of the following categories: Good, fair, or poor locations were those in which subjects were placed within an area of less than 25 ha, 25 - 50 ha or more than 50 ha, respectively.

3.4 Daily Movement and Activity Patterns

Daily Movement: An index of same-day movement was obtained by measuring the straight-line distance between locations of radio-tagged individuals on successive days. Records with no movement were excluded; a cat was considered to have moved if, when relocated, its position had changed by at least 200 m. Linear distance between successive locations at intervals of one to five days were calculated for each snow leopard. When more than one location was made in a given day, only the first location or the most precise location was used in the analysis. Locations whose area of fix exceeded 100 ha were omitted from the data-set.

Same-day movements were derived by computing the linear distances between repeated locations made during a single day, and by following pugmark sets of tagged and untagged snow leopards during periods of snowfall. Distances moved and distance between individuals were tested for homogeneity of variance with Bartlett's test (Sokal and Rohlf 1981). When excessive deviation from normality and homogeneity of variance was detected, or when sample size was small, the Mann-Whitney U test (Daniel 1978) was used to test the null hypothesis that the distances moved by male and female snow leopard were similar. Distance between individuals of the same and different sex were compared using the Kruskal-Wallis one-way analysis of variance.

Activity: Activity patterns of snow leopards were examined by monitoring the activity level during one-minute sampling intervals at consecutive 5-minute periods throughout the day and night, for a total of 4,060 activity samples (♂♂ = 3,051; ♀♀ = 1,009). Determination of activity was based on transmitter pulse rate (active or inactive transmission modes caused by presence or absence of head movement) and changes in signal strength during the monitoring period. A short reset interval was employed in the transmitter's tip switch sensor, enabling the investigator to distinguish activity from normal periods of inactivity (Garshelis et al. 1982). Changes in pulse rate that were less frequent indicated the animal was moving its head, but was basically inactive. The following information was taken during each sampling period: signal behaviour (constant or variable in strength, as with a signal fading in and out); signal strength on a relative scale of 1 (barely audible) to 5 (very strong); and whether active or inactive. The following activity categories were recognized: (1) active (travelling) = active pulse rate with frequent, and usually wide fluctuations in signal strength as animal moves behind objects which absorb or deflect signals; (2) active (locally) = active pulse rate with less frequent and lower deviations in terms of signal strength, usually followed by periods of prolonged inactivity; and (3) inactive (resting) = inactive pulse rate, of constant strength. However, since frequent relocations are required to distinguish between travelling and locally active animals, these categories were lumped for the purpose of analysis.

Inferential analyses were undertaken in order to examine the following hypotheses:

H_1: Activity levels do not differ between individual snow leopards

H_2: Activity is independent of time of day

H_3: Activity is independent of the time of year (season)

Weather as a factor was not examined, since microclimatic conditions may vary substantially within short distances due to topographic and structural diversity associated with the mountainous terrain. I assumed that temperature, cloud-cover, wind intensity and precipitation data gathered at one location (base camp) would not be applicable to other study locales.

In order to better meet the assumption of independence, data gathered during consecutive 5-minute sampling intervals were combined and averaged over a 30-minute period (proportion of intervals monitored in which active signals were logged) for a total of 48 distinct periods during the 24-hour day/night period. These were then grouped into hourly intervals and four time periods. Three seasons were designated, each corresponding to relatively distinct social interaction phases exhibited by snow leopards (Ahlborn and Jackson 1988): fall/winter or generally the pre-oestrus period (November-February); spring or the post-oestrus period (March - May 15); and summer (16 May through late June or early July when the field season ended).

A chi-square test for independence was conducted to determine if activity was independent of sex. A Chi-square goodness-of-fit was employed to test whether the frequency of activity was proportionately distributed with respect to the time of day, according to 4 time intervals (night = 2000 - 0355 hours; dawn = 0400 - 0755 hours; day = 0800 - 1555 hours; and dusk = 1600 - 1955 hours Nepal Standard Time).

I compared snow leopard activity among the snow leopards sampled using ANOVA techniques, with data from M1 being excluded as it was not studied over the same time frame as the other four animals. This analysis compared activity among four snow leopards for a total of 3,646 samples, 3 seasonal periods, and four or 24 time intervals. Several models were constructed to examine main, interaction and nested effects of different error factors involved in snow leopard activity, using a least-squares analysis of variance procedure, PROC GLM for unbalanced designs (*SAS* version 6.04, SAS Institute, Cary, North Carolina). Each model permitted comparisons between activity and each factor, independent of the compounding effects of all other factors, so that activity is designated as a probability of being active under the stated condition(s) rather than as an actual percentage of observations where activity is noted (Garshelis and Pelton, 1980; Garshelis et al. 1982; Villarrubia 1982). Activity was categorized as either active or inactive, based on the dominant activity shown during each consecutive half-hourly interval. Pairwise comparisons were performed within the context of ANOVA using Dunn's procedure, in which overall main effects are tested for significance. If an overall effect is detected, each pairwise test is made at the 0.05 significance level. Generally, Bonferroni adjustments to pairwise comparisons were precluded on the basis of the large number of categories employed in the model. In order to determine which means were different from others in the model, a LSD (least significant difference) test (Fisher's LSD) was conducted. The least square means, rather than the arithmetic percent active was used to graph activity probability for each animal, as well as sex.

The first model (Model 1) examined the relationship between activity level, individual and the time of day (24 intervals). Model II substituted month for time of day, while Model III investigated time of year (season) and time of day (4 intervals, with each individual being analyzed for time and seasonal effects. A similar analysis was performed by replacing individual cat variations with sex as the main effect (Model IV). The final model (Model V) included nested effects of sex within individual and sex within month and cat number.

The data were examined with respect to the following assumptions: (1) randomness, representativeness and equality of sampling among individuals; (2) independence; (3) use of mutually exclusive categories; (4) data is normally distributed; and (5) multicollinearity among variables. Limitations of the data-set included an unequal sampling effort during the hours of darkness compared to daylight and with respect to individual and sex. Sampling effort totalled some 1,150 hours for male and 330 hours for female snow leopards. Although continuous 24-hour activity sampling was conducted, the times between 11 pm and 5 am (Nepal Standard Time) were under-represented in the data-set, with relatively sparse data for months other than January through May. Except for M1, no monitoring of snow leopard activity was undertaken between July and November.

3.5 Home Range Size and Spatial Utilization

Home range size and configuration was calculated using several techniques: minimum area polygon method, defined by connecting the outermost locations (Mohr 1947 and Southwood 1966); the concave polygon (Clutton-Brock et al. 1982); the 95% bivariate normal ellipse (Gipsen and Sealander 1972, Jennich and Turner, 1969); the 95% weighted bivariate normal ellipse (Samuel and Garton 1985); the Fourier transformation (Anderson, 1982); and the Dixon and Chapman (1980) harmonic mean measure, as revised by Samuel and Garton (1987). The software program *McPaal* (Smithsonian Institution, Washington, DC) was used to compute estimations for the concave polygon and the Anderson Fourier Transform. Bivariate ellipse and harmonic mean measure area and activity estimates were made using the PC-based program *Home Range* (Ackerman et al. 1990).

Information describing how animals utilize different portions of their home range are biologically more meaningful. I examined spatial patterns by (1) comparing cat use to the Poisson distribution (Sokal and Rohlf 1981:84) and (2) developing harmonic mean measures aimed at identifying core areas and centers of activity (Dixon and Chapman 1980, Samuel and Garton 1987). Under a technique pioneered by Dixon and Chapman, harmonic estimators are computed using an algorithm based upon distances between all animal locations and all intersections of a grid lattice superimposed upon the home-range area in question. A utilization distribution is derived using the harmonic mean measure at each grid point, with utilization contours being estimated as percentiles of the utilization distribution. Grid points with harmonic values that exceed the highest harmonic value for any animal location are considered to be outside the home range and are therefore excluded from the utilization distribution. The potential utilization is estimated at each grid point by dividing the total number of animal locations by the squared harmonic value at each grid point. Potential utilization is summed over all grid points within the home range and scaled to 1.0 to create a utilization distribution. Percentages of utilization are then determined from the ordered sum of grid points. Animal observations were relocated to a constant mean distance from the nearest grid point, in order to compensate for excessive sensitivity to scale parameters (Spencer and Barrett 1984). This distance is the mean radius of the grid, so that harmonic mean measures reflect grid size (Samuel et al. 1985). The program *Home Range* implements an algorithm which adjusts the grid cell size depending upon the number of animal locations and their density within the home range boundary. Core-area use was quantified according to Samuel et al. (1985), and statistically significant core areas were identified using a X^2 test (Samuel and Green 1988) which compares observed data to a uniform, cumulative distribution model.

Since the harmonic mean method is based upon average travel distances among animal locations and the lattice of grid points, it is not strictly required that sequential locations be independent. For the purpose of spatial use analysis, the assumption that locations be selected randomly (i.e. equal probability for all locations) must be satisfied. The study team made special effort to ensure that sampling intensity remained relatively constant through time and that all parts of the study area were searched until animals were located. A constant scale and set of grid parameters was employed in order to permit comparisons between individual home ranges. Advantages of the harmonic mean estimator include the ability to support multimodal activity centers, which need not be in the center of the distribution and which are more robust to changing use patterns that other methods. The influence of outliers is less pervasive, and locations are not as sensitive to concerns of serial correlation (Ackerman et al. 1990). However, large sample sizes (50 - 100 locations per season) are required to produce stable distributions.

Key assumptions relating to spatial and temporal sampling include (1) independence of locations; (2) the search effort should not be unduly biased toward accessible parts of an animal's known or potential home range; and (3) observations should be randomly distributed with respect to season, activity or the 24-hour period (Harris et al. 1990). Autocorrelation of observations was minimized by ensuring that successive locations were separated by a period of 12-18 hours or more, a time interval judged sufficient to allow animals to move from one end of their home range to the other (Swihart and Slade 1985a). This time interval was based on observations showing all tagged individuals were easily capable of moving from one extreme of their home range to the other within a 24-hour period. Special effort was devoted to searching inaccessible areas for missing signals by visiting high adjacent ridgelines, and by using two teams of observers. It should be noted that aerial surveillance is the only reliable means of detecting animals when they are located in relatively inaccessible areas. Given the rugged terrain and ground-based tracking, it was usually not possible to locate animals during the hours of darkness. Most locations were made while animals were bedded or locally active about their day-time bedding site; therefore, the locational data collected reflect the snow leopards' daytime home range use pattern only.

Day-after-capture locations, fixes with an error polygon exceeding 50 ha in extent and duplicate same-day locations were excluded from data-sets used in home range estimates and activity center analyses. For those days with more than one location, the first or location having the smallest error polygon was selected through the use of weighting values. A cumulative area curve of home-range size was developed by computing the area within successive two-week minimum area polygons, in order to assess the adequacy of the sample. The *Home Range* program was used to detect serial autocorrelation, identify outlier locations, and to compute home range statistics, such as significant core and utilization areas, minimum convex polygon size, and bivariate distribution tests using the Cramer-Von Mises goodness-of-fit statistic (Ackerman et al. 1990). The other technique employed for assessing spatial utilization involved allocating each location to its appropriate 0.25 x 0.25 km square grid cell, and then determining whether the observed distribution deviated spatially from an expected normal Poisson distribution. Home-range size between individuals were compared using the Kruskal-Wallis one-way analysis of variance. The Mann-Whitney U test was used to determine whether range size differed according to sex.

3.6 Habitat Mapping, Characterization and Utilization

Radiotelemetry is an invaluable tool for investigating spatial and habitat use patterns, especially in a secretive species like the snow leopard (Samuel and Fuller 1994). This study focusses upon second-order (home range) and third-order (use of habitat components within the home-range) selection processes described by Johnson (1980).

Habitat Delineation and Mapping Procedures: Maps depicting landform and vegetation distribution were prepared for the study area (Figures 2 and 3). This required developing a base map for the study area at a scale of 1:24,676 from a 1:50,000 scale *Survey of India* topographic (contour interval = 100 ft) map of the project area. Since stereoscopic aerial photographs were unavailable, landform and vegetation polygon types were hand-mapped, by systematically visiting high observation points (such as ridgelines and opposite valley slopes), and drawing the polygon boundaries of selected landscape and vegetation features with the aid of binoculars, spotting scope, sighting compass, and a clinometer. In addition, clues such as permanent or seasonal drainages, cliffs or other prominent landscape features shown on the topographic map were used for orientation. The study area contained numerous small drainages that aided in fixing a location and more accurately aligning polygon boundaries. Maps were updated whenever errors were detected until a reasonably accurate representation of landform and vegetation had been prepared for the primary study area. Landform and vegetation units smaller than 3.0 ha in size were not mapped.

Landform types were based on the amount of land-surface ruggedness and brokenness induced by terrain features such as gullies and other drainages, ridges, rock outcroppings, natural surface undulations, and related topographic elements (Beasom et al. 1983). This involved identifying and mapping each landform polygon boundary from visual, on-the-ground inspection, by examining topographic maps for the area, or by using a combination of techniques. Relative land-surface ruggedness was indicated by the number, density and complexity of contours, as well as the presence of seasonal or permanent drainages and related topographic features. Other indicators for land surface ruggedness included variation due to change in elevation, slope steepness and aspect over distances of 100 - 200 m or less.

Nine terrain types were distinguished, including 4 classes specifically describing land-surface ruggedness (cliff, very broken, broken and smooth-surfaced) and five classes defining essentially linear landforms like ice and glaciers, landslide and rockfalls, river bluffs, riverine terraces and river or major stream beds (Table 3). In addition to cliffs, these linear or "azonal" landform types appeared to typify areas most often used by snow leopard for travel purposes. Seven vegetation types were recognized, based on a combination of life-form and dominant plant species (Table 4). The availability of each habitat and vegetation type in the project area was computed using GIS (Tables 3 and 4).

Vector- and raster-based *Geographic Information Systems* (GIS) software facilitated habitat analysis and home range studies (Burrough 1986). Coverages were digitized using workstation *Arc-Info* (Environmental Systems Research Institute, Redlands, California) at the Midcontinental Ecological Science Center, National Biological Service in Fort Collins, Colorado. These coverages were transported to personal computer GIS software (*PC Arc-Info 3.4 D Plus*), and a comprehensive data-base of spatial attributes was developed and used to investigate spatial habitat use patterns. The GIS themes developed consisted of point, line and polygon coverages, including all cat locations, major drainages in the study area, and contours at an interval of 152 m (500 feet) derived from a topographic map enlarged to a scale of 1:24,676. In addition, maps of vegetation types and landform features described above were digitized at the same scale. A raster-based program (*IDRISI*, Clark University, Worcester, Massachusetts) was used to develop slope gradient and aspect DEM models of the study area, and to examine landscape pattern measures of habitat heterogeneity, including relative richness, diversity, dominance and fragmentation (Forman and Godron 1986).

Habitat Characterization: Selected habitat parameters were measured at randomly located plots (N = 150), in approximate proportion to the occurrence of each major landform and vegetation cover types in the core study area. Each sampled site consisted of a 100 square meter plot placed with one side parallel to the dominant aspect. Five one meter-square subplots were designated, one in each of the 4 corners with the remaining one in the center

Table 3: Description of landform types in the study area

Landform Type and Code	Land Ruggedness Index	Percent Occurrence	Description
Terrain Ruggedness or Zonal Type:			
Moderately Broken Terrain (2)	2	12.8	Terrain moderately to strongly broken by rocky outcrops, drainages (gullies) and ridges
Very Broken Terrain (3)	3	11.7	Very heavy broken cliff terrain with interrupted ridgelines
Smooth Terrain (4)	1	39.2	Smooth, relatively even-sloped, gently rolling terrain with few rock outcrops
Cliff (5)	4	33.7	Cliff (slopes generally exceed 50°) (C1 = cliff with rock and/or vegetative cover; and C2 = cliff inaccessible for blue sheep and snow leopard)
Azonal or Linear Terrain Type: [a]			
Landslides & Rockfalls (6)	n/a	0.7	Landslide and/or rockfall
Glacier (7)	n/a	not applicable	Glacier (see text)
River Bluff (8)	n/a	0.03	River bluff
River-bed (9)	n/a	1.8	River or major stream bed
Riverine Terrace (10)	n/a	0.1	Riverine terrace

Notes: Area computed from landform cover map (prepared in the field), based on 1,096 random points in the GIS data-set.

Zonal types = non-linear landform categories (see text); Azonal types = predominantly linear landform features (see text);

Ruggedness index = degree of land-surface ruggedness (structural diversity), ranked from 1 (low) to 4 (high) according to Beasom et al. (1983)

[a] Combined percent occurrence of types 6,8,9 and 10 = 2.6%

Table 4: Description of major vegetation cover types in the study area

Vegetation Type and Code	Percent of Study Area	Description
Barren (BA)	53.3	Less than 10% plant canopy cover. Dominated by exposed bedrock or talus materials with a few, often widely scattered plants.
Alpine Grassland (AG)	15.9	Grassland dominated by *Carex* spp. and a few perennial grass species with some scattered clumps of low shrubs. Usually found above elevations of 3,900 m.
Alpine Shrubland (AS)	16.1	A low shrub type dominated by *Caragana versicolor* and found between elevations of 3,800 - 4,400 m.
Mixed Shrubland (MS)	11.4	A species-rich shrubland generally found below 3,800 m. Typical sites contain low *Juniperus indica* trees with 6 or more common shrubs as high as several meters.
Riparian Woodland (RI)	2.0	Narrow and very discontinuous stands of *Populus ciliata*, interspersed with a variety of shrubs and found along permanent water-courses.
Birch Forest (BF)	1.2	Birch (*Betula utilis*) forest or scrub occupies the more mesic northerly aspects at elevations of 3,800 m or higher.
Pine Forest (PF)	0.2	Coniferous forest dominated by *Pinus wallichiana* with an understory of shrubs interspersed with shrubland.

Note: Based on estimates for general study area derived from the vegetation base map using the GIS data-set
* combined percent occurrence for tree cover-types = 3.4%

of the plot. The dominant elevation, slope, aspect, land-surface ruggedness type, vegetation type, and specific topographic feature (e.g., ridge, knoll, gully, cliff, landslide etc) were noted on a data-form, and its location plotted on a map. Vegetation was characterized by recording the percent life-form composition and canopy coverage (6 cover classes) present in the central meter square subplot, according to Mueller-Dombois and Ellenburg (1974). Life-form composition was defined as the percentage cover that each life-form (grass, forb and/or perennial herb, shrub, and tree) contributed to the total percent canopy cover of the plot. Percent canopy cover was estimated by projecting the extent of above-ground plant parts upon the ground surface. For each of four cardinal compass sectors (NW, NE, SW, and SE), the distance from the geographic center of the plot to the nearest shrub at least one meter in height, and the nearest boulder at least 1 m high and 1 m across, but located within the 100 meter square plot, was measured. A constant value was used for all features located outside the plot boundary. Rock and shrub heights were measured to the nearest centimeter.

In order to investigate the hypothesis that visibility may be an important factor in the snow leopard's selection of different habitat types, horizon distances were recorded. It was assumed that the distance to the nearest horizon is an acceptable index for assessing visibility under different terrain ruggedness (landform type) conditions. Distances were measured by having the observer stand at the center point of each plot and then successively look upslope, downslope and in either "across-slope" direction in order to determine horizon distances for each sector. These were either visually estimated or determined using a range-finder, with distances in excess of 120 m all being visually estimated. The horizon was considered to constitute the nearest visual obstruction as viewed from observer eye-level (i.e. about 2 m above the land-surface). Typically, the nearest physical horizon consisted of a gully, ridge edge, cliff, or rock outcrop, while obstruction due to vegetation varied according to the vegetation type present.

Blue sheep and Himalayan tahr sign was noted by tallying the number of pellet groups located within each of the five one-meter square subplots, while the number of beds lying at least 50% within the 100 m square plot was also recorded. The number of subplots or quadrants with pellet groups was also noted. Pellet groups with more than 50% of their mass located outside the quadrant boundaries were not included in the tally. The absence or presence of fresh tracks was noted.

Habitat profiles were developed using standard descriptive statistical analyses. One-way and two-way analysis of variance (ANOVA) was used to examine differences between habitat features found among each landform and vegetation type; when transformations failed to correct for heterogeneity of variance, the Kruskal-Wallis one-way analysis of variance was used. The Tukey HSD (Wilkinson 1990:222) and Dun multiple means test (Daniel 1978:212) were used to determine which parametric and non-parametric means differed significantly.

Habitat Utilization: Habitat use was determined by matching grid coordinates for snow leopard locations with vegetation and landform types indicated by mapped coverages, with additional information accruing from following pugmark track sets and by recording habitat-level placement of snow leopard sign like scrapes, scats and rock-scents. Habitat availability was determined by measuring the area of each habitat type present in two ways: (1) slope steepness, aspect and elevation were determined from a randomly located sample of 1,096 points overlain on the topographic map according to procedures described in Marcum and Loftsgaarden (1980); and (2) Landform and vegetation type, and distance to selected habitat types were computed using the GIS (Table 5), which also provided more precise estimates of coverage for each mapped type (Clark et al. 1993). Animal locations derived from radiotelemetry were assumed to represent a reasonably unbiased and serially independent sample of habitats utilized by snow leopards occupying the study area, particularly with regard to daytime bedding.

The hypothesis that snow leopards use available habitat categories in proportion to their occurrence was examined using methods described by Neu et al. (1974) and Marcum and Loftsgaarden (1980). Habitat use was compared to availability within the study area, and preference or avoidance of particular types determined. The Chi-square goodness-of-fit analysis determines whether use occurs in proportion to available habitat, with differences at the 95 percent probability level taken as indicating a significant difference between use and availability. Categories with low expected proportions of usage, such as azonal or linear landform types (categories 6,8,9 and 10), were combined into a single category for analysis (type 20). Vegetation types subalpine scrub (SA) and mixed scrub (MS) were also combined, since these communities differed little in structure, while low expected frequencies of the three tree types necessitated their combination as well. Glaciers were excluded from consideration because none were located within the home area of the radio-tagged leopards.

Table 5: Variable measurement techniques used in assessing habitat use by snow leopard.

Variable	Measurement Technique
1. Elevation	Measured from topographic map (100 ft contour interval) and DEM-generated model with a 500 ft interval
2. Aspect	Measured from topographic map and derived from DEM model
3. Slope steepness	Measured from topographic map and derived from DEM model
4. Ridgelines	First and second order ridges digitized from topographic map (1:24,676)
5. Drainages	First and second order drainages digitized from topographic map (1:24,676)
6. Landform Types	Digitized from specially prepared map (1:24,676)
7. Vegetation Cover Types	Digitized from specially prepared map (1:24,676)
9. Snow leopard locations	Digitized at 1:24,676 scale from triangulated data-base
10. Spatial buffering, distance estimators, area estimates and landscape diversity indices	Digitally computed using vector and raster GIS systems

Data-sets selected conformed with the following assumptions: (1) the use of mutually exclusive categories; (2) all samples had at least one expected observation in each habitat category examined; and (3) no more than 20% of all categories contained less than 5 expected observations. The data were also judged to satisfy the assumption that all snow leopards had equal access to the designated habitat types and that each observation had been gathered independently of the others, in a relatively random, unbiased manner. Bonferroni simultaneous confidence intervals were constructed to determine which categories snow leopards used significantly more (over-utilized or "preferred") or less (under-utilized or "avoided") than expected by chance alone (Miller 1966, Neu et al. 1974, Byers et al. 1984). In general, the terms "under-utilized" and "over-utilized" are preferable to "preferred" or "avoided" (see below). Circular distributions such as aspect were analyzed according to Zar (1974). Individuals were pooled by sex because of the small sample sizes.

For each parameter, chi-square tests of homogeneity (Daniel 1978) were conducted to determine if they differed significantly by sex; if no difference was reported at $P < 0.05$, data from each sex were lumped. If a significant difference was found, the samples were not combined. Habitat data were also pooled, possibly obscuring seasonal differences.

Selection implies that an animal is choosing among alternative habitats or foods available to it (Johnson 1980). Use of a specific habitat type is selective if it is exploited disproportionately to its availability. It is important to emphasize that selection does not necessarily imply *preference*, which can only be determined independently of availability: thus animals must be offered access to different resources on an equal basis, a procedure typically requiring enclosure experimentation. The approach used in this investigation corresponds with the second study design described by Thomas and Taylor (1990:324), in which data on resource use is gathered for each individual but pooled across individuals and repeated observations of individuals. Thus, pooling of location observations (in reality subsamples or "pseudoreplicates") from different individuals serves to mask individual differences and may introduce bias if some individuals contribute more substantially to the sample than others (i.e., snow leopards M2, F1 and F5 in this case). Aebischer et al. (1993) recommended a log-ratio technique of compositional analysis which addresses problems related to (1) inappropriate level of sampling and sample size; (2) non-independence of proportions; (3) differential habitat use by groups of individuals; and (4) arbitrary definition of habitat availability. However, my study does not meet their minimum required sample size of at least 6 individuals. Similar constraints precluded use of fractal analysis as a means for investigating individual habitat preferences within the core use area (Gautestad and Mysterud, in prep.).

Due to intense solar insolation, which caused any snow-cover to melt rapidly, the Hargis and McCullough (1984) technique for characterizing habitat along travel routes had limited applicability, although it served to identify or substantiate terrain features used by snow leopard for travel.

Core and Non-Core Area Use and Classification: Use of habitat by snow leopard was compared with respect to core and non-core area locations, in order to examine the hypothesis that the core area contained more suitable habitat than non-core areas. Specifically, I hypothesized that the strong preference shown by radio-collared snow leopards for the geographically smaller core zone reflected (1) closer proximity to ridges, river-beds and other linear features used for travelling and social marking; (2) enhanced availability of landforms and vegetation associations preferred by snow leopard; and (3) more favorable habitat for blue sheep, the snow leopards' principal prey item.

The two-sample t-test and Mann-Whitney non-parametric equivalent were used to compare mean values for a wide range of spatial habitat measures derived from the GIS model, following procedures described previously. For methods used in assessing blue sheep use and habitat suitability, see Section 3.8. Discriminant Function Analysis (DFA) was used to develop a model that accurately classified sample sites according to snow leopard core or non-core areas (Afifi and Clark 1984). Based upon habitat patterns shown by radio-tagged animals and a review of the available literature, a selection of variables were subjected to R-type orthogonal factor analysis, and the 3-5 variables with the highest factor coefficients were used in the DFA (Capen 1981; Johnson and Pelton 1981). Sample size was large relative to dimensionality in order to maximize discriminate robustness (Williams et al. 1990). The proportion of variables to sample size was kept low. After transforming non-normally distributed data, and to satisfy the assumption of independence of variables, highly correlated habitat parameters ($r > 0.75$) were removed, and the remaining variables were entered in a stepwise DFA to create a linear combination of variables that most accurately separated the two groups. Values to drop variables were set at 0.10. Autocorrelation was considered critical if the correlation matrix value exceeded 0.7. The best model was considered that which exhibited the lowest Wilks' Lambda values and an F-ratio greater than 2 for each discriminant coefficient examined (Afifi and Clark 1984).

DFA requires that the following assumptions be satisfied (Afifi and Clark 1984): (1) habitat parameters are randomly sampled and resulting model variables (independent) are multivariately normally distributed (equality among variances-covariance matrices for all populations); (2) model variables are not autocorrelated, as indicated by covariances which exhibit homogeneity within-groups; and (3) Nonadditivity (i.e. no additivity among selected variables). DFA is extremely sensitive to unequal covariance, requiring large sample sizes. Variables found to be non-normally distributed were transformed, using an appropriate transformation. Outliers were identified and removed, and the problem of auto-correlated variables was avoided by selecting only one of each set of variables known or suspected of being correlated. The magnitude and sign of the canonical coefficient values was used to assist in selecting variables most useful in explaining variation within the data-set. Finally, I assumed that no other core areas were available to the snow leopards within the range of the radio-tagged snow leopards, and that harmonic mean activity centers reasonably reflected their spatial utilization pattern.

Landscape Diversity and Habitat Fragmentation Assessment: A raster GIS was used to compute selected measures of habitat relative richness, diversity, dominance, fragmentation and interspersion (Turner 1989). Landform and vegetation maps were rasterized using a cell size of 15 x 15 m; index values were then computed for each cell across the entire study area using a roving 3x3 pixel window (Eastman 1992:130). Statistical comparisons were then made between random and cat sites, using tests previously described.

3.7 Social Interaction and Marking Behaviour

Social Interaction: Residents were defined as adult or subadult snow leopards which showed site attachment, and were continuously resident in a predictable area (home area or home range) for at least 6 months or more (Hemker et al. 1984). Subadults were assumed to have dispersed when they left the defined area they had used for at least a year. Transients were classified as those individuals that showed site attachments of less than 6 months. Individuals, other than members of family groups were judged as being "in association" if located no more than 200 m apart on the same day. The degree to which snow leopards socialize was studied by two means: (1) Computing straight-line distances between each individual located on the same day; and (2) interpretation of sign (pugmarks, scrapes, scats, scent-sprays and claw rakes) found throughout the study area as well as long-term, repeated "sign transects" (see section on marking behaviour).

Linear distances between individuals on the same day were computed using the first location for each individual on that day. The Kruskal-Wallis one-way analysis of variance was used to test the null hypothesis that distances between individuals of the same and different sexes on the same day did not differ. If the null hypothesis could be rejected, a non-parametric multiple comparison test (Daniel 1979: 211 - 214) was used to determine which mean was different.

Marking Behaviour: Studies of marking behaviour were led by Gary Ahlborn, and are summarized here in order to promote a better understanding of topics covered by this thesis. The reader is referred to Ahlborn and Jackson (1988) for a detailed account of the methodology employed.

A transect nearly 5 kilometers in length and located in the center of the snow leopard ranges was demarcated and selected features characterized (see Figure 19, Chapter 9). It was sampled at regular intervals (every 10 days or whenever a tagged leopard was known to be in the area) over a two-year period (December 1983-June 1985) for all snow leopard sign, including pugmarks, scrapes, scats and scent-sprays. Each item of sign observed was identified and catalogued, and each site was unobtrusively marked for future identification and monitoring. Criteria were developed for measuring and aging sign consistently, and a record maintained of the appearance and eventual disappearance, through aging, weathering or other factors, of each sign item.

Sign changes were attributed to a particular individual only when there was good evidence to implicate its presence in the area. The number of times when cat tracks were observed along a section of the transect were designated as "known visits". The frequency of transect crossing by radio-tagged snow leopards was estimated by connecting each individual's consecutive locations with a straight-line, then counting the number of intercepts with the transect. Cat transect crossings were used as an index for visitation rates. Known and suspected visits were compared with the frequency and numbers of sign type changes to estimate the likelihood and intensity of marking during two seasons, as well as throughout the entire period monitored.

Detailed habitat information was recorded at random points along each transect (scrape sites = 58; random sites = 53). Particular attention was given to characterizing topographic features (eg., promontory, rock outcrop, riverain terrace, cliff etc.) in relation to marked sites. In addition to the repeated sign transect, a total of 49 "one-time only" transects were conducted in various parts of the study area to investigate the hypothesis that density of sign is related to snow leopard density and differentially associated with various landscape and terrain types, as well as specific topographic features. Each time snow leopard sign was encountered along the transect, the type of sign (scrape, feces, tracks, rock-scent and tree-rake), as well as its abundance and location were noted. The visibility of each scrape was noted and sites with scrapes were judged as relic or non-relic. Transect lengths and distances between marked sites were determined by pacing. Three hundred and twenty-one systematic sampling plots, located at 200 m intervals, were used to characterize vegetation, habitat, terrain and topographic features along each transect. In addition, a tracking medium quality index was calculated (Van Dyke et al. 1986), and the presence/absence and relative abundance of ungulate sign was recorded.

Scent-sprayed sites were detected by their characteristic odor, especially during winter and spring when most scent spraying activity occurred. Accompanying evidence of leopard use included discoloration of the marked face by urine, pugmarks showing where the cat had backed up to a boulder, facial hair attached to the sprayed surface indicating cheek rubbing, and rarely, claw marks where it had reached up to investigate the scent. Odor was found to be a more reliable indicator than discoloration for validating scent-sprayed rock faces. Sprayed sites were characterized by noting such habitat parameters as elevation, aspect, slope, type of feature marked and dimensions (overhang of surface, height, length and width of mark and marked surface), relative strength of odor, and presence of leopard hair (an indicator of cheek-rubbing). Horizon distances were measured as described earlier (Section 3.6). The density and height of shrubs and boulders greater than 1 m in height, but within 10 m of the site was determined. The presence/absence and placement of scrapes was noted, and if found, their relative visibility and dimensions were recorded. Twenty-five spray-sites were permanently marked and mapped, and then visited at regular intervals to quantify visitation rates.

3.8 Food Habits and Prey Species Investigations

Food Habits: Food habits were primarily studied through the analysis of scats, as attempts at examining the kills of radio-tagged cats proved exceptionally difficult due to precipitous terrain that often precluded access to the suspected kill site. Snow leopard scats were identified on the basis of size, color and location, but there was little danger of confusing them with other species. Snow leopards were not sympatric with forest leopard in the core study area, although overlap existed south of the Langu River (an area not used by any radio-tagged individual) and to the west of the core area, near Dolphu (also not utilized by tagged animals). Generally, it is extremely difficult to distinguish between scats from the two species, although important differences exist with respect to marking behaviour

(Ahlborn and Jackson 1988; Jackson and Hunter 1995). Scats were prepared according to Johnson and Aldred (1982), and Korschgen (1980); identification of prey items was made by comparing hair surface scale patterns of guard hairs with those of a reference hair collection comprising potential prey species from the same area (Weingart 1973). Cross-sectioning of hairs was necessary (Hilton and Kutscha 1978; Berwick, 1974), with the medulla-cortex shape offering additional clues for discriminating prey species. Mukherjee et al. (1994) recommended examining at least 20 hairs/sample in order to detect multiple prey species. We compared our criteria with those developed independently by Oli (1993) for identifying mammalian hair found in snow leopards scats collected in the Annapurna region of Nepal. Scat contents were reported as frequency of occurrence (percent of total scats in which an item was found) and the percent occurrence (number of times a specific item was found as percentage of all items found).

Successive-day movements of radio-tagged snow leopards were used to estimate the frequency with which they killed prey large enough (blue sheep or Himalayan tahr) to detain them for more than a day in one place. Except for females with sedentary cubs, all stationary locations were considered to constitute suspected kills; in most cases, we were unable to visit sites to confirm predation because of the extremely rugged terrain, or our ability to detect prey remains was hampered by thick cover and scavengers like the Himalayan Griffon vulture that quickly disposed of the remains left by snow leopards. Kill rate estimates were based on consecutive locations in which no more than 7 calendar days elapsed between consecutive locations.

Prey Species Studies: Information on the prey species was gathered by K.B. Shah, who collected data on the number, distribution and sex-age ratios for blue sheep and Himalayan tahr through the regular census of 6 censusing blocks from fixed observation points, using a spotting scope with 22-X and 60-X eyepieces. Blue sheep and tahr were classified according to the age classes described by Schaller (1973a & b, 1977) and Wilson (1981). For each herd or individual sighted, the following information was recorded: number, sex and age class in group, elevation, slope, aspect, vegetation type, distance to nearest escape cover, position on slope, activity and distance to observer. Each sighting was mapped. In addition, herd activity was studied at 5 or 10 minute intervals throughout the daytime by noting the number of individuals inactive (standing and lying), the number active but not feeding, and the number active and feeding.

Blue Sheep Habitat Utilization Patterns: I investigated habitat preferences of blue sheep using sign as an index of relative abundance and use (White and Eberhardt 1980). The presence, absence and abundance of ungulate sign was noted during habitat sampling (see Section 3.6). Pellet abundance was assumed to reflect bedding and foraging use. Differences in the mean number of pellet-groups, tracks and beds in randomly sampled plots along transects were used to assess the extent to which blue sheep preferred different vegetation and landform types. Since defecation rates may vary with respect to type of activity (Collins and Urness 1981), indices of track and bed site abundance, as well as incidental observations were used to verify conclusions derived from pellet group distribution surveys. Differences in pellet-group means were examined using a maximum likelihood estimator robust to measures of contagion, and not requiring assumptions of a common *k* value (White and Eberhardt 1980). Statistical analyses were conducted using the PC-based computer program *PELANAL* developed by these investigators. A non-parametric multiple comparison test was used to determine which means differed significantly (Daniel 1979:211-214). Finally, these data were used to develop a spatial habitat suitability index model for blue sheep, which is described in Section 8.4.

3.9 Statistical Analysis

Except as noted, all statistical analyses were undertaken on 386 and 486 based PC computers, using *SYSTAT* as the primary software package (Wilkinson 1990). Spreadsheet software (*1-2-3*, Lotus, Inc. or *Quattro-Pro*, Borland, Inc.) was used to prepare and manage data for input to statistical packages. Sample distributions were examined for shape, outliers and normality using univariate graphing techniques such as normal probability plots and stem-and-leaf diagrams, in addition to standard measures of skewness and kurtosis. Data were examined for homogeneity of variance using Bartlett's test (Sokal and Rohlf 1981). Where required, outliers were removed and standard transformations used to correct non-normally distributed variables prior to detailed statistical analysis. Where data remained abnormally distributed even following transformation, non-parametric tests were employed. The Kolmogorov-Smirnov one sample test was used with nominal data to examine goodness-of-fit, while comparisons of location and dispersion with respect to two samples were made with the Kolmogorov-Smirnov two-sample test. Unless otherwise stated, the 95% significance level was used to accept or reject the null hypothesis. See preceding sections for specific analysis procedures employed.

Attaching a radio-collar to snow leopard No. 3 - 1983

© Darla Hillard

Cat 02, a male, on its release following immobilization and attachment of the radio-collar

© Rodney Jackson

PART II RESULTS

CHAPTER 4 STUDY ANIMALS

4.1 Capture and Immobilization

Results of live-trapping and chemical immobilization are described in detail by Jackson et al. (1990). A brief summary follows:

Capture: Traps were placed at 16 sites along the Langu River and monitored for a total of 3,899 trap-nights. The overall trapping success was 0.59 percent, although success at live-trapping varied between 0.37 and 0.92 percent during the four year period. Snow leopards were trapped 23 times, but in 13 instances the animal was able to extricate itself and escape prior to immobilization. No animals were caught after the beginning of May and most were trapped in March or April, a time period generally corresponding with the snow leopard's mating season. All the radio-collared individuals revisited the area where they had been trapped, although most detoured around the actual site of capture to rejoin the trail further along. Pugmark searches indicated that on at least 30 occasions, snow leopards travelled within 50 m of a trap site. Although various attractants were used, no obvious patterns could be detected. No major trap-related injuries were observed, but several important modifications to trap design and placement were recommended by Jackson et al. (1990).

Immobilization: Three male and two female snow leopards were immobilized and radio-tagged, with two males (M3 and M2) being recaptured once and four times respectively, for a total of 10 immobilizations. The snow leopards immobilized exhibited a wide tolerance to ketamine hydrochloride, but relatively high dosages were required to induce adequate ataxia, presumably because entrapped snow leopards were highly excitable and metabolizing the drug more rapidly. No animals were lost as a result of immobilization. All individuals exhibited varying degrees of salivation, but only in two cases was the administration of atropine sulfate deemed advisable. However, substantial muscular rigidity was noted in all immobilizations, and the use of a tranquillizer or muscle relaxant such as xylazine in association with the ketamine hydrochloride is strongly recommended, provided its effect is chemically reversed with yohimbine hydrochloride prior to release of the animal. Jackson et al. (1990) recommend that future immobilizations of snow leopard utilize a dosage of 7 - 9 mg/kg ketamine with 1 - 1.5 mg/kg xylazine and reversal with 15 mg yohimbine hydrochloride (*Antagonil*) per adult animal. Schaller et al. (1994) used CI-744 or *Telazol* (A.H. Robins Co., Richmond, Virginia.), a combination of tiletamine hydrochloride (HCl) and zolazepam HCl, at a dosage of 3.7 mg/kg to immobilize snow leopards in Mongolia.

4.2 The Study Population

Radio-tagged Animals: Table 6 indicates the sex, age and body measurements for the five snow leopards which were radio-tagged. Judging by body size, weight and testicle prominence, M1 was a fully grown, reproductively active male. Contact was lost some four months after his capture, although large male snow leopard pugmarks continued to be periodically sighted each field season and M1's transmitter could have therefore malfunctioned. However, the relative paucity of large-sized pugmarks suggested either a vacancy in the home range occupancy of fully grown male snow leopards or a situation in which the dominant male(s) roams over a much larger area than that utilized by the two more youthful males radio-tagged, M2 and M3. At capture, these males were classified as subadults, aged about 30 and 35 months respectively. They could have been litter mates, as they were similar in size and appeared to be relatively tolerant of each other, at least during the initial months they were radio-tracked. When M2 was recaptured a year later, he showed facial scars suggestive of intraspecific fighting. Long-distance vocalizations and movements by M2 during the time F1 copulated suggest that he may have at least tried to breed with her. About this time, contact was lost with M3, suggesting that either he left the area, or that his radio-transmitter malfunctioned. The presence of pugmarks of similar size class were found in areas where telemetry confirmed M2 had not recently visited, indicating that M3 or another young adult snow leopard was using the same general area concurrently.

Female F1 was judged to be at least 4 years of age, and nipple coloration and size indicated that she had given birth previously. Several months later, in early June of 1984, she gave birth again to at least two cubs (whose tracks were seen at the start of the next field season). Despite frequent attempts at establishing visual contact, she was not seen with her two cubs until they were just a year old, on June 10, 1985. Although the position of radio-tagged cats could be established with reasonable accuracy, the extremely rocky, broken

Table 6: Sex, age and physical features of radio-tagged snow leopards

Animal Identification Number	Age Class/Sex	Body Weight (kg)	Body length (cm)	Tail Length (cm)	Capture Date
M1	Adult ♂	50-55 (est)	n/a	96	3 April 1982
M2	Subadult ♂	28 (1st capture) - 37 (14 months later)	114	98	15 December 1982
M3	Subadult ♂	34	102	90	1 May 1983
F1	Adult ♀	39	113	96	23 March 1984
F2	Subadult ♀	21	96	89	30 April 1984

terrain and often dense shrub cover made sightings extremely difficult, and this female was especially wary while her cubs were young.

Female F2 is the presumed daughter of F1 as they associated for three days, a month before she gave birth again. The daughter's age at capture was estimated at 18 to 22 months. Thus, F2 was tracked over a time when she was apparently establishing her home range within that of her presumed mother.

Study Area Population: The sex and age composition of the study area's population is uncertain for not all individuals present were collared or observed and classified. Sex determination based upon pugmark size and shape can only reliably separate fully grown males, as subadult male tracks overlap in size with those of adult females. Not only was sandy or fine soil scarce as a tracking medium in the study area, but differences in slope steepness, soil depth and soil texture resulted in considerable variation with respect to track size, shape and detail, even for the same set of pugmarks made over a relatively short distance. Even with the benefit of multivariate statistics and extremely large samples, it is doubtful that snow leopard track sets could be reliably classified with respect to individual, sex or age class as suggested by Panwar (1979) for tiger and Smallwood and Fitzhugh

(1993) for puma.

Based upon concurrent observations of radio-tagged animals, sign (pugmarks, scrapes and scent-sprays), and visual sightings, the resident and transient snow leopard population of the core study area numbered between five and possibly as many as 12 individuals, including F1's two cubs. In early 1984, the population consisted of two young adult males (M2 and M3), a subadult female (F2) and at least one adult female (F1); tracks indicated three or four uncollared animals about the size of M2 and F1, as well as at least one larger and apparently widely roaming adult male in the roughly 80-100 km^2 area. This amounted to an adult snow leopard density in excess of 5 animals per 100 km^2 or at one adult snow leopard per 20 km^2. If subadults and cubs are taken into account, the snow leopard density may have exceeded one animal per 10 km^2.

Age of Independence, Reproduction and Mortality: The age of independence in wild snow leopards is not known. However, snow leopard F2 was 18 to 22 months of age when she was captured, suggesting she had not been on her own for more than a few months. F1 was judged to be at least 4 years old when she gave birth to a litter of two (and possibly more) cubs in early June, 1984. When field work was terminated in July 1985, both cubs were still travelling with their mother, and were fully dependent upon her for their food and protection. Thus, the interval between births is at least 2 years, judging by this particular individual. The age at first breeding cannot be established, except to note that a female aged about 20 months at capture had not produced cubs a year later (at least judging by her movement patterns), while a 40-45 month-old male (M2) may have attempted to breed with F1, judging by his frequent vocalizations and movement pattern.

Breeding appears to be strongly seasonal in wild snow leopards. Mating vocalization or "yowling" was recorded on 7 occasions, between the months of January and March. Yowling was more frequently heard in 1984, when F1 was in oestrus, suggesting that it helps mating pairs locate each another. Both sexes yowled and these calls were audible over distances of at least 300 or 400 meters, even with the background sound of the Langu River. Most yowling occurred in the late evening (especially between 7-10 pm) and again around midnight. In one three hour bout, 25 yowls were heard, apparently made by an adult male (G. Ahlborn, pers. comm.). In another instance, M2 yowled, followed by another individual shortly afterwards. The incidence of yowling was greatest in late February, coinciding with increased marking activity (see Chapter 7).

All animals handled during the study had very low ectoparasite loads, and generally appeared to be in good health. Mortality was not documented, except for instances of hunting preceding this study, when local villagers regularly killed snow leopards by placing poisoned spears along trails frequented by them (Jackson 1979a). The sale of pelts was considered an important source of potential income for some hunters.

4.3 Discussion

I gathered very little information on birth and survival rates, although with at least 12 snow leopards (adults, subadults and cubs) within the approximately 100 km^2 study area, the Langu Valley clearly supports a very dense snow leopard population. While surveys have been made in widely-separated parts of the snow leopard's enormous range, most are derived from incidental observation of tracks (spoor) and other sign, supplemented by interviews with local residents -- rather than from populations with known, marked (radio-tagged) individuals; all such estimates should, therefore, be viewed cautiously. Estimated snow leopard densities from other areas range from about 0.36 - 0.53 animals per 100 km^2 in the Taxkorgan Reserve of the Xinjiang Autonomous region in China (Schaller et al. 1987), one snow leopard per 150 km^2 in parts of central Ladakh (Mallon 1984), to as many as 4.3 animals per 100 km^2 in the Manang area of the Annapurna Conservation Area of Nepal (Sherpa and Oli 1987). Based upon a subsequent radio-telemetry study conducted in the same area, Oli (1994) revised his density estimate upward to 4.8 - 6.7 adult snow leopards per 100 km^2. Fox et al. (1991) placed the snow leopard density at between 0.4 - 0.6 animals per 100 km^2 in central Ladakh and the Kulu-Manali area to the south of the main Himalayan range. Jackson et al. (1994a) estimated about 100 snow leopards inhabit the Qomolangma Nature Reserve of southern Tibet -- a crude density of about 0.3 per 100 km^2, with a few areas containing as many as 5 per 100 km^2. Judging by sign, Schaller et al. (1988b) estimated snow leopard densities at one per 25-35 km^2 in four areas of Qinghai Province, located near the northern edge of the Tibetan Plateau. On average, he surmised the density at one cat per 100 km^2 for this region. In the more arid central portion of the Altai Range of Mongolia, Schaller et al. (1994) judged at least 10 snow leopards (including large cubs) frequented one 275 km^2 area surveyed, for a density of

3-4 cats per 100 km^2. Other nearby areas contained few or no snow leopards, while the 30 or so snow leopards in the 44,190 km^2 Great Gobi National Park (Sector "A") are restricted to a few isolated, small mountain massifs. Differences in habitat quality, population fragmentation and other factors greatly complicate comparisons between these climatically and topographically different areas (unpub. data).

Information accruing from this study is insufficient to establish reproductive and survival rates for wild snow leopards. In captivity, snow leopards reach sexual maturity at 3 - 6 years of age (Blomqvist and Sten 1982). The age at first reproduction averaged 3.9 years in a sample of 42 captive females, but only 14% bred at 3 years of age (Blomqvist and Sten 1982). According to these authors male snow leopard reach sexual maturity at about the same age as females. Females continued to produce litters through 11 years of age, after which productivity declines markedly. One female gave birth when she was about 18 years old, but this is clearly unusual. The median interval between births was two years for wild-caught and one year for captive-bred females in a sample analyzed by Rieger (1982).

Seventy seven percent of 384 estrus periods in captive animals occurred between January and March (Blomqvist and Sten 1982), with a peak during February. According to these investigators the duration of oestrus ranged from 1-16 days, with an average of 5 or 6 days. Sadlier (1966) reported an average oestral duration of 6.2 days, Rieger (1980) 10-12 days and Kitchner et al. (1975) a range of 2 to 8 days. This study supports late January through mid-March as the mating period (Ahlborn and Jackson 1988), based upon scent-marking patterns, mating vocalizations and other social interactions. Mallon (1982) reported that mating occurs in late March or April in Ladakh, a time during which local shepherds often hear the cats calling at night. Schaller (1977) reported that mating occurs between February and early April in the Himalaya; these authors agree that most cubs are born in June and July, although Schaller felt that one cub he observed had probably been born in August. In the Soviet Union, cubs are said to be borne between April and June (Andriuskevicius 1980). By contrast, captive snow leopards are born between late March and early September, with a peak in May (Blomqvist and Sten 1982; Rieger 1982; Freeman and Hutchins 1978). Litter size in captivity ranges from one to four cubs, with an average of 2.2 (Blomqvist and Sten 1982; Rieger 1982). Litter size in wild populations range between 1-5 and average 2 or 3, according to Novikov (1956), Stroganov (1962) and Schaller (1977).

These observations are generally consistent with our observations on radio-tagged snow leopard F1 which gave birth to cubs around June 13-15. She subsequently raised 2 cubs, but there could have been more at birth for her litter size could not be confirmed until 6 months later. Assuming a gestation period of 96-105 days (Jones 1973; Kitchner et al 1975; Marma and Yunchis 1968), this female bred in early to mid-March.

No estimates of mortality rates are available, but these must be high in most parts of the cat's range, partly judging by lack of consistent sightings and hunting pressure from humans. Like other felids, young and subadult snow leopards die as a result of disease, inadequate nutrition, abandonment, or at the hands of man. In Ladakh, cubs are occasionally taken from maternal dens or dispatched while with their mother at a livestock kill (Mallon 1984). Reports of snow leopard being stoned to death in Ladakh (India) and Baltistan (Pakistan) after entering livestock enclosures are not uncommon. Elsewhere, snow leopards are killed using rifles, pit-traps and possibly poisoned bait for their valuable pelt or in retribution for livestock depredation (Schaller 1988a & b; Jackson 1979b; Jackson et al. 1994b; Tan and Liao 1988; Nath 1982; Mallon 1984; Simon 1976; Rodenburg 1977). One of the males in this study (M2) showed evidence of facial scratches, which could possibly have been the result of intraspecific aggression. Aside from unnatural mortality (i.e. road kills, poaching), Maehr et al. (1991) consider aggression between males as the most common form of mortality in Florida puma.

Other than man, the only natural enemy of snow leopard appears to be other large carnivores, notably the wolf (*Canis lupus*) (Schaller, pers. comm.). One cat in Ladakh appropriated a kill from a pack of 4 wild-dogs (*Cuon alpinus*) by chasing them off it (Anon. 1993). Snow leopards may also be killed in avalanches according to Mallon (1984), who reported the demise of a female and her two cubs in Zanskar. Occasionally, a snow leopard may misjudge its stalk and lose its footing on a cliff, falling to its death (Nath 1982). However, one instance of a snow leopard falling off a cliff that was relayed by villagers to Mallon (1984) may in fact have been suspect. In captivity, mortality among cubs is generally attributed to stillbirths, mistreatment by the parent, pneumonia and enteritis (Marma and Junchis 1968; Freeman and Hutchins 1978; Wharton and Mainka 1994). Longevity among captive animals has increased since 1970 from a maximum of 13 years to about 17 years, in large part due to improved management.

Nepalese associate radio-tracking from the rolling alpine grasslands of Tillisha mountain - 1983

CHAPTER 5 MOVEMENT AND ACTIVITY PATTERNS

5.1 Radio-locations

The five tagged animals were relocated a total of 711 times using radio-telemetry. Eighty-two percent of the relocations were assigned to good and fair location classes (i.e. less than 50 ha in extent). The tracking frequency and interval for the five snow leopards which were fitted with radio-collars is shown in Table 7. The number of locations per individual ranged from 36 to 245. On average, animals were relocated at intervals of 1.5 - 3.6 days, or 28 - 68% of time I or other team members spent in the field. Not only was M1 tracked before any other animal had been tagged, but its activity and movements were the least studied of all of the tagged snow leopards. Leopards M2 and F1 were located most frequently. Contact with F2 declined during the second year it was being monitored, possibly reflecting this female's efforts at consolidating her home area through increased movement.

Radio contact was lost with three of the tagged snow leopards (M1, M2 and M3) after periods of some 4, 18 and 10 months of monitoring respectively. Signal contact with M1

Table 7: Radio-location data for 5 snow leopards

Cat No.	Number of Locations	Number of Days Located	Mean number of consecutive days between successive locations	Percentage of days contacted	Time Period Tracked (month/year)
M1	36	28	3.61	27.7	4/82 - 8/82
M2	222	199	1.77	56.3	12/82 - 6/84
M3	75	69	2.70	37.1	5/83 - 3/84
F1	245	206	1.47	68.0	3/84 - 6/85
F2	133	109	2.43	41.1	4/84 - 6/85
Totals	711	611			

and M3 was abruptly lost, suggesting transmitter failure or the individual's sudden departure from the study area. Large male pugmarks periodically seen after the failure of M1's transmitter could have been left by this or another fully-grown male. Contact with M3 terminated after a period during which two similar-sized, tagged male snow leopards (M2 and M3) used a common area. Facial scars and other wounds found on M2 when it was immobilized in early February of 1984 may have resulted from intraspecific contact with other males, including M3. Fifteen days later, contact was lost with M3; this animal appeared to be travelling more extensively at the time, and may have been forced out of the area by M2. When last contacted, M3 was travelling in a northerly direction, toward the high mountain range that demarcates the study area's northern boundary. Despite regular attempts, contact was never re-established with any of these snow leopards.

Following several weeks of malfunctioning, M2's radio-transmitter was replaced on 14 February, 1984, some 14 months after it was first attached. Normal transmission resumed and continued until late June, 1984 when inactive signal pulses were repeatedly obtained, suggesting either death or the shedding of its radio-collar. Triangulation placed the transmitter location in a high, U-shaped valley near the northern perimeter of the core study area. The entrance to the valley was blocked by a deep, inaccessible gorge, its perimeter by high cliffs or extremely steep and dangerous talus slopes. Several attempts at visiting the collar site were thwarted by inclement weather, including deep snowfall; it was not until nearly a year later that a successful search was mounted and the radio-collar was recovered on 10 June, 1985 at an elevation of 4,450 m. It was lying 15 m downslope of a prominent boulder, above a small rockfall and other lateral or terminal morainal debris, in alpine grassland and fell-fields near the confluence of the Mangar and Tillisha streams. The collar bolts were intact, but imbedded in bovid rumen material, while the transmitter box contained two long scratches that could have been made by a felid clawing at its surface. An intensive search of the area revealed no bones or body remains, although an old blue sheep kill was located under a large boulder in a rockfall 225 m below the radio-collar recovery site. Evidently M2 shed its collar, but I can only speculate how this might have happened. One possibility is after M2 had successfully stalked and killed a fully grown male blue sheep and was dragging the carcass downslope to the rockfall noted above; during this process, the blue sheep's horn-tips could have become caught and locked beneath the radio-collar, thereby causing the snow leopard to claw and pull the radio-collar off over its head. Had the cat died here, I would expected to find some evidence like hair, skin or bones even if the site had been disturbed by vultures and other scavengers. Pugmarks of the same size class as M2 were regularly sighted after the transmitter failed, indicating the continued presence of snow leopards of this size class in the study area.

5.2 Movements

There was no evidence to indicate that capture and radio-marking disrupted subsequent activity and movement patterns, for tagged animals regularly travelled through the area where they were captured (Sunquist 1981, Samuel and Fuller 1994). In fact, M2 and M3 were recaptured within several days, just meters away from their initial capture sites. Snow leopards were found in a different place on 72% of all consecutive days on which they were located (N = 232, data from five leopards pooled). Tagged snow leopards were located in a different grid square (6.25 ha) 64 - 74% of their locations, indicating that all radio-tagged animals tended to choose a different resting site each day unless on a kill, or in the case of females with newly born cubs, constrained to their maternal den-site.

The mean minimum distance (straight-line) moved by a radio-tagged snow leopard between consecutive daily locations ranged from 0.85 to 1.61 km (Table 8), excluding stationary locations (i.e., when located at a known or presumed kill-site, or locations that were separated by distances of 200 m or less). Males moved slightly farther than females, but the difference was not significant (Mann-Whitney U = 7547; $P > 0.057$). The mean linear distance moved was 1.12 km (N = 232), with considerable variation (ranging from 0.21 to 6.72 km) between and among the different individuals. Linear distance between consecutive daily locations provides an index of daily movement, rather than actual distance moved, which typically involves a far greater distance. Home range size was not significantly correlated with daily distances moved (Kruskal-Wallis ANOVA = 8.717, df 4, $P < 0.069$). Snow leopards moved significantly shorter distances after leaving a kill compared to pre-kill distances (before kill $\bar{X} = 1.6 \pm$ S.E. 0.24 km, N = 50; after kill $\bar{X} = 0.9 \pm$ S.E. 0.13 km, N = 58; Mann-Whitney U = 1869.0, df 1, $P < 0.01$). No differences in distance between successive kill sites was detected with respect to either sex or season.

Nearly 90% of consecutive day movements involved a distance of 2 km or less, and in 58% of the sample the distance moved was less than a kilometer (Table 8). Frequency

Table 8: Linear distance (in kilometers) between locations of radio-tagged snow leopards on consecutive days

Cat No.	Number of Consecutive day locations	Mean Distance ± SE (km)	Maximum Distance	Frequency Distribution (percent)		
				< 1.0	1.0 - < 2.0	≥ 2.0
M1	12	1.61 ± 0.31	3.37	33.3	33.3	33.3
M2	68	1.31 ± 0.13	4.74	52.9	30.9	16.2
M3	19	0.95 ± 0.13	2.15	63.2	26.3	10.5
F1	88	1.09 ± 0.11	6.72	55.7	35.2	9.1
F2	45	0.85 ± 0.09	2.35	73.3	17.9	8.9
Males	99	1.27 ± 0.10	4.74	52.5	30.3	17.2
Females	133	1.01 ± 0.08	6.72	61.6	29.3	9.0
All cats	232	1.12 ± 0.06	6.72	57.8	29.7	12.5

Note: Stationery locations (< 200 m) are excluded

distributions indicated that 82.8% of male and 90.9% of female successive day movements encompassed distances of two kilometers or less, hardly surprising given the rugged and elevationally extreme terrain of the study area (Figure 1). Only 3 and 2.25% of the male and female sample respectively involved consecutive-day straight-line distances in excess of 4 km. Nearly half of the sample involved consecutive day movements of 0.75 km or less.

On average, males moved linear distances of 1.16 ± 0.40 km during the same day (N=13 locations; range 0.20 to 5.65 km), and females an average of 0.64 ± 0.10 km (N=27 locations; range 0.22 to 2.25 km). No difference in same-day movements between sex was detected (Mann-Whitney U = 803; p > 0.300). The average day-time distance moved by a snow leopard of either sex was 0.81 ± S.E. 0.15 km (N=40).

Snow leopard F1's movements were significantly reduced after she gave birth to a litter of at least two cubs on June 13-15, 1984. During the first 4-5 days, she apparently did not wander from the den-site, presumably because she was regularly nursing. On June 19 she

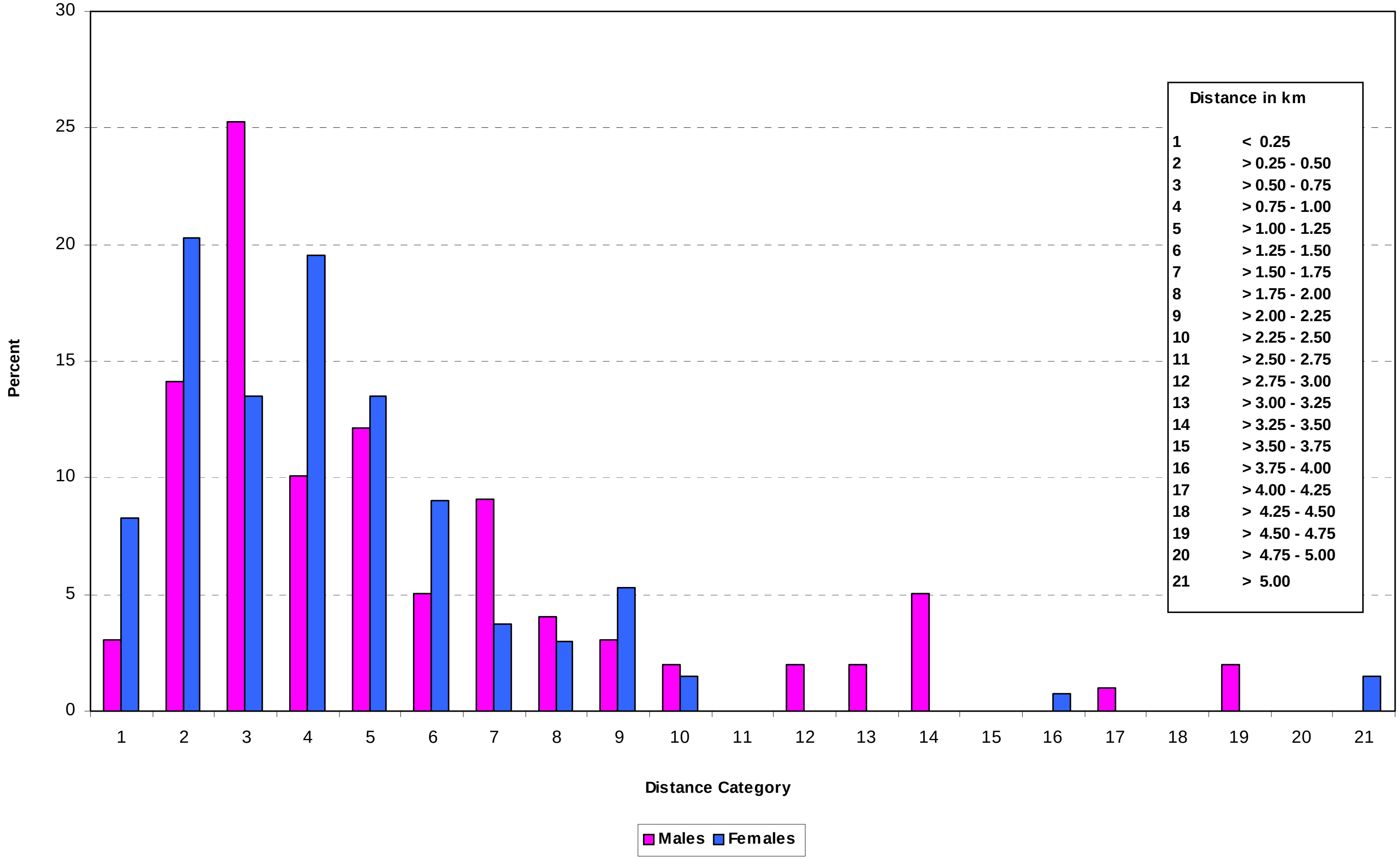


Figure 4: Frequency distribution for distances moved between consecutive days for 5 snow leopards

left the den for 1.5 days, possibly to hunt: during this time she was located in several different places, all within 400 m of her den-site. She was at the maternal den again on June 21 and evidently remained there with her cubs until June 23. F1 returned after spending a full day almost a kilometer to the south-east, where she may have been feeding upon a kill. She stayed at the den for another 3 days, then travelled to another site slightly over a half kilometer away in the opposite direction. The mean daily distance F1 moved during the 10 days prior to the birth and the 15 days following this event averaged 0.66 ± S.E. 0.11 km (N = 14). Due to the impending monsoon and associated logistical constraints, I had to leave the study area at this point (June 30) and was therefore unable to determine at what age she first moved her cubs to a new den site. When I returned five months later, F1 and her two cubs were changing their bedding sites daily. Between ages 6 and 12 months, the mean daily linear distance travelled by the trio was 1.23 ± S.E. 0.17 km (n = 51), compared to a mean daily distance of 1.01 ± S.E. 0.09 (N = 23) which F1 travelled prior to giving birth. The differences in movement before, during and after births were marginally significant if compared among all groups (Kruskal-Wallis ANOVA statistic = 5.408, df 2, P < 0.067); however, these differences were significant if natal movements were compared with those of the pre-birth period (Mann-Whitney U = 236, P < 0.019) or the post-maternal denning period (Mann-Whitney U = 485, P < 0.041).

5.3 Activity Pattern

Percent activity and sampling effort for the 5 animals studied are shown in Table 9. These data include records in which activity is very localized, such as that occurring in bedding sites when an animal shifts its head or body position. Sample size varies widely between sex, individual and time interval (for example activity records totalled 13,830 records for males (N = 3) compared to only 3,946 for females (N = 2); interpretation of activity data must therefore be made cautiously. Activity by male radio-tagged snow leopards differed significantly between the four time intervals of day and night, with greater than expected activity during dawn and dusk and less than expected during daytime ($\chi^2 = 36.231$; df 3; $P > 0.001$). Female activity ($\chi^2 = 11.223$; df 3; $P > 0.005$) differed for the dusk time period only, when they became more active.

Factors affecting Activity in Snow Leopards: Individual behavioral differences among snow leopards (variable "catno"), with some being more active than others, contributed most significantly to variation in activity levels, as did the differing response of some individuals to time of day and the time of year.

Time of day was found to be highly correlated with the activity pattern exhibited by snow leopards of the Langu Valley, with activity levels differing according to the particular individual, time of day and individual response to time of day respectively (Table 10 - Model I). Activity differed with respect to individual and time of day for all snow leopards. Fishers LSD test indicated that M2 differed significantly from the other three individuals sampled, whose mean overall activity did not differ significantly. Snow leopard F1 was most active, while M2 was the least active. Dawn hour (0500-0855 hrs) and dusk hour (1600-1900 hrs) activity levels differed significantly from the remaining daylight hours (0900-1555 hrs), but with less consistent differences from the night-time intervals between 2000 - 0355 hours, thus confirming a crepuscular activity pattern in the population sampled. All individuals showed this basic pattern, although there was considerable variation between animals (Figure 5). Figure 6 shows the probability of activity for male and female snow leopards, based on least square means. Both figures indicate activity peaks during dawn (04:30 - 08:25 hrs) and dusk (16:00 - 19:55 hrs), with reduced activity during the daytime (08:30 - 15:55 hrs) and nighttime (20:00 - 04:25 hrs) periods. It is not known why the two females showed so much more activity during the evening activity peak than the two males (Figure 6).

A similar crepuscular activity pattern is shown when daily activity is averaged over the entire year, with two peaks of activity (one around 0700 hrs and the other at 1800 hrs). Typically, snow leopards became active an hour or so before dawn, remaining active for 5-6 hours, and then resting during the middle of the day. Activity intensified again around 1500 h, with animals remaining active for several hours following darkness. Although activity varied greatly between individuals (Figure 6), all animals were generally most active around dawn and dusk.

Activity differed according to month (Model II), although the diurnal differences were not as strong (Table 11) and in the case of one individual (F2) these were not significant. In terms of daily activity, the crepuscular pattern is pattern is most pronounced during the

Table 9: Activity of 5 snow leopards according to four time periods

Cat No	Nighttime (0200-0355 hrs)		Dawn (0400-0755 hrs)		Daytime (0800-1555 hrs)		Dusk (1600-1955 hrs)	
	Percent active	Sample Size	Percent active	Sample Size	Percent active	Sample Size	Percent active	Sample Size
M1	55.1	377	77.9	261	35.3	721	73.9	485
M2	34.8	2,036	49.1	1,190	39.5	4,500	44.4	1,964
M3	52.5	654	62.5	379	51.4	1,458	54.5	741
F1	47.5	680	73.1	243	52.2	974	71.3	840
F2	58.2	270	44.6	196	48.8	514	49.6	368
♂♂	41.9	2,874	55.4	1,712	42.1	6,237	50.8	3,007
♀♀	50.6	919	60.1	429	51.0	1,427	64.6	1,171
All	44.1	3,793	56.4	2,141	43.8	7,664	54.7	7,178

Note: Sample Size = number of 30 minute intervals in the data subset. Each 30 minute interval consisted of up to 6 individual activity readings, taken at consecutive 5-minute periods; these figures were averaged to obtain the proportion of each interval in which the animal was considered to be active.

fall/winter and spring sampling periods; the increased day over dawn activity noted during the summer may have reflected the limited sampling effort of this time period, rather than a real pattern of snow leopard activity (Figure 7).

Model III (Table 12) examined activity under the additional influence of time of year and time of day (according to 4 broad categories), indicating that time of year based on the three seasons was not significantly correlated with activity. Sex was found to be highly correlated with activity in snow leopards, along with time of day and interactions between sex, season and time interval (Model IV, Table 13). This relationship involving sex, however, did not hold when examined in terms of month of year: F-values for this model (V) are shown in Table 14, suggesting the effect of sex is nested within individual snow leopards and interaction between cat and month.

Table 10: Analysis of variation (MODEL I) in activity of snow leopards in the Langu Valley with respect to time of day and difference among individuals (1982 - 1985)

Source of variation	d.f	MS	F & Probability Level
Total	3646		
Catno (n = 4)	3	37.428	10.08 P = 0.0001
Time Interval [1]	23	12.436	3.35 P = 0.0001
Cat x time interval	69	6.217	1.67 P = 0.0005
Residual	3551	3.713	

Note:

[1] Hourly time intervals, based on Standard Nepal Time

No significant differences were detected between activity levels during the mating and non-mating seasons for either individual (F = 1.55, df 1, P < 0.213) or sex (F = 1.12, df 1, P < 0.289), although overall activity levels in males were highest during March, the peak of the mating period. However, female activity was lower during this month compared to other times of year. This situation may possibly reflect a sexual difference, with males roaming widely in search of oestrous females and females being more sedentary during the mating period. Interestingly, activity did not differ according to month in F2, a non-breeder. However, given the very small sample size, more research is clearly needed before valid conclusions can be made.

Presumably these patterns reflect differences among sampled snow leopards with respect to age, sex and other individual characteristics. Overall, females tended to be more active than males (Least Square means ♀ = 0.61; ♂ = 0.49). Some of this difference may have been due to M2's apparently less sensitive activity sensor, which was replaced in February 1984. This could also explain why this individual was significantly less active than the other snow leopards' monitored; one would have expected this individual to be more active if it had been in the process of establishing itself as the dominant male, as I suspect may have been the case.

Table 11: Analysis of variation (MODEL II) in activity of snow leopards in the Langu Valley with respect to time of year (month) and difference among individuals (1982 - 1985)

Source of variation	d.f	MS	F & Probability Level	
Total	3646			
Catno (n = 4)	3	35.194	9.53	P = 0.0001
Time of Year (month) [1]	6	8.670	2.35	P = 0.0289
Cat x month	16	21.492	5.82	P = 0.0001
Residual	3621	3.694		

Note:

[1] Model does not examine all months of the year (see methods)

5.4 Discussion

Movement Pattern: The Langu Valley snow leopards were relatively mobile, changing their location from one day to the next, unless they were on a blue sheep or tahr kill. Given the strongly precipitous terrain within their respective home ranges, it is not surprising that these snow leopards moved straight-line distances of only a kilometer or so between consecutive days. Actual distances moved are greater than the telemetry data indicate, as pugmarks showed all cats typically traveled a circuitous, zig-zag route. However, no estimates of actual distances travelled were made, but movements in excess of 1.5 times the airline distance are likely, as observed in the puma studied by Sweanor (1990). A snow leopard would occasionally move from one end of its range to the other within a 12- to 24-hour period, thereby covering a linear distance of 7 km. or more.

Daily movements of a kilometer or less in snow leopard were also reported by Chundawat (1990a) who monitored a radio-collared male over a 35 day interval in late winter in the Hemis National Park of Ladakh. In Mongolia, Schaller et al. (1994) noted that a male

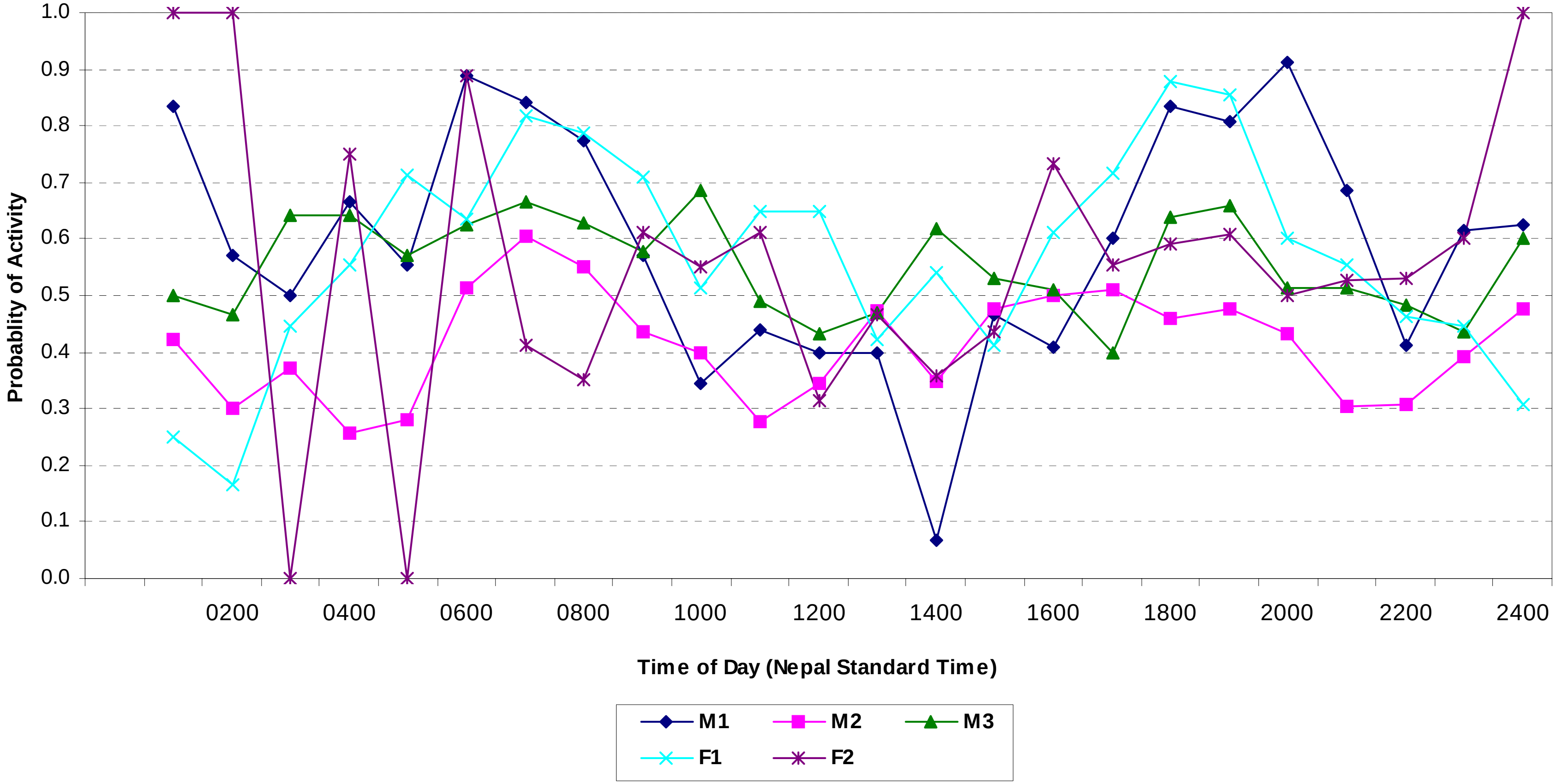


Figure 5: Probability of activity according to 30 minute intervals for 5 snow leopards

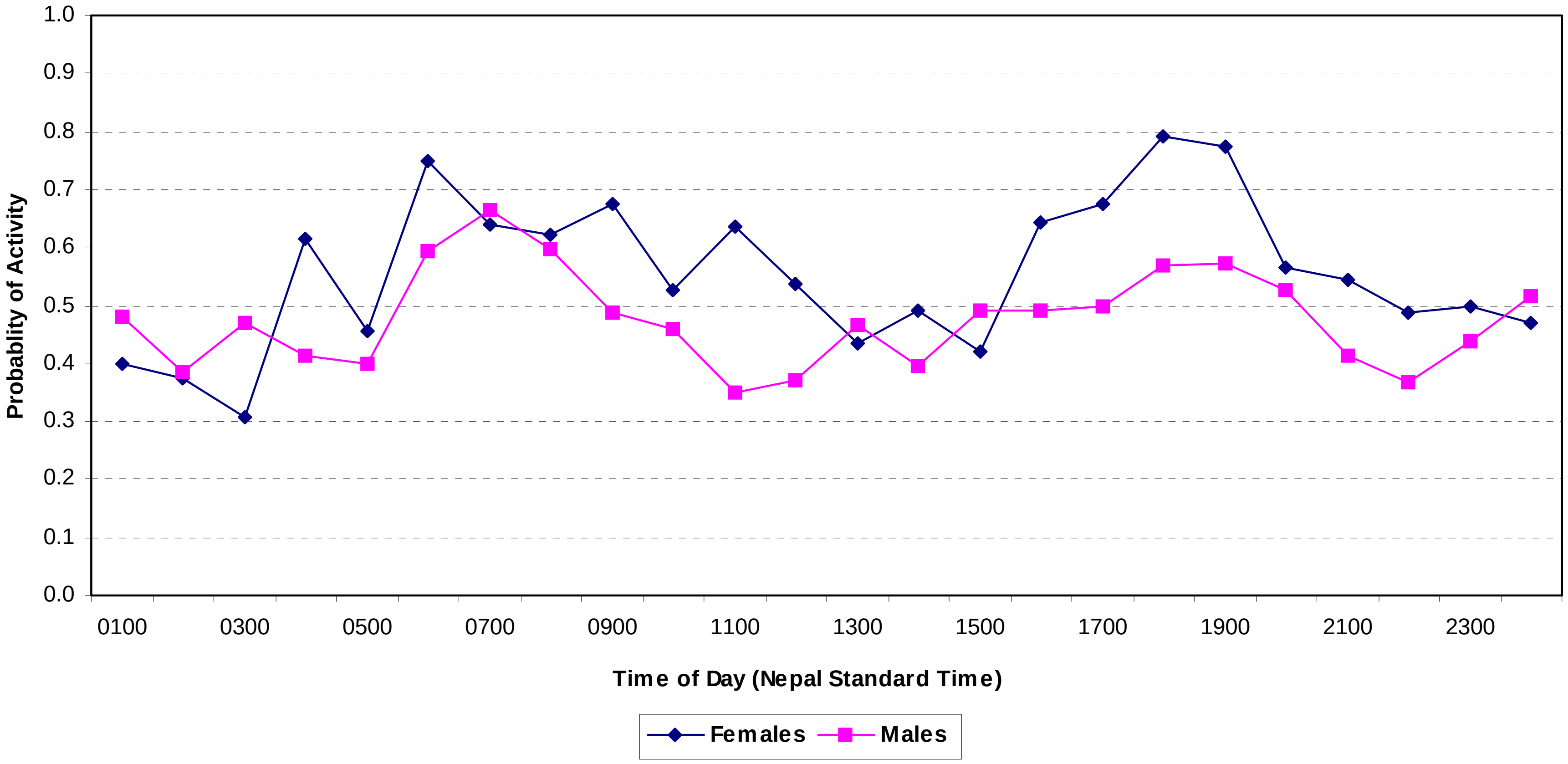


Figure 6: Probability of activity for male and female snow leopards

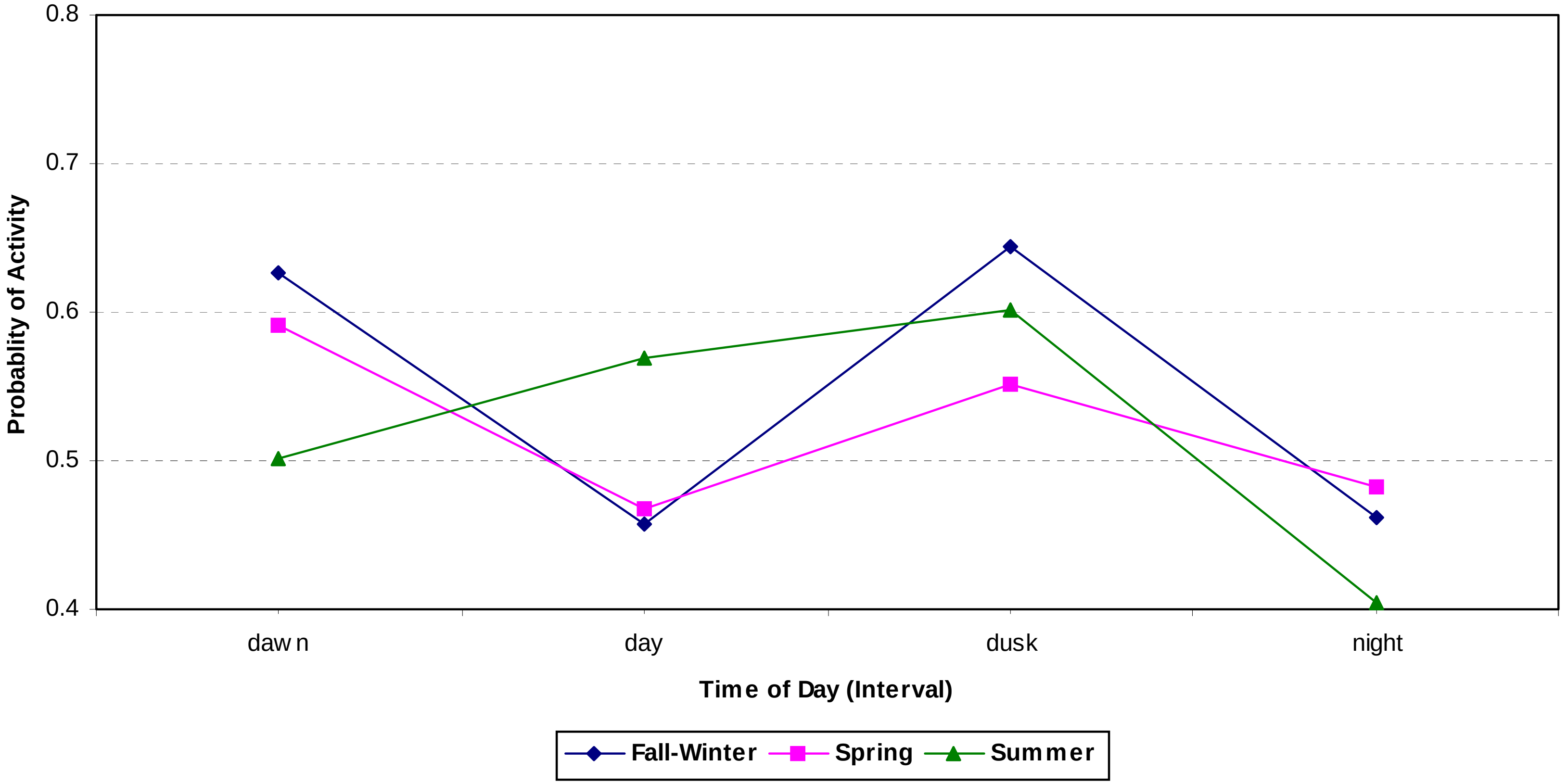


Figure 7: Probability of activity in snow leopards according to three seasons

Table 12: Analysis of variation (MODEL III) in activity of snow leopards in the Langu Valley with respect to time of year (season), time of day (interval), and differences among individuals (1982 - 1985)

Source of variation	d.f	MS	F Value & Probability
Total	3646		
Catno (n = 4)	3	6.5562	27.98 P = 0.0001
Season [1]	2	0.0872	0.37 P = 0.6894
Time Interval [2]	3	1.9257	8.22 P = 0.0001
cat x time interval	9	0.5533	2.36 P = 0.0118
cat x season	6	1.4627	6.24 P = 0.0001
season x time interval	6	0.7032	3.00 P = 0.0063
cat x season x time interval	18	1.0365	4.42 P = 0.0001
Residual	3599	0.2343	

Note:

[1] Seasons sampled are fall/winter (November - February); spring (March - May 15); and summer (May 16 - July)

[2] Time intervals sampled are night (20:00 - 04:25 hours Standard Nepal Time); dawn (04:30 - 08:25 hrs); day (08:30 - 15:55 hrs); and dusk (16:00 - 19:55 hrs)

Table 13: Analysis of variation (MODEL IV) in the activity of snow leopards according to time of year (season), time of day (interval), and differences between sexes (1982 - 1985)

remained within an area of 12 km^2 during the 41 days it was radio-tracked, and repeatedly used a favoured daytime resting site. Oli (pers. comm.) determined similar mean daily distances for 3 snow leopards he tracked in the Annapurna region of Nepal, an area comprised of considerably less rugged terrain than the Langu Valley.

Tigers, jaguar and puma, for example, were found to travel linear distances about twice as much (Schaller and Crawshaw 1980, Seidensticker et al. 1973, Sunquist 1981). Norton and Henley (1987) reported that common leopards moved mean daily distances of 2.3 to 4.2 km, observing that they also rested in different places each day. Common leopards in the Kruger National Park were stationary on only 5% of all consecutive days monitored (Bailey 1993). The average distance between daily locations of Bailey's radio-collared leopards was 1.7 km/day, with 40% of all locations being less than 1 km apart; these

Source of variation	d.f	MS	F Value & Probability
Total	4059		
Sex	1	8.9301	37.07 P = 0.0001
Season [1]	3	0.1191	0.49 P = 0.6099
Time Interval [2]	2	4.5325	18.82 P = 0.0001
sex x time interval	3	0.3290	1.37 P = 0.2313
sex x season	2	1.7189	7.14 P = 0.0008
season x time interval	6	0.5199	2.16 P = 0.0441
sex x season x time interval	6	1.5096	6.27 P = 0.0001
Residual	4036	0.2409	

Note:

[1] Seasons sampled are fall/winter (November - February); spring (March - May 15); and summer (May 16 - July)

[2] Time intervals sampled are night (20:00 - 04:25 hours Standard Nepal Time); dawn (04:30 - 08:25 hrs); day (08:30 - 15:55 hrs); and dusk (16:00 - 19:55 hrs)

adult males moved 1.9 times further than adult females. Mean daily distance moved was not significantly correlated with snow leopard home range size, as Hamilton (1976) found in the case of common leopard in Kenya. Not surprisingly, movement in one female with immobile cubs was significantly less than that recorded prior to birth, or before the cubs had attained six months of age. Bailey (1993) speculated that home range patrolling and maintenance, along with the location of mates were the main factors explaining the greater daily movements of males.

No seasonal differences in the daily movement rates of snow leopard were detected. In common leopard, Bailey (1993) found that adult females travelled significantly greater distances between successive days during the peak breeding period (July through September) than at other times of the year. The average daily distance travelled by adult

Table 14: Analysis of variation (MODEL V) in activity of snow leopards in the Langu Valley with respect to time of year (month), sex and individual, with nested effects due to sex, cat number and month.

Source of variation	d.f	MS	F Value & Probability
Total	3646		
Sex	1	3.100	0.84 P = 0.3597
Month [1]	6	8.568	2.32 P = 0.0308
month x sex	6	11.067	3.00 P = 0.0064
cat (nested by sex)	2	25.705	6.96 P = 0.0010
cat x month (nested by sex)	10	25.107	6.806 P = 0.0001
Residual	3621	3.694	3.00 P = 0.0063

Note:

[1] Model does not examine all months of the year (see methods)

males did not increase significantly between nonbreeding and breeding periods. Female leopards moved 50% further during the breeding season. Females with cubs moved significantly shorter distances each day than females without cubs: three females without cubs averaged 1.9 km/day compared to 1.2 km/day for 3 females with cubs. The distance moved decreased from 1.4 km/day to 1.1 km/day after parturition, with movement being most restricted during the first six months after birth. One common leopard female monitored by Bailey remained within an area of only 12.3 km^2 near the *kopjie* (rocky outcrop) that concealed her cubs for the eleven-month period that she was monitored. Bailey also found that female leopards raising young typically sought the secluded cover of rocky outcrops or riparian reed-beds.

Radio-telemetry indicated that snow leopards preferred to bed on or near ridgelines, cliffs or other sites with a good vista (see Chapter 9). The species preference for travelling along a prominent terrain features or edge has been documented in other areas (Koshkarev 1984; Mallon 1984; unpub. data). While snow leopards often select a prominent feature as a resting place, such as a large rock outcropping or ridgeline promontory, they seem to prefer its base rather than lying in an well-exposed position on top. Promontories provide shade as well as a close-by vantage point from which the animal could survey the immediate area once it had become active again. The base of rock outcrops used as resting sites are usually well-marked with scrapes and scats. The Langu snow leopards also rested under low juniper bushes or along the edge of a low rock outcropping, but no instances of tree-climbing, as reported from the Ala-Tau region of Kyrgyzstan, was recorded. Here Guggisberg (1975), citing Stroganov (1962), noted that snow leopards rested in the nests built by black vultures in low junipers. The large amount of shed fur suggested that this was a regular habit of the snow leopards in this area, but this behaviour has not been observed elsewhere. In India, Dang (1967) reported that snow leopards spent the daytime lying in rocky lairs, and other resting sites include rocky caverns, crevices or overhangs (Heptner and Sludskii 1992; Schaller 1977).

The Langu snow leopards tended to travel a shorter distance after leaving a kill than they did beforehand. By contrast, adult male common leopards moved significantly greater distances after leaving a kill compared to pre-kill distances (1.5 compared to 4.7 km/day) (Bailey 1993). This investigator found that consecutive kills of adult male leopards were farther apart than those of other leopards, with dry seasons kills being most widely separated. He suggested that the daily movements of leopards were influenced by prey abundance, with greater movement occurring in prey-poor areas. This relationship could not be examined in this study, since the entire study area offered prey-rich habitat for the snow leopards. However, I would expect average daily movements to be significantly greater in areas where ungulate density is less than 1-4 animals per square kilometer; hopefully studies underway in Mongolia will provide comparative data on snow leopard movements in prey sparse habitat (T. McCarthy, pers. comm.).

No information was gathered on dispersal movement, and none of the snow leopards monitored showed exploratory movements of the type documented by Bailey (1993) or Sunquist (1983) for the common leopard. However, I cannot exclude the possibility that M3 left the study area for a new home range elsewhere. Bailey's data (1993) indicates that some common leopards did not disperse from their natal range until they are about 3 years of age. The availability of resources and competition with resident leopards are the primary factors influencing the variability in age of dispersing leopards in South Africa. Animals are more likely to remain in the vicinity of their natal range in the absence of competing resident adults, and as noted, land tenure in the Langu Valley may have been in a state of flux, with no evidence to indicate frequent visitation by a fully grown male snow leopard to the core use area.

Activity pattern: Although my sample size is clearly very limited, two basic patterns emerge: (1) snow leopard activity is primarily crepuscular, but with considerable variation between individuals and within an individual, from one day to the next; (2) snow leopards tend to spend the middle of the day and night bedded on cliffs, in rocky outcrops or other secluded and protected places.

Studies of captive snow leopards indicate that they are most active early in the morning and again in the evening at nightfall, with only short activity phases during other hours of daylight (Hemmer 1968; Freeman 1975). In the wild, recent work (Oli, in prep; Schaller et al. 1994) confirms this crepuscular activity pattern, contrary to the popular and scientific literature which portrays the species as being strongly nocturnal in its activity. The Langu snow leopards were most active after dawn and around dusk, but occasionally moved around during the middle of the day as well. The extent of daytime movement seems to be partially related to ambient temperature and whether an animal is on a kill or not: mid-day activity movement is more likely to occur on cloudy days or in animals that had not recently killed. Radio-tagged snow leopards were most inactive at night between the hours of 10 pm and 3 am. Their activity pattern appears to be adapted to that of their principal prey species for blue sheep show a strongly diurnal activity with early morning and late afternoon activity peaks (unpublished data). At night, blue sheep move to cliffs and other steep places to bed down for the night. Presumably snow leopards are more likely to make kills in or close to such terrain (see Chapter 8).

Oli (in prep.) monitored 3 radio-collared snow leopards in the Annapurna Conservation Area in Nepal for a two-month period during winter and found they exhibited a crepuscular activity pattern. Overall, activity averaged 43.5%, with the highest peak (60.3%) occurring during dusk (16:00 - 19:55 hours) and the lowest activity during the nighttime. Animals were more active during dusk and less active than expected during the night. Schaller et al. (1994) reported that a male snow leopard studied in the Altay Mountains of Mongolia was crepuscular. Over a three-day period in early December, he remained active for about 53% of the time. Similar activity levels were observed in the

Langu snow leopards. Typically, a snow leopard remained resting in a small area for several hours or even several days, occasionally shifting its body position. If not on a kill or if a week or more has passed since the last kill, a snow leopard is more likely to exhibit higher levels of movement, frequently shifting from one part of its range to another.

As noted, many authors consider snow leopards to be primarily nocturnal in their activity (Novikov 1962; Mallon 1984; Roberts 1977). Novikov, for example, wrote that snow leopards in the former Soviet Union were most active at twilight and at night, although they were occasionally to be seen moving about during the daytime. Mallon (1984) reported the same situation in Ladakh. I suspect that the species is relatively inactive during daytime where disturbed, but even then it can be seen on kills (Fox and Chundawat 1988). Snow leopards appear to be far more willing to travel by day in those areas little visited by either people or livestock. For example, Dang (1967) reported midday activity in the secluded Nanda Devi sanctuary in India. However, daylight movement can easily pass unseen, thanks to the snow leopard's excellent cryptic camouflage and its tendency of moving quietly away, unseen upon the arrival of any humans. It is reasonable to conclude that snow leopards are able to adjust their behaviour in response to the type of disturbance and level of threat they encounter. Mallon (1984) felt that the nocturnal habits of snow leopard in Ladakh resulted from their tendency to subsist upon domestic livestock, thus leading to hunting and other forms of retribution. Snow leopard sightings in Ladakh have increased in recent years, possibly attributable to the increased emphasis upon wildlife conservation, and resulting protection of wild ungulates like blue sheep and ibex. Also, a decreased dependence upon animal husbandry as an income source may be another factor in this apparent trend.

Crepuscular activity has been reported in puma as well (e.g., Seidensticker et al. 1973; Sweanor 1990). Sunquist (1981) found tigers in Chitwan to be more active by night (92%) than day (42%), presumably an adaptation to the higher ambient temperatures of tiger habitat. This diurnal difference is even more marked in common leopard inhabiting the same area: nighttime activity averaged 74 percent versus only 12 percent during the daylight hours. Hamilton (1976) found common leopards to be three times as active during the nighttime as daytime. Bailey (1993) noted a similar pattern in the southern African population he studied, with male leopards being more active than female leopards during the night; while age did not significantly influence the activity pattern, females with cubs tended to be more active during night than females without cubs. Daytime activity was found to be greater during the wet season than the dry season. Seasonal variations in temperature, cloud cover, precipitation and wind velocity had little influence on activity patterns, although daytime movements tended to increase on overcast days. Although the influence of weather on snow leopard activity could not be easily studied because of its variability across short distances, the Langu cats remained active longer on overcast days than on days with more solar insolation. There appeared to be a tendency for snow leopards to rest earlier or longer on hot days compared to cold or cool days; however, animals could easily seek relief from heat by resting along windy ridge-tops or among shaded rocks. This option is not as easily available to the tiger or common leopard, both of which reside primarily in the tropics.

This study found no significant difference in activity level between the seasons, although activity rates varied according to month of the year. However, these patterns appear to have been masked by variation between individuals and a small sample size, so that it is not easy to determine if overall activity levels increase during the mating season, or are higher in winter than summer. Studies have indicated distinct seasonal patterns exist in tiger (Sunquist 1981) and common leopard (Bailey 1993), which appear to be related both to ambient temperature and prey availability. Bailey (1993) concluded that seasonal differences in leopard activity patterns may be related to vegetative cover and the activity patterns of impala (*Aepyceros melampus*). Seidensticker et al. (1973) observed that puma in Idaho increased their daytime activity in summer in apparent response to the diurnal activity of ground-squirrels, a key food item of this time of year. Similar shifts may occur in snow leopard for some populations rely heavily upon marmot during summer months.

CHAPTER 6 HOME RANGE CONFIGURATION AND UTILIZATION PATTERNS

6.1 Home Range Size and Configuration

Cumulative minimum area polygon curves indicated that initial asymptotes were reached after animals had been located once every 2-4 days over a period of at least 40 to 65 days (Figure 8). Home-range size continued to periodically increase in individuals monitored for time intervals in excess of 280 days. This trend is attributed to the difficulty of sampling each individual's home area, given the rugged mountainous terrain and reliance upon ground-based radio-tracking. The radio-tagged snow leopards tended to be fairly widely dispersed, and capable of moving rapidly from one part of their home range to another. The long-term increase in the home area utilized by M2, M3 and F2 may have resulted from their youthful age, because each appeared to be in the process of establishing its respective home area. Periodic increases in F1's home range after 180 days of monitoring may be related to the increasing food demands of her two young cubs. Her home range increased about 44% in area after 197 days of relocation, 38% after day 239 and a further 60% after 292 days of monitoring (Figure 8). Radio-telemetry indicated the cubs were born in mid-June, 1984, after F1 had been located on almost 100 separate days. Their estimated ages at the 197, 239 and 292 day intervals were 8, 9 and 12 months respectively. She probably had to travel more widely in her effort to secure sufficient prey for herself and her offspring, in order to maintain hunting success while accompanied by untrained cubs.

Minimum area polygons for the 5 radio-tagged snow leopards are shown in Figure 9, and these suggest considerable overlap between individuals of the same and different sex. The minimum area polygons were several times longer than wide, reflecting local physiography -- a deep river gorge bounded by precipitous, rocky ridges and peaks exceeding 5,100 m in elevation. None of the animals monitored were observed south of the Langu River, which appeared to constitute the southern home range boundary for all tagged individuals. During mid-winter, when flows were at the annual low, a snow leopard could easily have crossed in several places, simply by jumping across a series of boulders. The tagged animals may occasionally have ventured across the 5,150 m range bordering the northern part of the study area, but this was not confirmed.

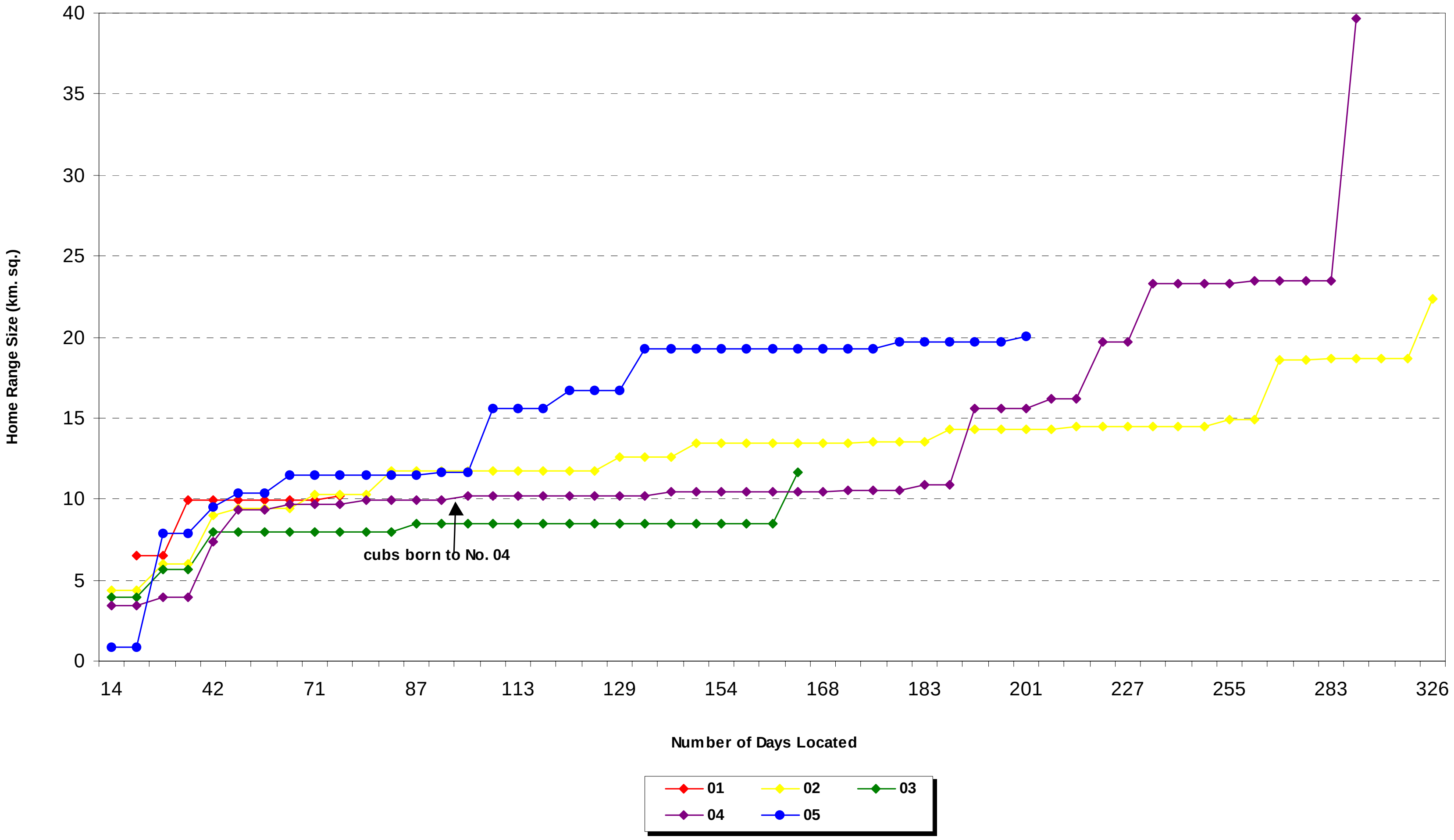


Figure 8: Cumulative area curves for home ranges of 5 snow leopards

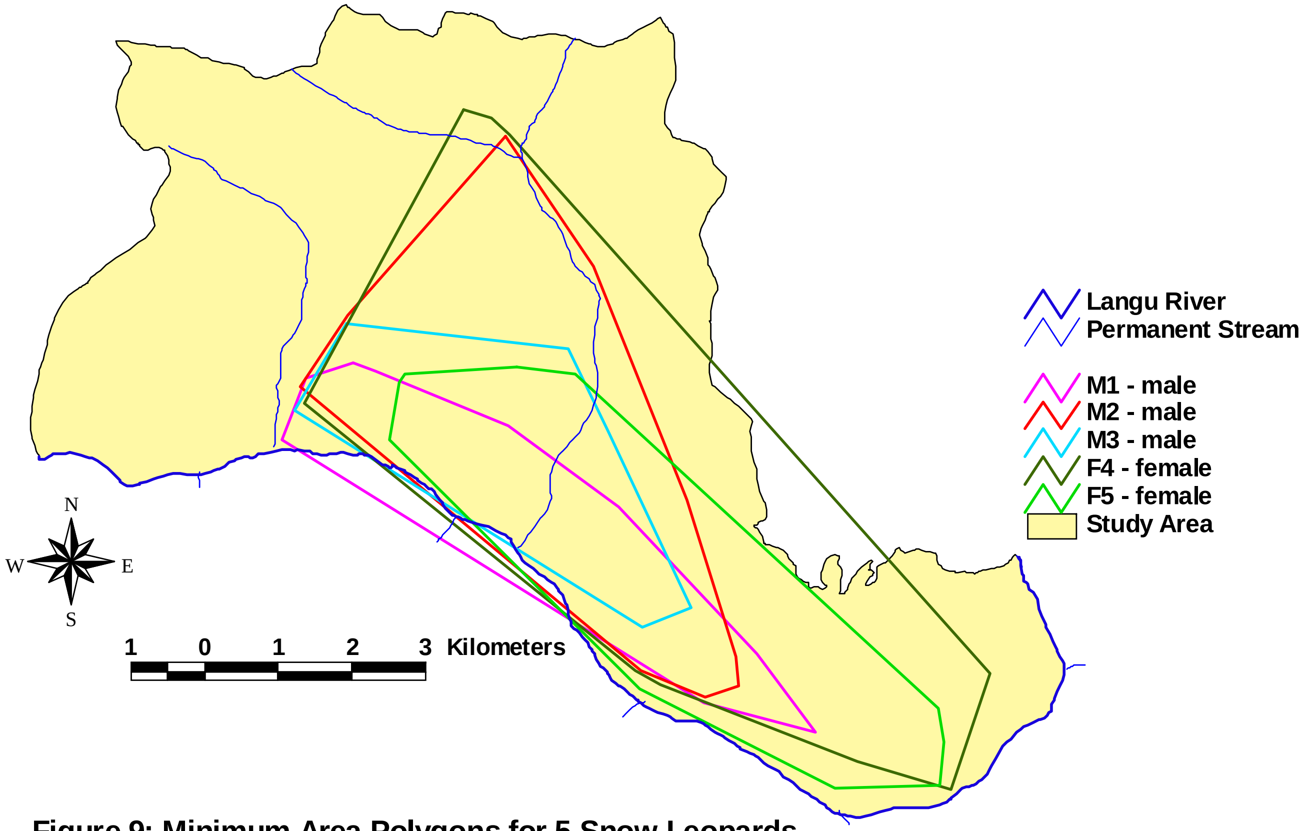


Figure 9: Minimum Area Polygons for 5 Snow Leopards

Home range size varied from about 11 to 36 km^2 according to the minimum area polygon method (Table 15). However, these estimates do not account for the considerable topographic relief present within the study area, which could increase surface area by as much as 20-25 percent. Limited access to key parts of the study area precluded effective tracking of the first snow leopard tagged (M1), and as a result its home area is significantly under-estimated. The construction of three cable bridges in December 1982 enabled us to cross the Langu River after the spring snow-melt, and we were subsequently better able to monitor leopard movements. Home range size may also have been greater in M3, which was tracked over two successive seasons, during a time that it entered adulthood and appeared to be attempting to establishing its own home area.

Home range size depends upon the computation method utilized. Home range estimates using five different techniques commonly cited in the literature are shown in Table 16. The concave polygon technique (Clutton-Brock et al. 1982) provided the lowest areal estimate, while the Fourier transform method (Anderson 1982) produced the largest estimates for home range size. These data indicate home areas ranging from 11 km^2 to more than 179 km^2. Each method has its own advantages and disadvantages, and except for the concave polygon and the Fourier transform, all appear to offer reasonable estimates for the area utilized by the five tagged snow leopards investigated. The minimum convex polygon method is extremely sensitive to outliers, and may include little used areas within the designated home range limits (Ackerman et al. 1990). By contrast, the concave polygon technique may exclude used areas from consideration, and its algorithm is difficult to apply unambiguously. The Fourier transform and harmonic mean measure represent nonparametric estimation techniques based on utilization distributions, but home range estimates derived from small samples have a strong tendency for bias. In view of the difficulty of establishing a limit to the "real world", Anderson (1982) recommended that the 50% utilization distribution be afforded priority over the 95 percent distribution for estimating home ranges with the Fourier transform technique.

Areal projections using the Anderson fourier transformation and Dixon-Chapman harmonic mean measure 95% activity isopleth were large and encompassed unused habitat located to the south of the Langu River. As indicated below, estimates based on lower valued isopleths (30 - 56%) appeared to more reasonably reflect areas actually utilized.

Table 15: Home range sizes of 5 snow leopards in the Langu Valley, based on the minimum area method of Mohr (1947)

Cat No	Minimum Area (km^2)	Length (km)	Width (km)	Length / width Ratio	No of Locations
M1	11.07	8.4	1.8	4.66	34
M2	20.58	7.5	4.4	1.70	152
M3	10.66	6.0	2.7	2.22	52
F1	36.23	10.4	4.6	2.26	168
F2	18.60	8.3	2.5	3.32	101
Mean ± standard error	19.4 ± 4.64	8.1 ± 0.71	3.2 ± 0.55	2.8 ± 0.53	

6.2 Core Area and Home Utilization Patterns

Expected Poisson distribution frequencies were computed for snow leopards' M2, M3, F1, and F2, using 6.25 ha square grid cells (i.e. 250 x 250 m grid size). The spatial distribution of utilized grids differed significantly ($P < 0.0001$) from an expected random distribution, indicating a strongly clumped spatial pattern. These four cats used a total of 208 grid cells (Table 17); males and females shared 47 or 22.6% of these cells. The shared grid cells contained 39% of all male locations and nearly 52% of all female locations, suggesting heavy use of common areas by snow leopards of either sex.

Harmonic mean distance utilization distributions for these 4 snow leopards (M2, M3, F1 and F2), based upon the entire period that each was monitored, are graphically depicted in Figures 10 to 13. These include the statistically significant "core area", the 30 percentile harmonic contour, the harmonic activity center, and the arithmetic center of activity for each individual. Small sample size precluded inclusion of M1 in the analysis, and instead this individual's home use is depicted using the 100% minimum area polygon and the arithmetic center of activity (Figure 14).

Table 16: Size of yearly total home ranges (in square kilometers) as determined by 5 different home range estimation techniques

Cat No	No of Locations	Percent Convex Polygon (100%) (1)	Concave Polygon (2)	Weighted Bivariate Ellipse 95% (3)	Anderson Transform. (4)	Dixon Harmonic Mean (95%) (5)
M1	26	11.07	1.98	18.23	n.a.	n.a.
M2	152	20.58	11.66	16.39	100.72	42.86
M3	52	10.66	3.83	7.82	46.31	18.07
F1	168	36.23	12.97	16.44	179.94	65.06
F2	101	18.60	9.22	28.61	93.03	20.59
Mean ± S.E.		19.42 ± 4.64	7.93 ± 2.16	17.49 ± 7.42	105.00 ± 27.72	36.65 ± 10.99

n.a. = sample size too small for estimation; S.E. = standard error.
(1) Bowen (1982); Samuel and Garton (1985)
(2) Clutton - Brock et al. (1982)
(3) Gipson and Sealander (1972); Jennich and Turner (1969)
(4) Fourier transform utilization distribution (Anderson 1982)
(5) Harmonic Mean Measure, 95% isopleth (Dixon and Chapman 1980).
The Concave Polygon and Fourier Utilization was estimated using *McPaal*, version 1.1 (Smithsonian Institution, Washington DC); the 100 Percent Convex Polygon, 95% Weighted Bivariate Normal Ellipse and Harmonic Measure was calculated using *Home Range* (Ackerman et al. 1990, University of Idaho, Moscow)

The activity contour plots indicated that relatively large numbers of locations were concentrated within a relatively small part of the home range, denoting high intensity of use within the center of activity (Figures 10 - 13). Harmonic mean centers of all four snow leopards were located within several kilometers of each other. The 95% and 75% activity isopleths approached circularity in all animals, and enclosed relatively large areas of unused habitat, especially to the south of the Langu river. Core use was more convincingly modelled using the core area polygon (herein termed the *significant core area*) automatically generated by the home range program and based upon the chi-square goodness of fit test. It is defined as the maximum area where the observed utilization distribution, based on harmonic values, exceeded a uniform utilization distribution (Ackerman at al. 1990). By contrast, the 30 percent isopleth best denoted "central areas of consistent and intense use"

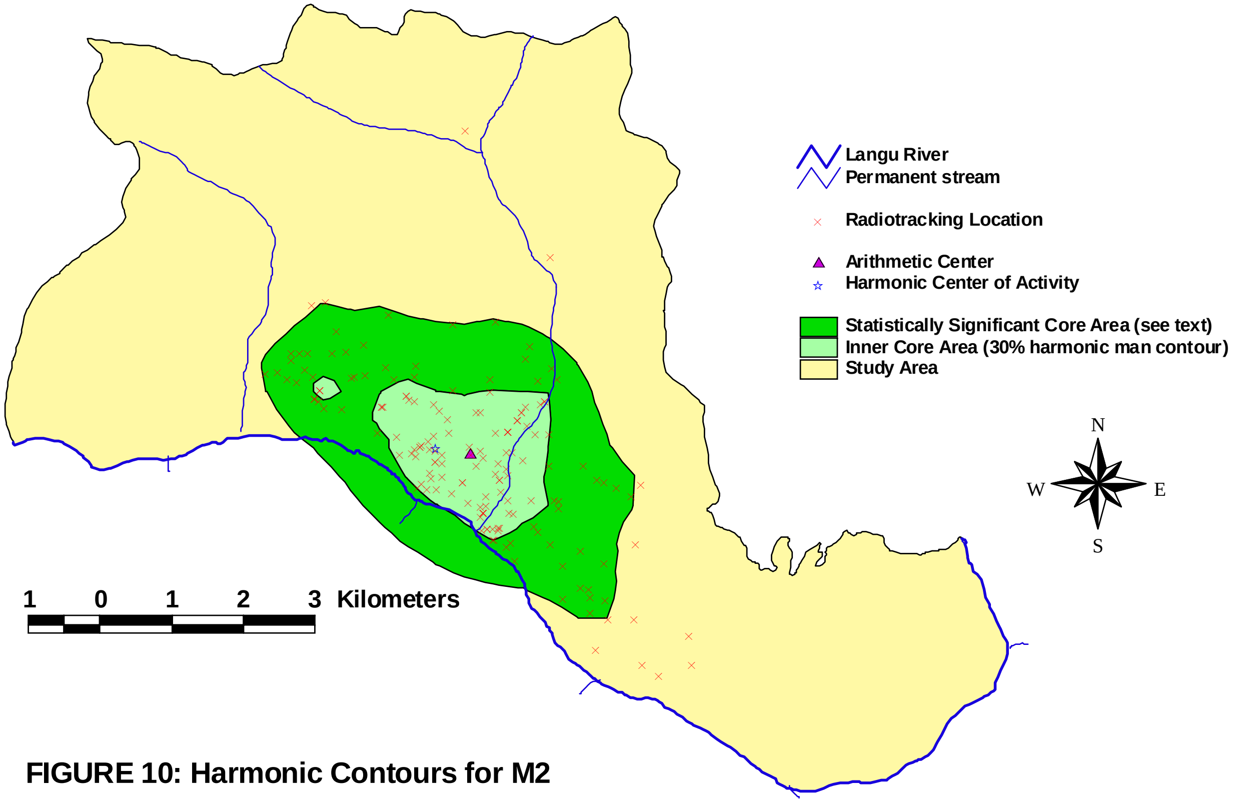


FIGURE 10: Harmonic Contours for M2

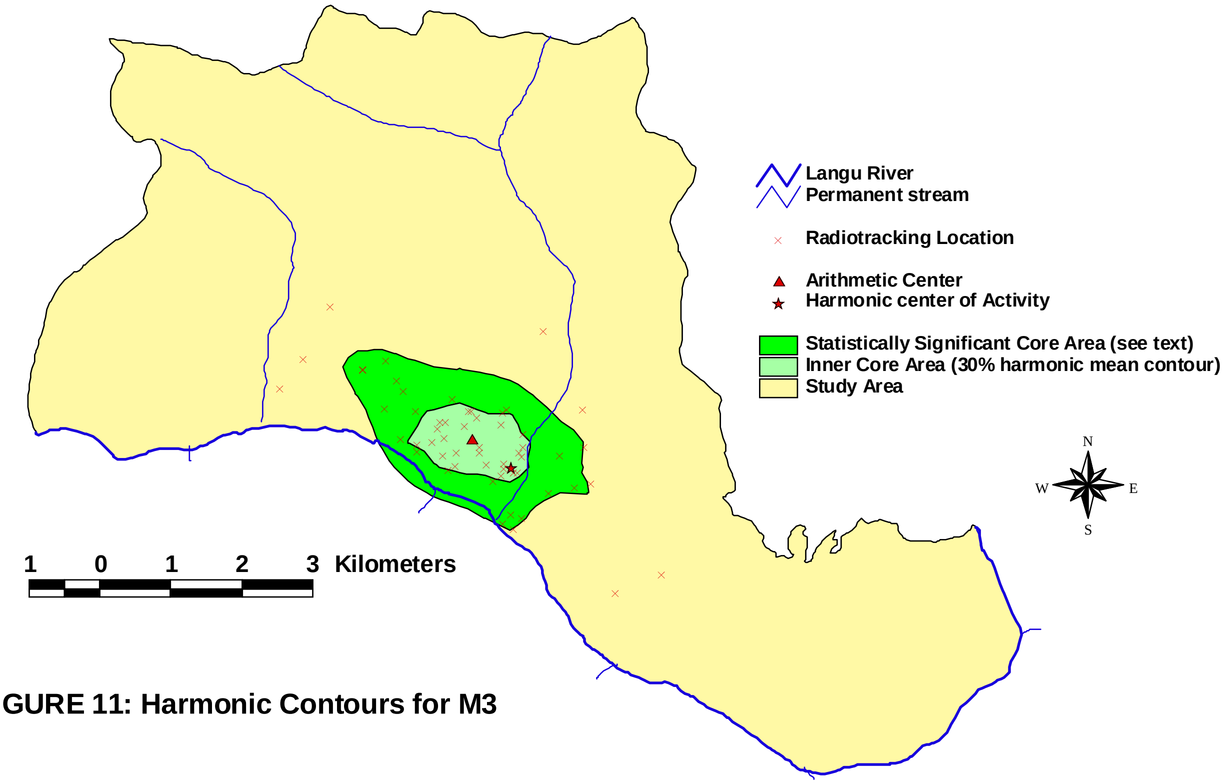


FIGURE 11: Harmonic Contours for M3

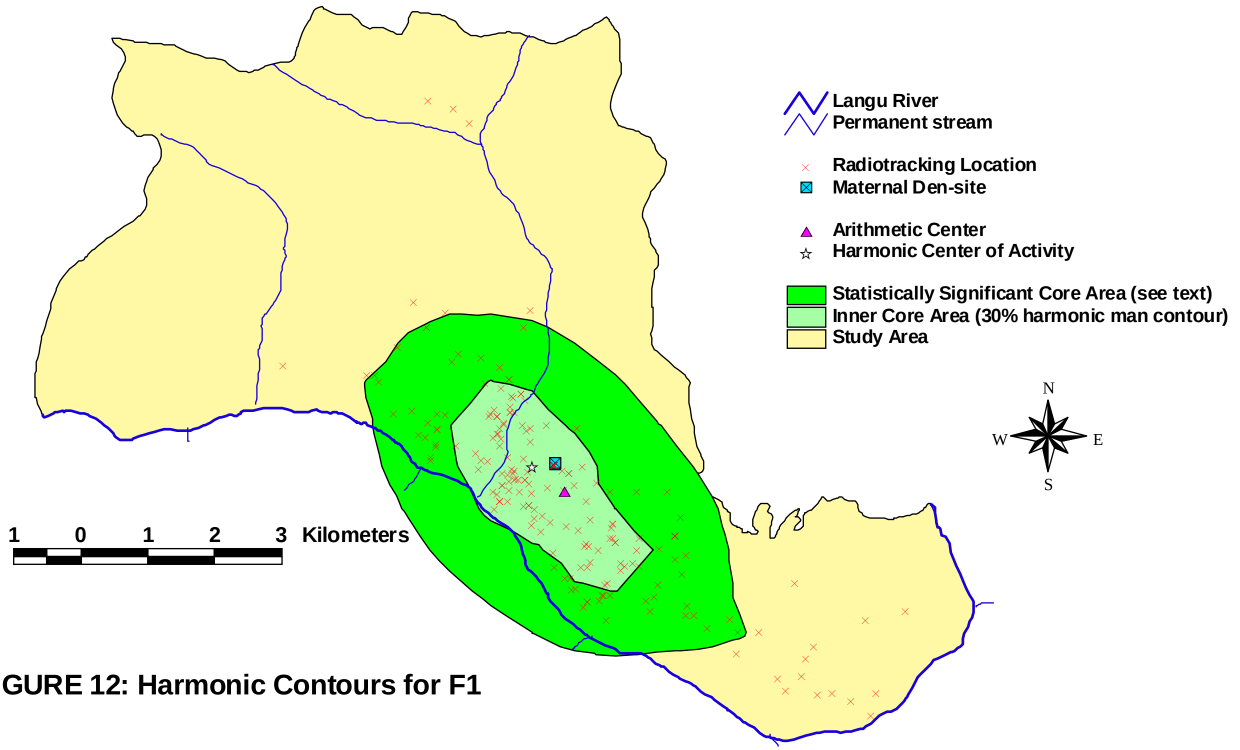


FIGURE 12: Harmonic Contours for F1

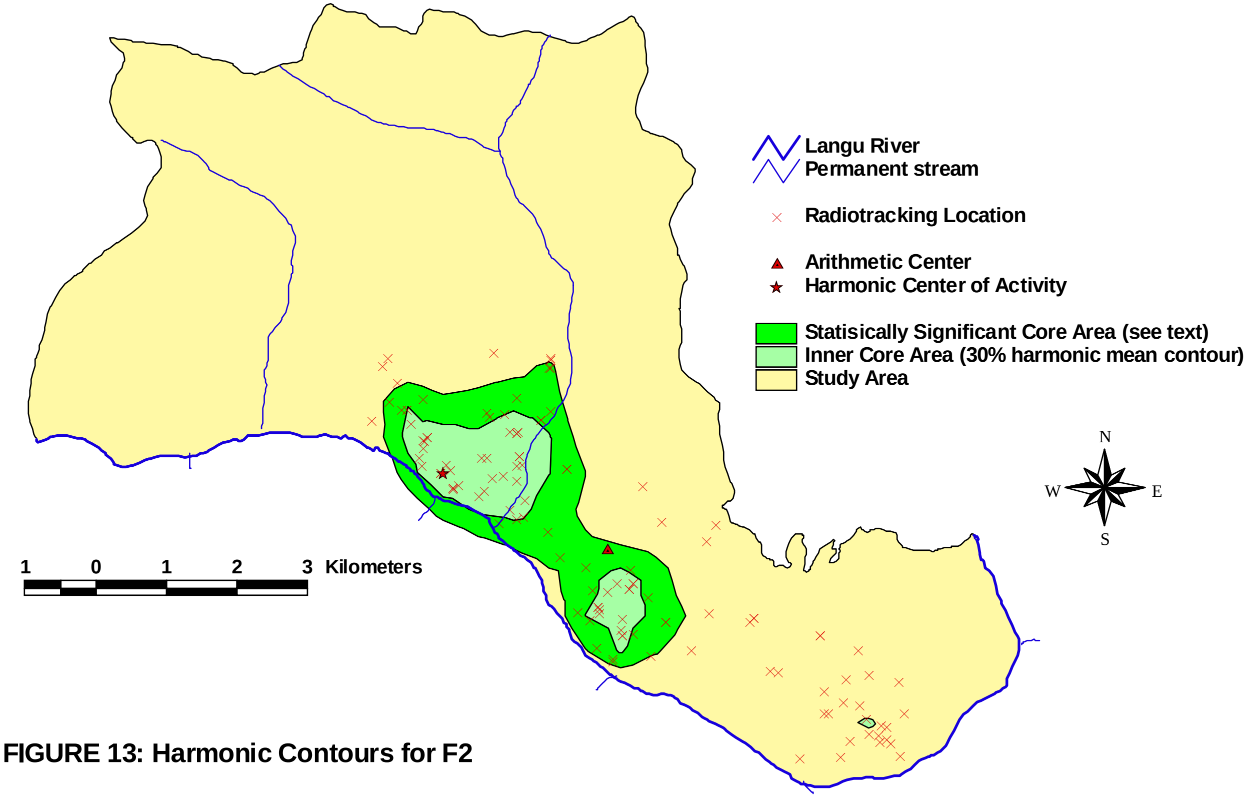


FIGURE 13: Harmonic Contours for F2

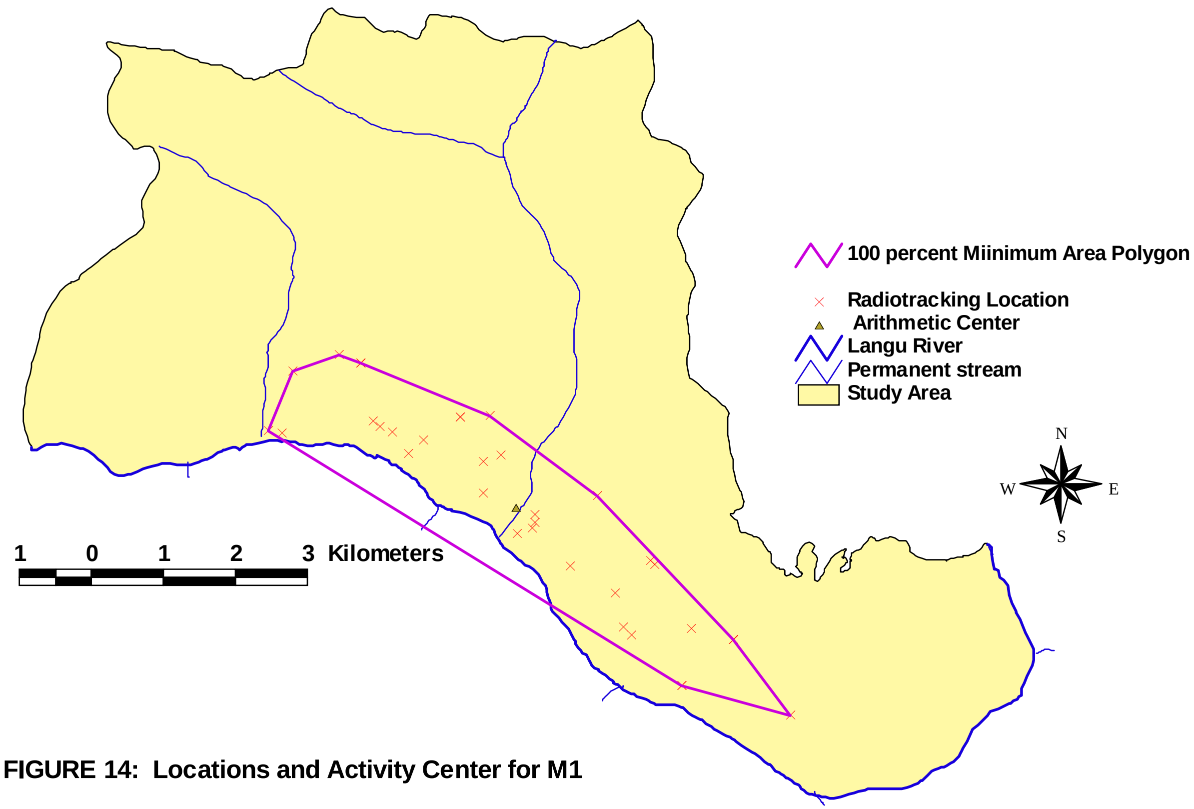


FIGURE 14: Locations and Activity Center for M1

(termed *inner core areas*). Inner core use areas also overlapped between individuals and across sex (Figure 15). The harmonic mean activity centers of the 4 snow leopards were located within 2 kilometers of each other, near the confluence of the Tillisha gorge with the Langu River, in an area of abundant snow leopard sign and a relatively high prey population (see Chapter 10). Male core areas tended to be located in areas west of the Tillisha - Langu confluence, while the two females tended to use areas more to the east.

The significant harmonic mean distribution ranged from 56.1 to 66.8 percent of the utilization volume (Table 18); thus, the statistically significant core areas ranged in size from 6 km^2 in M3 to 20 km^2 in F1. While core areas comprised between 26 and 37% of the total home range area, they contained 68 to 93 percent of all locations tallied. The figure in the last column of Table 18 provides a measure of the intensity of use within the core area of each snow leopard: these indicate M2, M3 and F1 were using their core areas most intensively. Utilization volumes based upon the 30% isopleth designated smaller internal, but comparatively more intensively utilized activity centers (Table 19). A relatively high percent of home range use (47 - 55%) occurred in the 30% isopleth core area, which encompassed only 6 - 15% of the animal's total home range area. F2 used her core area to the least degree with F1 showing the highest intensity of use. This may have been related to F1's natal den-site, which was located on a precipitous ridge overlooking the Tillisha gorge (Figure 12), very close to the harmonic activity center. The intensity of use ratio was several times greater for the *inner* core area compared to the larger *significant* core area. Furthermore, these areas overlapped greatly between different individuals, although their use of the core area polygon was temporally separated (see Chapter 8). The area of the combined, overlapping core area totalled 4.61 km^2, and encompassed the slopes around a major stream confluence formed by the Langu River and Tillisha Stream (Figure 15). The data indicated that 40 - 73 percent of locations were situated within the common (overlapping) inner core area, which comprised between 6 and 23 percent of the particular individual's total home range (Table 20).

Shifts between successive years in the use of the core area were detected in 3 of the 4 snow leopards studied. M2's center shifted 1.7 km southwest, F1's center about 1.1 in the same compass direction, and F2's center about 3.8 km to the southeast. The shift in the core activity area of F2 may reflect her attempt at establishing a home area within that of her presumed mother (F1), by concentrating her activity in areas less heavily utilized by F1.

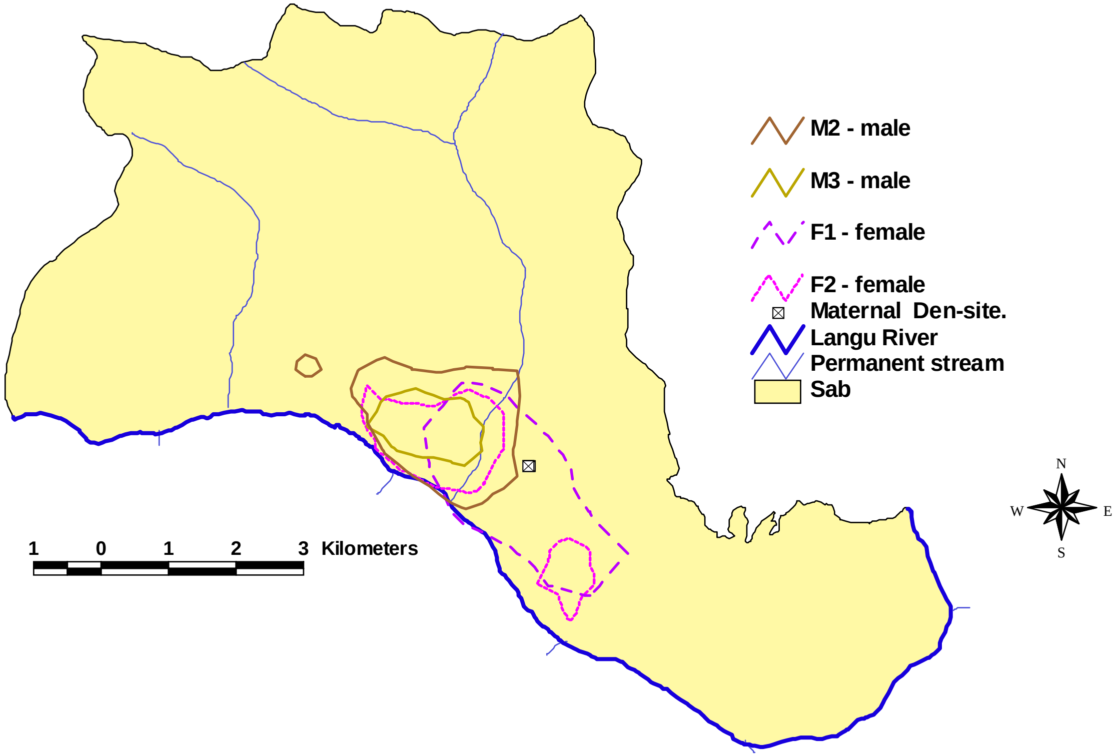


FIGURE 15: Inner Core Area Isopleths (30 percent) for 4 Snow Leopards

Table 17: Spatial distribution in 4 snow leopards based on grid cell method

Cat No	Number of locations	Number of grids used
M2	152	102
M3	53	37
F1	168	101
F2	98	66
Males	205	116
Females	266	139
All cats	471	208

Grid size = 6.25 ha (0.25 X 0.25 km^2)

However, these shifts may have partly resulted from bias introduced by small sample size and use of an algorithm contained in an earlier version of the program used to compute harmonic means (see Chapter 3, Home Range Size and Spatial Utilization).

Table 18: Harmonic activity isopleths for 4 snow leopards

Cat	Activity Isopleths (percent)[a]			Significant Core Area Statistics (see text)				
	95	75	30	Percent of Utilization Volume	No of Locations(USE)[b]	Area km^2	Percent of Total Home Range (HR)	Intensity of Use[c]
	Area (km^2)							
M2	42.86 (2)	21.20 (1)	4.10 (1)	66.8	141 (92.7)	15.25 (1)	31.07	2.98
M3	18.07 (1)	9.32 (1)	1.26 (1)	63.1	44 (84.6)	6.03 (1)	30.23	2.79
F1	65.06 (1)	29.52 (1)	4.34 (2)	66.5	150 (89.3)	20.07 (1)	26.25	3.40
F2	20.59 (1)	13.14 (2)	3.25 (2)	56.1	74 (68.5)	7.74 (2)	36.96	1.85

[a] Figure in brackets indicate number of polygons forming each activity isopleth

[b] Figure in brackets indicates percent of locations within significant core area

[c] Intensity of Use = USE ÷ HR

Adapted from Samuel et al. 1985

Table 19: Thirty percent isopleth core area use patterns for 4 snow leopards

Cat No.	Total Number of Loci [a]	Number of Loci in Core Area	Core Area Size (km^2) [b]	Percent of Home Range Within Core Area (HR) [c]	Percent of Home Range Use within Core Area (USE) [d]	Intensity of Use INTEN [e]
M2	152	83	4.10	8.35	54.6	6.54
M3	52	21	1.26	6.31	40.4	6.40
F1	168	92	4.34	5.68	54.8	9.65
F2	102	48	3.25	15.52	47.1	3.03

[a] Total No of loci = number of loci used to compute home range and core area size
[b] Core area = area enclosed within 30% harmonic measure isopleth for each cat
[c] HR = Percent of home range with core area
[d] USE = Percent of animal locations found within the core area
[e] INTEN = A measure of intensity of use within the core area derived from USE÷HR

Table 20: Use pattern within common overlapping core area

Cat No.	Total Number of Loci [a]	Number of Loci in Core Area	Common Inner Core Area Size (km^2) [b]	Percent of Home Range Within Core Area (HR) [c]	Percent of Home Range Use within Core Area (USE) [d]	Intensity of Use INTEN [e]
M2	152	82	4.61	9.39	53.9	5.74
M3	52	38	4.61	23.12	73.1	3.16
F1	168	73	4.61	6.03	43.4	7.19
F2	102	41	4.61	22.02	40.2	1.83

[a] Total No of loci = number of loci used to compute home range and core area size
[b] Common Inner Core = area enclosed within overlapping 30% harmonic measure isopleths of 4 individuals
[c] HR = Percent of home range with core area
[d] USE = Percent of animal locations found within the core area
[e] INTEN = A measure of intensity of use within the core area derived from USE÷HR

6.3 Discussion

Given a secretive behavior and the difficulty of making observations, it is hardly surprisingly that home range size, land tenure and movements in snow leopard remained essentially unknown until some animals could be radio-tagged (Jackson and Ahlborn 1989). Relying upon ephemeral pugmarks, Schaller (1977) was only able to conclude that the snow leopard's home range size was unknown, but it had to be quite large given the long intervals between visits of animals to a particular valley. This view was also held by Guggisberg (1975) who stated that snow leopards "have vast territories, within which they move about a great deal, covering long distances in the process." Citing Schaposchnikov (1956), Hemmer (1972) concluded: "Obviously, individuals have expanded hunting grounds through which they roam regularly in the course of about one week." Dang (1967) reported that snow leopard had regular beats and ranges, returning regularly to fixed abodes such as sheltered overhangs or caves.

To date, this is the only study that has monitored snow leopards for more than a few months. Sweanor (1990) found that at least 35 locations over a 10-month period were necessary to adequately measure home range size in resident male and female puma. The estimation of snow leopard home range size required a similar effort. My study demonstrates that snow leopards may occupy remarkably small home ranges in areas with a prolific wild prey base. Elsewhere, snow leopard ranges appear of comparable size, although none of the other three studies conducted to date have monitored animals for longer than three months. Chundawat (1990a) radio-tracked a single adult male snow leopard for 70 days during late winter in the Hemis National Park of north-western India, and estimated its home range at about 19 km^2. In Mongolia, Schaller et al. (1994) reported that a radio-tagged male remained within a 12 km^2 area during most of the 41 days it was tracked. In the Annapurna Conservation Area of Nepal Oli (in prep.) found that home range size ranged between 13.9 and 22.3 km^2, and averaged 19.1 km^2, for the three cats (2 ♀♀; 1 ♂) monitored in winter and early spring. However, samples based on short-term monitoring tend to under-estimate total home range size, as indicated by the cumulative area curve shown in Figure 8. At least two of these studies (Oli and Schaller) were conducted in relatively favorable snow leopard habitat, with fairly dense large ungulate populations. Larger home ranges than these are anticipated in snow leopards inhabiting marginal habitat sparse in prey, areas with heavy winter snowfall, or places subject to summer livestock grazing and associated human disturbance.

The snow leopard home ranges were similar in size to those reported for common leopard from different areas of Africa (Bailey 1992; Hamilton 1976; Smith 1978), but smaller than the 40-49 km^2 adult male home ranges reported for African leopards in a mountainous area (Norton and Henley 1987) and larger than common leopard home ranges in Asia (Seidensticker et al. 1990; Eisenberg and Lockhart 1972). Home ranges of male leopards in South Africa varied between 16 and 96 km^2, and were much larger than the female ranges (6 - 30 km^2) (Bailey 1993). By contrast, puma range over an area exceeding 60 km^2 in females to well over 450 km^2 for males (Anderson 1983, Hemker et al. 1984, Hopkins et al. 1986, Maehr et al. 1991; Neal et al. 1987; Seidensticker et al. 1973), with relatively smaller ranges in puma that do not migrate seasonally (Sweanor 1990). Male puma ranges are typically two to three times larger than those of females; both sexes migrate between summer and winter ranges in those areas experiencing deep winter snowfall, such as Idaho (Seidensticker et al. 1973) or Wyoming (Logan et al. 1986).

A quick review of the literature clearly substantiates the wide variability in home range size in a species such as the puma; the same may well apply to snow leopard, which also lives primarily in mountainous habitats. Home range size may vary depending upon the stage of an animal's reproductive life cycle. Thus, the home range of snow leopard F1 increased after her cubs were 8 months age and more mobile, a trend also reported in puma (Sweanor 1990). Bailey (1993) noted that female common leopard ranges changed with their own age and the mobility of their cubs. His study population did not maintain distinct seasonal ranges, although home range size and activity radii changed between seasons, apparently in response to prey population density and availability. Overall, female ranges tend to be more stable than those of males, at least in tiger and puma (Smith 1984; Sunquist 1981; Sweanor 1990). As noted in the discussion section of Chapter 8, male ranges sow varying degrees of temporal change due to the death of a resident male, the arrival of a new male, or the pressure exerted by a more aggressive individual.

Anderson et al. (1992) concluded that puma home ranges were more accurately sampled with the harmonic mean estimator, especially when compared to the minimum convex polygon method. My analyses suggest that estimates based on the harmonic measure resulted in somewhat larger home ranges for snow leopard; presumably, this reflects the linear nature of snow leopard home ranges in the Langu Valley. Here, snow leopards were found to occupy home ranges of 11 - 37 km^2 using the minimum area polygon method or 9 - 29 km^2 using the 75% harmonic mean utilization isopleth. These figures should be taken as approximations only, since they are strongly influenced by factors such as the estimation technique employed, sample size and autocorrelation between locations. Swihart and Swade (1985b) found that positive autocorrelation resulted in the underestimation of home range size. Although I collected only one locational observation every 24 hours for each animal as recommended by these investigators, autocorrelation proved to be a persistent problem, at least statistically. The statistical algorithm employed by Ackerman et al. (1990) detected autocorrelation even when locations were separated by a week or more, apparently reflecting the snow leopard's proclivity for intensively utilizing a small area for a week or more before shifting to another focal place. Harris et al. (1990) concluded that the biological and logistical considerations which result in autocorrelated data do not necessarily bias home range estimates derived using the harmonic mean isopleth method. Since a majority of locations in my study were taken during daylight hours, these home ranges may not adequately portray the area used during hours of darkness. This bias is partly offset by the fact that snow leopards are quite inactive during much of the night, being more active near dawn or dusk, when their locations could be more easily fixed. Snow leopards usually spent more than half of their time in or around their day-time beds.

No indication of distinct seasonal ranges was detected in this snow leopard population (Jackson and Ahlborn 1989). Although little or no monitoring was undertaken between the months of July and November, other factors suggest there is little need for animals to change areas seasonally. Snow accumulation is not a significant constraint, given the predominantly south-facing aspect of the Langu Valley and rain-shadow effect from the adjacent Kanjiroba Range. Seasonal prey movements are limited to a narrow elevational corridor, with no evidence for any long-distance or intra-valley movement. There are no people or livestock to force snow leopards or wild ungulates into higher, more remote regions, which typically occurs when livestock are being grazed on alpine pastures during the summer (Roberts 1977; Mallon 1984). Seasonal elevational movements have been reported in snow leopard populations in Pakistan, India and Krygystan (Roberts 1977; Koshkarev 1989).

No evidence was found to indicate that snow leopards patrolled their home-range boundary (Jackson and Ahlborn 1989). Resident animals visited most portions of their range at intervals of several days to two weeks or more; on rare occasions, they crossed their entire home area within a 24-hour period, while at other times they remained within tracts as small as a 1 km^2 for a week or more. Typically, they resided for several weeks in a general area several kilometers in extent before unpredictably shifting to another part of their range. Although Norton and Henley (1987) found no evidence to suggest common leopard patrolled home range edges, they noted that animals regularly and rapidly crossed their home area. On average, rapid back and forth movement in snow leopard was observed every few weeks. Bailey (1993), Rabinowitz & Nottingham (1986) and Sunquist (1981) reported similar intra-home range movements for leopard, jaguar and tiger respectively.

While the ranges of the four of the snow leopards using the study area overlapped almost entirely (both within and between sex), this population was apparently dominated by relatively young individuals (see Chapter 4). While the area was visited by a fully grown, uncollared male, its pugmarks were infrequently sighted, suggesting that it may have roamed quite widely. In early 1984, two subadult males (M2 and M3), a subadult female (F2) and at least one adult female (F1) shared the central portion of the study area; pugmarks indicated the presence of another female, at least one and probably 2 or 3 uncollared subadults, as well the large adult male. The two young males (M2 and M3) shared a common range for about a year, until M3 evidently left the area. In another radio-tracking study, the home ranges of a single male and two female snow leopards were found to overlap extensively (Oli, in prep.). This investigator found the three leopards shared a common overlapping zone of 8.1 km^2 or nearly 40 percent of the largest home range reported, a similar amount of overlap to that documented in my study population.

An animal's home range has been defined as the area used by the particular individual during its normal activities, including food gathering, mating and the caring for young (Burt 1943). However, resources needed by animals are generally not distributed evenly within the home range. Typically, animals inhabit a heterogenous environment, with certain areas rich in resources, scattered throughout areas poor or much poorer in resources. The harmonic mean values indicated that snow leopard home range use was significantly concentrated into relatively small areas or a core area. Identifying these areas is an important part of better understanding which ecological factors may influence spatial use patterns (Samuel et al. 1985). These investigators (1985:712) observed that "core areas are those areas used more frequently than any other areas and probably contain the homesites, refuges, and most dependable food sources" Kitchener (1991) visualized the home range as an area which "consists of a series of trails which link together hunting areas, drinking places, resting areas, lookout positions, and denning sites where kittens or cubs can be safely reared."

While researchers have shown that felid home ranges may vary greatly in size and shape with respect to time, position, space and the degree of overlap between conspecifics, our understanding of the underlying causal factors is fragmentary. A better appreciation of home range dynamics depends upon an understanding of the spatial characteristics of habitat in the study area, especially with respect to core and non-core use areas (Chapter 7), and the role of social interaction and communication (Chapter 8). Information on the food habitats of snow leopards in the Langu Valley and elsewhere, along with a review of the relevant aspects of the ecology of its principal prey species, blue sheep is presented in Chapter 9. The significance of the spacing and habitat pattern observed in my study is discussed in Chapter 10, along with speculation on how utilization patterns may differ in less heterogeneous environments.

CHAPTER 7 HABITAT USE PATTERNS

Habitat selection and use was examined using the snow leopard locations obtained from the radio-tracking data-set. Habitat characterization was based upon plot sampling (N = 147) of the major landform types found in the study area, and from a random sample of points (N = 1,096) using the Geographic Information System database. This chapter summarizes results of these investigations, and examines utilization patterns by snow leopards in the Langu Valley, especially with respect to core and non-core home range use.

7.1 Habitat Characteristics of the Study Area

7.1.1 Landform or Terrain Types

The most widespread landform types in the study area are smooth-surfaced terrain (39.2%) and cliffs (33.7%) (Figure 2). See Table 3 (Chapter 3) for a description of each landform type. The four major landform types, smooth, moderately broken, heavily broken and cliff, differed with respect to such environmental features as elevation, slope, life-form composition, canopy composition, horizon distance and the density of shrubs or boulders in excess of a meter high (Table 21). Cliffs occurred at lower elevations than the other three landform types, but mean elevation among the landform types varied by 250 m or less (Kruskal-Wallis H = 25.6, df 3, $P < 0.0001$). Habitat sampling indicated that slope steepness was positively correlated with increasing land-surface ruggedness, from an average of 32° for smooth terrain to 62° for cliffs ($r^2 = 0.57$; $P < 0.0001$). Mean slope steepness differed significantly among landform types (Kruskal-Wallis H = 85.7, df 3; $P < 0.0001$), except for cliffs and heavily broken terrain which showed similar slope steepness on average; in general, the latter were 1.5 times as steep as less broken terrain types. Aspect was not found to be correlated with landform type. Heavily broken and cliff areas supported comparable vegetation canopy coverage, while smooth and moderately broken areas had significantly more vegetative cover (Kruskal-Wallis H = 48.9, df 3; $P < 0.0001$). Thus, vegetation canopy cover decreased slightly with increasing terrain brokenness ($r^2 = 0.15$, $P < 0.0001$). Sample plots in the different terrain types differed significantly in terms of the percentage composition of grass and shrub, but not tree composition (Table 21). The proportion of shrub cover was significantly lower for plots

Table 21: Characteristics of landform types in the Langu Valley based on habitat plots

Parameter / statistic	Landform Type				
	Smooth LF = 4	Moderately Broken LF = 2	Heavily Broken LF = 3	Cliff LF = 5	Test Statistic
Elevation (m)					
Sample Size	46	40	27	34	
Mean ± Std. Error	3733 ± 80.4	3500 ± 53.5	3578 ± 64.9	3251 ± 42.1	H = 25.62 ***
Minimum	2990	3050	3010	2995	
Maximum	4625	4560	4285	3980	
Slope Steepness (°)					
Sample Size	46	40	27	33	
Mean ± Std. Error	32 ± 1.2	39 ± 1.2	50 ± 2.2	62 ± 2.3	H = 85.71 ***
Minimum	5	17	25	27	
Maximum	50	62	75	85	
Mean Aspect ± Std. Error (°)	85 ± 37.3	116 ± 45.9	112 ± 47.6	125 ± 37.6	n.s.
Avg Life-Form Composition (percent)					
Sample Size	46	41	29	34	
Grass	33.1	26.8	31.9	35.1	F = 4.89 ***
Shrub	64.2	65.6	61.8	41.5	F = 8.77 ***
Tree	0.4	2.7	2.1	5.1	n.s.
Canopy Cover (%)					
Sample Size	46	41	29	34	
Mean ± Std. Error	26.7 ± 3.2	19.8 ± 2.9	10.2 ± 2.5	4.3 ± 0.7	H = 48.91 ***
Minimum	0	0	0	0	
Maximum	87.5	67.5	67.5	17.5	
Mean Horizon Dist (m)					
Sample Size	46	41	29	34	
Down-slope	101.3 ± 6.5	73.6 ± 6.7	46.7 ± 7.5	98.1 ± 10.2	F = 9.75 ***
Up-slope	71.8 ± 6.6	48.3 ± 5.3	22.1 ± 3.6	20.8 ± 5.8	H = 55.19 ***
Across Slope 1	69.1 ± 6.3	48.8 ± 5.5	25.8 ± 7.3	46.6 ± 9.3	F = 6.13 **
Across Slope 2	61.6 ± 5.6	51.9 ± 6.3	19.4 ± 4.0	47.3 ± 8.9	H = 34.05 ***
Avg (4 directions)	75.9 ± 3.8	55.7 ± 3.5	28.5 ± 3.2	53.2 ± 4.9	H = 49.49 ***
Mean Distance (m) to:					
Nearest Shrub	9.9 ± 0.7	9.5 ± 0.6	10.1 ± 0.6	12.2 ± 0.5	F = 3.41 **
Nearest Rock	13.7 ± 0.3	10.7 ± 0.5	8.5 ± 0.2	11.1 ± 0.9	H = 31.58 ***
Average Height (m) of					
Nearest Shrub	1.5 ± 0.1	1.8 ± 0.2	1.5 ± 0.1	1.34 ± 0.1	n.s.
Nearest Rock	1.7 ± 0.2	1.2 ± 0.1	9.9 ± 3.6	7.0 ± 4.8	H = 14.37 **

Notes:

H = Kruskal-Wallis one-way analysis of variance test value; F = F-ratio ANOVA test value
* = $P \leq 0.05$, ** = $P \leq 0.001$, *** = $P \leq 0.0001$, n.s. = not significant

sampled on cliffs than the other three landform types examined (F-ratio = 8.8, df 3; $P < 0.0001$). Mean percent grass cover ranged between 27 and 35%, with differences too weak for the LSD test to indicate which landform or landforms differed.

Eighty-six percent of areas mapped as a cliff and over half (64%) of the areas mapped as consisting of very broken terrain supported little or no vegetative cover (Appendix A-1, barren vegetation type). Vegetation cover in moderately broken areas is typically dominated by the barren, subalpine shrub and mixed shrubland types, whereas smooth terrain tends to support alpine grassland, barren, subalpine shrub and mixed shrub in decreasing order of occurrence.

Judging by the distance to the nearest rock a meter high or more within each sampled 10 x 10 m square plot, cliff, moderately and heavily broken landforms contained significantly more surface boulders than smooth-surfaced terrain (Kruskal-Wallis H = 31.5, df 3, $P < 0.0001$) (Table 21). Smooth and moderately broken terrain tended to support more dense, tall shrub cover than cliff areas (F-ratio = 3.4, df 3, $P < 0.019$). While the average height of shrubs varied little between landforms, rocks tended to be 4 - 5 times higher in cliff and heavily broken sites than either smooth-surfaced or moderately broken areas (Kruskal-Wallis H = 14.4, df 3, $P < 0.002$).

Horizon distances varied according to both direction of view and type of landform (Table 21). The furthest horizon tended to occur in the downslope direction, with more constrained distances along the upslope and across the slope horizon. One-way analysis of variance indicated significant differences among landform types for each of the four horizons sampled (Downslope F-ratio = 9.7; upslope Kruskal-Wallis H = 55.2; across slope #1 F-ratio = 6.1, $P < 0.0001$; across slope #2 Kruskal-Wallis H = 34.0, $P < 0.0001$; df 3). A multiple means test ($P < 0.05$) indicated smooth-terrain had significantly further downslope horizon distances compared to moderately or heavily broken terrain; generally, mean downslope distances decreased progressively from about 100 m for a cliff or smooth type to 74 m in moderately broken terrain and 47 m in heavily broken areas. Upslope horizons increased from about 20 m in heavily broken or cliff areas to twice as much (48 m) in moderately broken areas and three times as far (72 m) in the plots sampled within smooth terrain areas. A multiple means test indicated significantly greater ($P < 0.05$) mean distances for moderately broken sites compared to heavily broken sites; similarly, upslope horizons were significantly further away in smooth-surfaced sites compared to cliffs or heavily broken areas sampled. Across-slope horizons were significantly greater in moderately broken and smooth areas compared to the more dissected terrain found on cliffs or in heavily broken areas.

Descriptive statistics for elevation, slope, aspect and spatial characteristics of the four major landform types in the study area based on GIS locations are summarized in Appendix A-2. Slopes are under-estimated, in large part because these were derived using a DEM (Digital Terrain Model) based upon a coarse contour interval (500 feet or 152.5 m). Smooth terrain differs from broken or very broken terrain in being less steep, and further from the nearest travel corridor, linear feature, stream or other landform edge. This landform is more closely associated with the upper mountain slopes or wide, U-shaped valleys, such as occur in the upper Tillisha and Mangar basins (Figure 2). The second most-widespread landform type found in the study area are cliffs, distinguished as steep or very steep exposed rock slabs and strata with a slope steepness of at least 50°. As Appendix A-2 indicates, the DEM-derived slopes are under-estimated, with cliffs showing a mean slope steepness of only 44°. Cliffs which are not too steep, offer ledges and which contain vegetative or rocky cover are used as bedding sites and travel lanes by snow leopards, especially those at lower elevation (see Section 7.3 for additional information). Radio-tracking and pugmark sign indicated that leopards also utilized other linear landforms, such as landslides, rockfalls, riverine terraces and river-beds, for travel purposes. These terrain features are characterized by having a more gentle slope, close proximity to permanent watercourses, adjacent landform or vegetation edge, and increased distance from a ridgeline (Appendix A-2).

7.1.2 Vegetation Associations

More than 53 percent of the study area supports the barren vegetative type, where the canopy cover is less than 10 percent (Figure 3). Alpine grassland totals 15.9 percent, while the coverage of alpine shrubland and mixed shrubland is 16.1 and 11.4 percent respectively (Table 4, Chapter 3). Coverage by riparian woodland totals two percent, while there are a number of small, isolated patches of birch (1.2%) and pine (0.2%) forest. Alpine grassland and subalpine shrub are primarily associated with areas of smooth-surfaced terrain, while the barren type mostly occurs on cliffs (Appendix A-3). Bare rock and ground

Table 22: Characteristics of vegetation types in the Langu Valley based on habitat plots

Parameter	Vegetation Type				
	Barren	Mixed Shrub	Subalpine Shrub	Alpine Grassland	Test Statistic
Elevation (m)					
Sample Size	68	57	15	8	
Mean ± S.E.	3351 ± 42.5	3431 ± 31.4	4144 ± 72.9	4458 ± 42.1	H = 56.7 ***
Minimum	2940	2990	3595	4315	
Maximum	4560	3900	4570	4625	
Slope (°)					
Sample Size	66	59	16	8	
Mean ± S.E.	53.6 ± 1.93	37.9 ± 1.56	35.5 ± 2.83	33.1 ± 4.14	F = 18.48 ***
Minimum	0	5	18	17	
Maximum	80	85	55	50	
Mean Aspect (°)					
Sample Size	66	59	16	8	
Aspect ± S.E.	131 ± 43.4	97 ± 40.7	75 ± 56.5	67 ± 17.4	F = 4.79 **
Avg Life-Form Composition (%)					
Sample Size	68	59	16	8	
Grass	38.6	20.3	23.7	83.8	H 25.88 ***
Shrub	43.6	77.2	75.6	16.2	H 49.39 ***
Tree	2.5	2.5	0.6	0	ns
Canopy Cover					
(%) Sample Size	68	59	16	8	
Mean ± S.E.	4.0 ± 0.4	24.5 ± 1.6	26.2 ± 4.9	42.5 ± 8.4	H = 99.62 ***
Minimum	0	2.5	7.5	17.5	
Maximum	17.5	87.5	67.5	87.5	
Horizon Distance					
Sample Size	68	59	16	8	
Down-slope	81.2 ± 6.9	80.2 ± 6.1	90.1 ± 11.6	95.0 ± 16.1	ns
Up-slope	29.3 ± 4.5	52.1 ± 4.9	58.9 ± 10.4	82.3 ± 18.9	F = 7.55 ***
Across Slope 1	43.0 ± 5.9	54.8 ± 5.2	55.7 ± 9.5	67.5 ± 21.2	ns
Across Slope 2	37.7 ± 5.2	55.3 ± 5.1	53.7 ± 9.5	68.6 ± 19.6	F = 2.73 *
Average	47.8 ± 3.6	60.6 ± 3.5	64.6 ± 7.1	78.4 ± 10.7	F = 4.52 **
Distance (m) to:					
Sample Size	68	59	16	8	
Nearest shrub [a]	11.6 ± 0.4	7.9 ± 0.5	11.9 ± 1.0	15.0 ± 0.0	H = 42.96 ***
Nearest rock [b]	10.5 ± 0.6	11.8 ± 0.4	12.0 ± 1.1	11.8 ± 1.1	ns
Avg. Height --					
Nearest Shrub	1.4 ± 0.6	1.4 ± 0.1	1.0 ± 0.2	none present	ns
Nearest Rock	7.9 ± 2.7	2.4 ± 0.4	1.5 ± 0.4	2.5 ± 0.3	ns

Notes:

[a] Distance to nearest shrub at least 1 m in height

[b] Distance to nearest rock or boulder at least 1 m high and 1 m wide or long

H = Kruskal-Wallis one-way analysis of variance test value; F = F-ratio ANOVA test value

* = $P \leq 0.05$, ** = $P \leq 0.001$, *** = $P \leq 0.0001$, ns = not significant predominates at elevations in excess of 4,600 m, where plant growth is greatly impeded by low temperatures, poor soils and a short growing season.

Selected characteristics of the four dominant vegetation types are summarized in Table 22. Mean elevation differed significantly between all vegetation types, except for subalpine shrubland and alpine grassland (Kruskal-Wallis H = 56.7, df 3, $P < 0.0001$). Barren sites tended to be more southerly in their aspect than the other vegetation associations (F-ratio = 4.8, df 3, $P < 0.003$), and contained significantly steeper slopes (F-ratio = 18.5, df 3, $P < 0.0001$). They also supported significantly less vegetation cover than the other types (Kruskal-Wallis H = 99.6, df 3, $P < 0.0001$). In terms of vegetation life-form composition, alpine grassland supported significantly greater amounts of grass cover than the other communities (Kruskal-Wallis H = 25.9, df 3, $P < 0.0001$). Similarly, mixed and subalpine shrub areas contained more shrub cover than the other two communities sampled (Kruskal-Wallis H = 49.4; df 3, $P < 0.0001$).

Mean horizon distances differed between the four vegetation types (F-ratio = 4.5, df 3, $P < 0.005$). Barren areas had significantly lower overall horizon visibilities, presumably attributable to the presence of larger boulders (see below) in sampled plots (Table 22). No differences were detected between vegetation types in downslope visibility or across slopes in the left direction. Upslope horizons differed significantly between vegetation types (F-ratio 7.5, 3 df, $P < 0.0001$) with considerably shorter horizon distances (29 m versus 52-82 m) in barren sites (Table 22). Shrub density, as indicated by the mean distance to the nearest shrub, was greatest in mixed shrubland followed by subalpine shrub and barren sites respectively (Kruskal-Wallis H = 42.9, df 3, $P < 0.0001$). No shrubs were present within plots sampled in alpine grassland. The mean height of shrubs did not differ among vegetation types sampled, and no significant differences in terms of boulder density or height were detected.

Mixed shrub and tree stands tend to occur at lower elevation than the other vegetation cover types (Appendix A-4). Habitat features tend to reflect those of the landforms with which each vegetation cover type is most closely associated. For example, alpine grassland sites are less steep, located relatively far from the nearest vegetation or landform edge, or a travel route and ridge; a similar pattern exists in areas of smooth terrain. The small, mostly linear patch size and shape of vegetation types dominated by trees (birch and pine forest and riparian woodland) is reflected by a relatively close proximity to the nearest other vegetation type (38 m), travel corridor (204 m), or river (182 m), and relative remoteness (318 m) from a ridge compared to other vegetation types.

7.1.3 Size and Configuration of Landform and Vegetation Types

The size and perimeter for habitat polygons found in the study area vary with respect to landform type and vegetation association (Appendix A-5). In general, cliff and smooth landform polygons were larger than those of moderately or very broken terrain areas; if the linearly contiguous areas of stream and riverbed are excluded (with their associated riparian tree cover), stands of birch averaged 11.8 ha, compared to 2.3 ha for the pine forest type. Alpine grassland areas were nearly 3 times as large as mixed shrub or subalpine shrub habitat polygons, indicating they occurred in relatively contiguous stands in less broken terrain at higher elevation. GIS tabulations indicates barren areas are substantially larger than other vegetation associations, but this figure is somewhat misleading for it is based upon a few artificially large computer generated polygons. In reality, barren areas tend to be contiguous, linked together via narrow gaps that would normally constitute an edge for wildlife. Most low or mid-elevation barren sites are heavily dissected or broken by other cover types (Figure 2).

Patton's diversity index offers a measure of ecotonal habitat availability or patch size (Hays et al. 1981; Patton 1975). With this measure, the ratio of edge to area of a plot is compared to that of a circle having the same area. Not surprisingly, linear and cliff terrain types support the most edge, with heavily broken areas containing the least amount (Appendix A-5). Barren and tree cover types supported 3-5 times as much ecotonal edge as mixed shrub, subalpine shrub or alpine grassland.

7.2 Habitat and Spatial Utilization Patterns in Snow Leopards

Descriptive statistics (sample size, mean, minimum and maximum values) of selected environmental parameters at random sites, and male and female snow leopard locations are listed in Appendices A-6 and A-7. Comparisons between random sites (N = 1,096 and snow leopard locations (N = 593) for 21 spatial parameters are listed in Table 23, which

Table 23: Selected habitat and spatial variables at snow leopard and random locations

Habitat Parameter [a]	Random Locations (n = 1,096)		Leopard Locations (n = 593)		Test Statistic[b]
	Mean	Std. Error	Mean	Std. Error	
Elevation (m)	4,177	20.5	3,519	17.8	U = 136106.5 *** χ^2 = 360.90
Slope (degrees)	38	0.4	43	0.5	U = 397521.5 *** χ^2 = 61.66
Aspect (degrees)	157	51.3	165	45.0	U = 368083 *** χ^2 = 20.36
Dist landform edge	69	2.4	40	1.8	U = 248898 *** χ^2 = 63.21
Dist veg edge	83	3.3	47	1.9	U = 252739.5 *** χ^2 = 56.99
Dist nearest LF 2	231	7.7	158	6.3	t = -3.71 ***
Dist nearest LF 3	303	10.4	173	6.8	t = -4.33 ***
Dist nearest LF 4	84	3.6	94	4.1	U = 373006 *** χ^2 = 26.186
Dist nearest LF 5	91	3.8	49	3.2	t = -6.28 ***
Dist Alpine Grassland	442	13.7	893	20.5	U = 490122 *** χ^2 = 298.47
Dist Barren cover	36	2.1	39	2.8	t = 0.90 ns
Dist Mixed Shrub	811	25.8	172	13.4	t = 18.15 ***
Dist Subalpine Shrub	265	8.6	296	11.7	t = 1.16 ns
Dist Tree cover	1,075	27.1	398	17.3	t = 12.52 ***
Dist DNOT4	138	4.8	122	4.5	t = -0.82 ns
Dist DNOT5	139	5.9	89	4.7	t = -5.25 ***
Dist river or stream	828	17.8	598	18.2	U = 253754 *** χ^2 = 55.4
Dist bluff	2,520	47.8	1,025	26.0	U = 132312 *** χ^2 = 405.49
Dist confluence	2,664	46.9	1,841	53.9	U = 203278.5 *** χ^2 = 161.77
Distance any ridge	250	6.1	161	5.9	U = 236402 *** χ^2 = 85.69
Dist major ridge	493	13.8	545	21.5	t = 0.55 ns
Dist minor ridge	855	13.9	713	15.3	t = 5.29 ***
Dist linear landform feature	1,012	23.2	391	14.9	U = 158510 *** χ^2 = 302.7
Dist travel lane	1,031	19.2	708	23.3	U = 214112 *** χ^2 = 134.25

[a] Dist = distance to nearest specified landform or vegetation type. All distances are measured in meters; LF = landform type; DNOT4 = distance nearest landform # 4 when not located in this type; DNOT5 = distance nearest landform # 5 when not located in LF 5;

[b] t = Two-sample t-test value, unequal sample size (pooled variances, df = 591); U = Mann-Whitney U

*** = $P \leq 0.0001$; ns = not significant

Variables transformed to meet homogeneity of variance requirement indicates means differed in all parameters except for distance to the nearest barren landform type, subalpine shrub type and the nearest major ridge-line. In addition, mean distance to the nearest patch of smooth terrain when not in this type did not differ between random and snow leopard sites. The same comparisons for male and female snow leopards are shown in Table 24; no significant difference was detected between males and females for over half of the parameters examined, suggesting a similar habitat pattern in both.

The following paragraphs describe specific habitat preferences and patterns exhibited by the 5 snow leopards I studied.

7.2.1 Landform Features

Elevation: Snow leopard locations were 650 m lower, on average, than the mean elevation for a random sampling of points within the study area, a significant difference (Table 23). Although mean elevation varied by sex (Table 24), the small difference involved (72 m) is not of biological importance; data from male and female snow leopards were therefore combined according to 8 elevational categories. Snow leopards exhibited a significant preference for those areas with an elevation of 4,050 m or less, while significantly under-utilizing areas above 4,200 m in elevation ($\chi^2 = 413.6$, df 7, $P < 0.001$) (Table 25). Approximately 60% of the study area is located above the 4,200 m contour, with less than 25% occurring below an elevation of 3,600 m.

Slope Steepness: Although snow leopards selected sites with a steeper gradient, these differed by only 5° from those available by chance alone. The data also showed that snow leopards avoided gentle slopes, especially those with a gradient of 30° or less. While mean slope steepness differed significantly between sexes, it amounted to less than two degrees (Table 24). Both sexes showed significant under-use or avoidance of less steep slopes ($\leq 40°$) and over-use or preference for slope categories in excess of 40° (Table 26). Female snow leopards sampled showed a stronger preference for slopes in excess of 40° than the males, as well as a more pronounced avoidance for areas with gradients of 20° or less (females $\chi^2 = 73.9$, df 4, $P < 0.001$; males $\chi^2 = 35.7$, df 4, $P < 0.001$).

Aspect: Although the mean aspect of snow leopard and random sites was significantly different, this amounted to only 8 degrees (Table 23). Snow leopards of both sex

Table 24: Habitat and distance preferences shown by 3 male and 2 female snow leopards

Habitat Parameter [a]	Male Locations (n = 265)		Female Locations (n = 328)		Test Statistic[b]
	Mean	Std. Error	Mean	Std. Error	t-value
Elevation (m)	3479.1	26.1	3551.6	24.3	2.03 *
Slope (degrees)	42.1	0.8	44.1	0.6	2.09 *
Aspect (degrees)	155.4	3.5	158.2	3.2	ns
Dist nearest landform edge	38.3	2.6	40.9	2.5	ns
Dist nearest vegetation edge [c]	45.4	2.6	48.1	2.7	ns
Dist nearest LF 2	153.9	8.9	161.9	8.8	ns
Dist nearest LF 3	183.2	9.9	164.9	9.3	ns
Dist nearest LF 4 [c]	87.3	6.3	100.3	5.4	2.49 *
Dist nearest LF 5 [c]	58.2	5.1	41.8	3.9	2.17 *
Dist nearest Alpine Grassland	865.8	30.2	915.9	27.9	ns
Dist nearest Barren cover type [c]	46.2	4.4	33.4	3.6	2.57 **
Dist nearest Mixed Shrub	131.8	15.7	203.8	20.5	2.52 *
Dist nearest Subalpine Shrub	320.6	17.9	276.5	27.9	ns
Dist nearest Tree cover type [c]	292.9	10.0	483.3	26.7	3.13 **
Dist DNOT4	118.1	7.3	124.6	5.7	ns
Dist DNOT5 [c]	99.6	7.1	80.2	6.3	ns
Dist nearest river or stream [c]	536.3	23.2	647.5	26.9	2.65 **
Dist nearest bluff	1031.3	38.3	1020.1	35.5	ns
Dist nearest confluence [c]	1492.8	48.6	2122.5	86.1	4.51 ***
Distance nearest ridge (any)	162.7	8.8	159.9	8.0	ns
Dist nearest major ridge [c]	443.1	27.7	627.8	31.1	2.85 **
Dist nearest minor ridge [c]	700.9	22.6	722.9	20.9	ns
Dist nearest linear landform feature [c]	360.6	18.9	415.9	22.3	ns
Dist nearest travel lane [c]	590.4	29.3	802.7	34.1	3.74 ***

a Dist = distance to nearest specified landform or vegetation type. All distances are measured in meters; LF = landform type; DNOT4 = distance nearest landform # 4 when not located in this type; DNOT5 = distance nearest landform # 5 when not located in LF 5;

b Two-sample t-test value, unequal sample size (pooled variances, df = 591)
* = P ≤ 0.05, ** = P ≤ 0.001, *** = P ≤ 0.0001, ns = not significant

[c] Variable transformed to meet homogeneity of variance requirement

Table 25: Observed and expected use of elevational categories by 5 snow leopards

Class Code	Elevation (meters)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
1	<=3300	0.123	194	72.9	0.327	+0.454	SD +
2	>3300 - 3450	0.053	98	31.6	0.165	+0.512	SD +
3	>3450 - 3600	0.051	60	30.5	0.101	+0.326	SD +
4	>3600 - 3750	0.065	65	38.4	0.110	+0.257	SD +
5	>3750 - 3900	0.051	51	29.9	0.086	+0.260	SD +
6	>3900 - 4050	0.061	57	36.2	0.096	+0.223	SD +
7	>4050 - 4200	0.051	25	30.5	0.042	-0.100	NS
8	>4200	0.544	43	322.8	0.073	-0.765	SD -

All Cats (593 locations): χ^2 = 657.14; df=7, P < 0.0001

1) Availability based on 1,049 random locations.
2) SD indicates that observed utilization (Pi) of the category is significantly (P < 0.05) greater ("+" indicates preference) or less ("-" indicates avoidance) than expected by chance and NA indicates no difference. Significance value indicated above.
3) Index of electivity (Ivlev 1961) = (obs - exp)/(obs + exp), values range from -1 to +1.

significantly under-utilized areas with a northerly and easterly aspect (i.e., slopes facing northwest through north and northeast), while over-utilizing sites with a southerly aspect (χ^2 = 83.2, df 3, P < 0.001) (Table 27). The index of electivity suggests that strong avoidance of north-facing areas (i.e., those with an aspect between 315° and 45°, and constituting approximately 12% of the study area), with greater than expected use of south-facing slopes (≥ 135° and < 225°) which constitute nearly half of the study area.

Table 26: Observed and expected use of slope categories by 5 snow leopards

Class Code	Slope Steepness (degrees)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
MALE CATS							
0	<20	0.091	17	24.2	0.064	-0.174	NS
1	20 to <30	0.131	16	34.8	0.060	-0.370	SD -
2	30 to <40	0.298	58	79.1	0.219	-0.154	SD -
3	40 to <50	0.535	17	83.2	0.442	+0.169	SD +
4	>50	0.293	57	43.8	0.215	+0.131	NS
FEMALE CATS							
0	<20	0.091	8	29.9	0.024	-0.578	SD -
1	20 to <30	0.131	20	43.1	0.081	-0.366	SD -
2	30 to <40	0.298	76	97.9	0.232	-0.126	SD -
3	40 to <50	0.314	126	102.9	0.384	+0.101	SD +
4	>50	0.165	98	54.2	0.299	+0.288	SD +

Males (locations=265): χ^2 = 35.67, df = 4, P < 0.001; Females (locations=328): χ^2 = 73.956, df = 4, P < 0.001; Both sexes: χ^2 = 99.25, df = 4, P < 0.0001

1) Availability based on 1,096 random locations.
2) SD indicates that observed utilization (Pi) of the category is significantly (P < 0.05) greater ("+" indicates preference) or less ("-" indicates avoidance) than expected by chance and NA indicates no difference. Significance value indicated above.
3) Index of electivity (Ivlev 1961) = (obs - exp)/(obs + exp), values range from -1 to +1.

Landform Type: Male and females significantly over-utilized cliffs (LF 5) and linear landforms (LF 20), while under-utilizing smooth or evenly-surfaced terrain (LF 4) (χ^2 = 82.9, df 4, P < 0.0001) (Table 28). Moderately and heavily broken areas are used in approximate proportion to their availability within the study area. Indices of electivity indicated strong preference for bedding in linear landforms while smooth terrain was avoided. Use levels increased progressively with increased terrain brokenness from smooth, open terrain to through moderately broken areas (LF 2) to cliffs (LF 5) and linear landforms (LF 20), with reduced use in areas of very broken terrain, as exemplified by

Table 27: Observed and expected use of aspect by 5 snow leopards

Class Code	Aspect (degrees)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
N	≥ 315° to < 45°	0.119	16	70.3	0.027	-0.629	SD -
E	≥ 45° to < 135°	0.180	64	106.6	0.108	-0.250	SD -
S	≥ 135° to < 225°	0.422	321	249.9	0.541	+0.124	SD +
W	≥ 225° to < 315°	0.280	192	166.1	0.324	+0.072	NS

All Cats (locations = 593): $\chi^2 = 83.215$; df = 3, $P < 0.0001$

Table 28: Observed and expected use of landform categories for 5 snow leopards

Landform Category	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
Moderately broken (LF 2)	0.128	89	75.7	0.150	+0.080	NS
Very Broken (LF 3)	0.117	73	69.2	0.123	+0.026	NS
Smooth (LF 4)	0.392	133	232.6	0.224	-0.273	SD -
Cliff (LF 5)	0.337	267	199.6	0.450	+0.144	SD +
Linear (LF 20)	0.026	31	15.7	0.052	+0.328	SD +

All Cats (593 locations): $\chi^2 = 82.86$; df=4 $P < 0.0001$

- See Table 26 for explanation of availability, statistical significance and index of electivity

landform type 3 (a category of landform which is heavily dissected in all three dimensions). The data, therefore, seem to reflect the snow leopard's predilection for bedding in steep, broken places and along linear landforms.

Adjacent Landform Type: The Langu snow leopards tended to select sites where the closest landform type consisted of a landslide, rockfall, river bluff or terrace and river bed (LF 20) more frequently than expected by chance (χ^2 = 71.8, df 4, P < 0.0001) (Table 29). This category of grouped landforms tends to be linear rather than areal or zonal in nature, and appears to be used by snow leopard as a "travel lane", especially within the core use area (see later). The significant under-utilization of cliffs as the nearest landform type probably reflects the likelihood that leopards are already using such areas within the immediate vicinity.

Distance to Nearest and Other Landform Edges: On average, snow leopards were significantly closer (40 m) to a landform edge than by chance alone, with the average distance to edges in the study areas being 69 m (Table 23). Leopards of both sexes over-utilized areas immediately close to the nearest landform edge, while under-utilizing sites more than 75 m away (χ^2 = 99.5, df 5, P < 0.001). The avoidance of sites 150 m or more from an edge is especially marked, as indicated by a high index of electivity value (Table 30). Leopards were respectively 32, 43, 46 and 61 percent closer to moderately broken terrain, very broken terrain, a cliff and a linear landform than on the basis of availability alone (Table 23).

Males and female snow leopards did not differ in terms of mean distance to the nearest moderately broken, very broken, and linear landform feature (Table 24). Mean distances to the nearest cliff and smooth terrain differed significantly between males and females, but this involved a small difference (cliff = 19 m; smooth terrain = 13 m) and one unlikely to be important from the viewpoint of either habitat selection or intraspecific competition.

Use-availability analysis indicated that snow leopards were located within 50 m of moderately broken terrain significantly more than expected by chance alone, while significantly under-utilizing sites more than 125 m away (χ^2 = 40.9, df 5, P < 0.0001). Similar patterns were detected with respect to cliffs (χ^2 = 70.4, df 5, P < 0.0001) and very broken terrain (χ^2 = 38.4, df 5, P < 0.0001), further evidence that snow leopards show strong preferences for being near a landform edge. While males showed no particular spatial preference with respect to smooth terrain, females significantly under-utilized sites within a distance of 50 m, while over-utilizing sites located at distances of 75 - 100 m ($\chi^2 = 53.2$, df 5, $P < 0.0001$). This suggests that female snow leopards are seeking daytime bedding sites located a greater distance from open, smooth-sloped areas than are males.

Distance to nearest Cliff when not located on this landform type (Variable DNOT5): The mean distance to the nearest cliff is 89 m for snow leopards and 139 m for random sites, a difference of 50 m (Table 23). No difference in male and female proximity to a cliff was detected when animals were not utilizing this landform type (Table 24). However, snow leopards tended to occur within 50-75 m of a cliff significantly more than expected by chance alone (Table 31), while under-utilizing areas more than 125 m away ($\chi^2 = 48.8$, df 5, $P < 0.001$), suggesting that they are located closer to a cliff than by chance alone, even when not using this landform feature.

Distance to nearest Smooth Terrain when not located on this landform type (Variable DNOT4): No differences in use of the same six distance categories were detected with respect to proximity to smooth terrain ($\chi^2 = 10.1$, df 5, $P < 0.07$); when not located in this type, no significant differences were detected between random and occupied sites (Table 23). Furthermore, mean distance to smooth terrain when bedded in another landform type was similar between male and female leopards (Table 24).

Distance to Moderately (DNOT2) and Heavily Broken Terrain (DNOT3) when not located in these types: Snow leopards of both sex significantly over-utilized areas within 50 m of moderately broken terrain, while under-utilizing sites more than 150 m away ($\chi^2 = 40.9$, df 5, $P < 0.0001$) (Table 32). A similar spatial use pattern exists in relation to areas of very broken terrain ($\chi^2 = 38.4$, df 5, $P < 0.0001$), suggesting that the study animals preferred to bed close to these types, even when not utilizing them.

Distance to the nearest Linear Feature (LF type 20) when not located in this type (DNOTLIN): Snow leopards of both sex were located significantly closer to a linear landform feature than by chance alone (Table 23). Chi-square use-availability analysis indicated that most sites within 125 m of a linear terrain type were significantly over-utilized, while sites further away were significantly under-utilized (χ^2 = 176.2, df 5, $P < 0.0001$) (Table 33).

Other Spatial Patterns: There is evidence to suggest that snow leopards frequently use ridges and stream or river-beds to move about their home ranges. For example, they were likely to be located on or near a ridge, with the mean distance to the nearest ridgeline being 161 m compared to 250 m for random points (Table 23). Furthermore, 58% and 60% of male and female relocations, respectively, were found to be located within 100 m of a major or well-defined ridge-line; use-availability analysis indicated significantly greater use than expected of sites within 50 or 75 m of a ridge-line, while sites located further than 150 m away were significantly under-utilized (χ^2 = 123.7, df 5, $P < 0.0001$) (Table 34). Sites within distances 75 to less than 150 m were used in proportion to their availability. On average, male snow leopards were located significantly closer (443 versus 628 m) to a major ridgeline than females (Table 24).

GIS was used to identify potential snow leopard travel routes within the study area, since the literature confirms the preference of snow leopards for moving along sharp ridge-lines, cliffs, river-beds and along other natural landform edges (Fox 1989; Heptner and Sludskii 1992; Koshkarev 1984; Schaller 1977). These were defined by establishing a 200 m wide buffer centered along the crest of a major or minor ridgeline, and a river or stream-bed (Figure 16). Male snow leopards tended to be some 200 m closer to a potential travel lane than the females, a significant difference (Table 24). The mean distance to a travel lane in the study area is slightly over a kilometer (Table 23). Although males were also closer (361 m) to a linear landform feature (landfalls and stream-beds, but not ridgelines) than females (416 m), this difference was not significant. Nearly 42 percent of male locations and 38 percent of female locations were situated within a potential travel lane.

Males and females differed significantly in terms of mean distance to the nearest stream and river confluence: males were over 600 m closer than the females sampled (Table 24). In addition, sites closer than 2 km to a river or major stream confluence were significantly more heavily utilized than expected by chance alone, while sites further than 2.5 km from a confluence were significantly under-utilized (χ^2 = 319.3, df 5, $P < 0.001$) (Table 35).

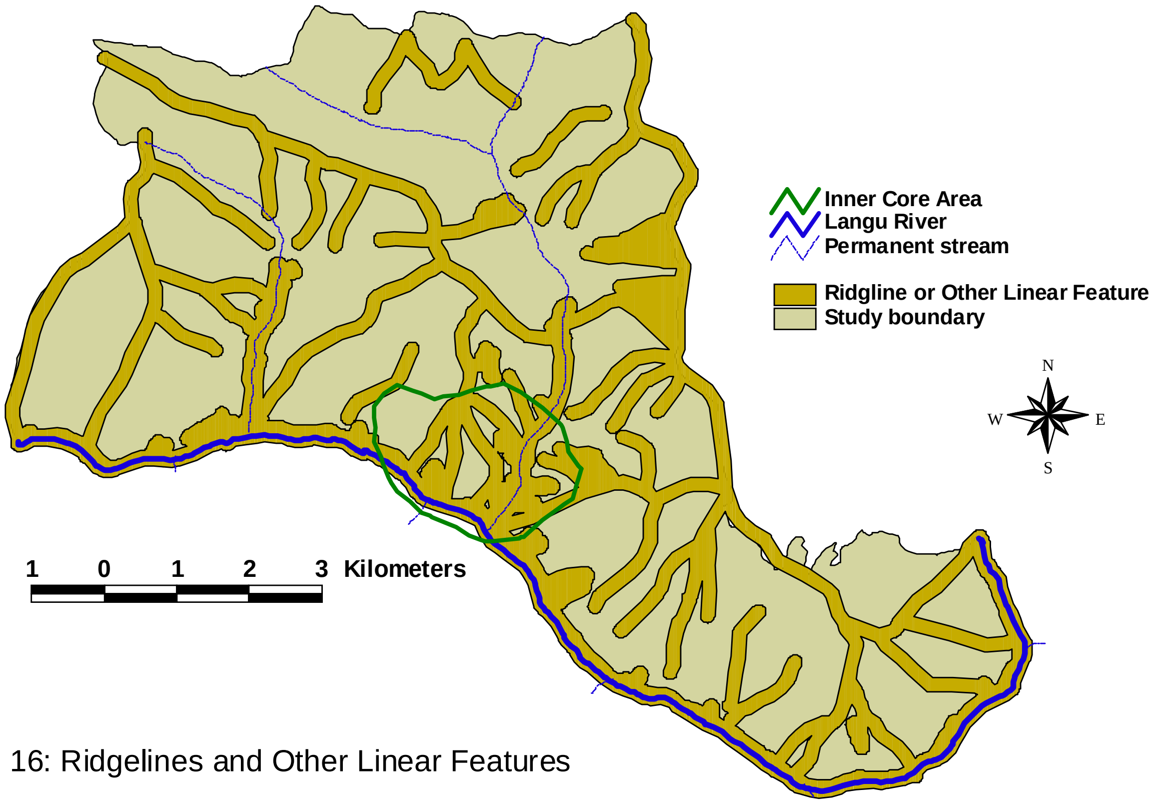


Figure 16: Ridgelines and Other Linear Features

Table 29: Observed and expected use of nearest landform type for 5 snow leopards

Landform Category	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
Moderately Broken (LF 2)	0.209	127	123.9	0.214	+0.012	NS
Very Broken (LF 3)	0.179	111	106.0	0.187	+0.023	NS
Smooth (LF 4)	0.222	134	131.5	0.226	+0.010	NS
Cliff (LF 5)	0.345	154	204.5	0.260	-0.141	SD -
Linear (LF 20)	0.046	67	27.0	0.113	+0.425	SD +

All Cats (593 locations): $\chi^2 = 71.823$; df = 4, $P < 0.0001$

- See Table 26 for explanation of availability, statistical significance and index of electivity

Table 30: Observed and expected use of distance to nearest landform edge for 5 snow leopards

Class Code	Dist. nearest landform edge (meters)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
1 & 2	≤ 50	0.564	438	334.4	0.739	+0.134	SD +
3	> 50 to ≤ 75	0.149	86	88.2	0.145	-0.013	NS
4	> 75 to ≤ 100	0.081	32	48.1	0.054	-0.202	SD -
5	> 100 to ≤ 125	0.048	15	28.7	0.025	-0.313	SD -
6	> 125 to ≤ 150	0.029	7	17.3	0.012	-0.424	SD -
7 - 16	> 150	0.129	15	76.3	0.025	-0.671	SD -

All Cats (593 locations): $\chi^2 = 99.493$; df = 5, $P < 0.0001$

- See Table 26 for explanation of availability, statistical significance and index of electivity

Table 31: Observed and expected distance to the nearest cliff when a snow leopard is not located on a cliff

Class Code	Distance to nearest Cliff (meters)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
1	≤ 25	0.167	68	54.3	0.209	+0.112	NS
2	> 25 to ≤ 50	0.157	62	51.2	0.190	+0.096	NS
3	> 50 to ≤ 75	0.110	54	35.9	0.166	+0.201	SD +
4	> 75 to ≤ 100	0.091	41	29.6	0.126	+0.161	NS
5	> 100 to ≤ 125	0.062	27	20.2	0.083	+0.144	NS
6 - 16	> 125	0.413	74	134.7	0.227	-0.291	SD -

Both sexes: $\chi^2 = 48.82$; df = 5, $P < 0.0001$

- Number cat locations = 326; random points = 726; see Table 26 for explanation of statistical significance and index of electivity

Table 32: Observed and expected distances to the nearest moderately broken terrain type (2) landform when a snow leopard is not located within this landform type

Class Code	Distance to nearest Type 2 (meters)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
1 & 2	≤ 50	0.145	109	73.3	0.216	+0.196	SD +
3	> 50 to ≤ 75	0.086	45	43.2	0.089	+0.020	NS
4	> 75 to ≤ 100	0.065	27	32.7	0.054	-0.095	NS
5	> 100 to ≤ 125	0.059	46	29.5	0.091	+0.218	NS
6	> 125 to ≤ 150	0.046	31	23.2	0.062	+0.144	NS
7 - 16	> 150	0.599	246	302.1	0.488	-0.102	SD -

Both sexes: $\chi^2 = 40.94$; df = 5, $P < 0.0001$

- Cat locations = 504; random locations = 956; See Table 26 for explanation of availability, statistical significance and index of electivity

Table 33: Observed and expected distances to the nearest linear landform (20) type when a snow leopard is not located within the same type

Class Code	Dist nearest Linear Landform (meters)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
1 & 2	≤ 50	0.032	52	17.9	0.093	+0.488	SD +
3	> 50 to ≤ 75	0.018	25	10.0	0.044	+0.428	SD +
4	> 75 to ≤ 100	0.020	22	11.1	0.039	+0.331	NS
5	> 100 to ≤ 125	0.015	25	8.4	0.044	+0.496	SD +
6	> 125 to ≤ 150	0.014	23	7.9	0.041	+0.489	SD +
7 - 16	> 150	0.902	415	506.7	0.738	-0.099	SD -

Both sexes: $\chi^2 = 176.22$; df = 5, $P < 0.0001$

- Cat locations = 562; Random locations = 1,067; See Table 26 for explanation of availability, statistical significance and index of electivity

7.2.2 Vegetation Associations

Vegetation Types: Snow leopards utilized mixed shrubland and tree cover types in excess of their availability, while significantly under-utilizing the alpine grassland and barren cover types ($\chi^2 = 229.7$, df 4, $P < 0.001$) (Table 36). Subalpine shrubland is used in approximate proportion to its availability. Preferences shown for mixed shrubland and a vegetation association dominated by trees are more pronounced, while alpine grassland is avoided for daytime bedding. Typically, the tree cover types found within the snow leopard home ranges are extremely small, and are presumably used primarily for daytime bedding. F1's selection of a cliff with a small birch forest for her maternal den also influences the strong electivity index for this vegetation cover type.

Table 34: Observed and expected use of distance to the nearest ridge for 5 snow leopards.

Code	Distance Interval to nearest ridge (meters)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
1/2	≤ 50	0.140	157	82.8	0.265	+0.310	SD +
3	> 50 to ≤ 75	0.057	56	34.1	0.094	+0.243	SD +
4	> 75 to ≤ 100	0.076	55	44.9	0.093	+0.101	NS
5	> 100 to ≤ 125	0.056	46	33.0	0.078	+0.164	NS
6	> 125 to ≤ 150	0.072	30	42.7	0.051	-0.175	NS
7 - 16	> 150	0.599	249	355.5	0.420	-0.176	SD -

All Cats (593 locations): $\chi^2 = 123.70$; df = 5, $P < 0.0001$

- See Table 26 for explanation of availability, statistical significance and index of electivity

Table 35: Observed and expected use of distance to the nearest river or stream confluence for 5 snow leopards.

Class Code	Distance to stream confluence (meters)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
1	< 500	0.021	46	12.4	0.078	+0.574	SD +
2	≥ 500 to < 1,000	0.070	93	41.7	0.157	+0.381	SD +
3	≥ 1,000 to < 1,500	0.142	142	84.4	0.239	+0.254	SD +
4	≥ 1,500 to < 2,000	0.146	127	86.6	0.214	+0.189	SD +
5	≥ 2,000 to < 2,500	0.170	84	100.6	0.142	-0.090	NS
6	≥ 2,500 to < 3,000	0.158	27	93.6	0.046	-0.552	SD -
7	≥ 3,000 to < 3,500	0.081	20	48.1	0.034	-0.413	SD -
8 +	≥ 3,500	0.212	54	125.5	0.091	-0.398	SD -

All Cats (593 locations): $\chi^2 = 319.29$; df = 7, $P < 0.0001$

- See Table 26 for explanation of availability, statistical significance and index of electivity

Table 36: Observed and expected use of vegetation types by 5 snow leopards

Class Code	Vegetation Type	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
AG	Alpine grassland	0.159	21	94.1	0.035	-0.635	SD -
BA	Barren	0.533	270	315.9	0.455	-0.078	SD -
MS	Mixed Shrubland	0.114	170	67.6	0.287	+0.431	SD +
SA	Subalpine Shrubland	0.161	97	95.2	0.164	+0.009	NS
TREE	Tree types	0.034	35	20.0	0.059	+0.272	SD +

All Cats (593 locations): $\chi^2 = 229.71$; df = 4, $P < 0.0001$

- See Table 26 for explanation of availability, statistical significance and index of electivity

Nearest Vegetation Type: Snow leopard locations were significantly closer to mixed shrubland and tree cover types than random sampling points (Table 23). The mean distance to all vegetation associations except for alpine grassland and subalpine shrub differed with respect to sex (Table 24). On average, females were 33 m from a barren area compared to 46 m for male snow leopards, but this may not be biologically meaningful. Spatial differences between sexes were greater in the case of mixed shrub vegetation, with males being located 80 m closer than females. Males were significantly closer on average (293 m) to a tree cover type than female snow leopards (483 m), although use of this type did not differ between the sexes.

Snow leopards preferred to use sites in which the nearest vegetation types are barren and mixed shrubland, while apparently avoiding areas closest to alpine grassland and subalpine shrub vegetation ($\chi^2 = 308.2$, df 4, $P < 0.001$) (Table 37).

Distance to Nearest Vegetation Edge: On average, random sites were 83 m from the nearest vegetation edge, compared top 47 m for the snow leopard locations, a significant difference (Table 23). No significant difference was detected between sex in terms of distance to the nearest vegetation edge (Table 24). However, sites closer than 50 m to a vegetation edge was used significantly more than on the basis of availability, while sites 100 m or further from an edge were significantly under-utilized ($\chi^2 = 140.8$, df 5, $P < 0.0001$) (Table 38). Thus, both male and female snow leopards were more likely to be located within 50 m of an edge than at a distance of 125 m or more. Electivity index values indicate strong levels of avoidance for all sites which are this distance or further from a vegetation cover edge, a pattern most evident in the two females sampled.

7.3 Comparison of Habitat Characteristics and Utilization between the Core and Non-Core Use Areas

The harmonic mean distributions strongly supported the contention that monitored snow leopards had preferred use areas within their respective home range, to which they returned frequently. These areas overlapped geographically to a large degree. The question then arises whether the core area offers higher quality habitat for snow leopard than the non-core area, or conversely, whether snow leopard core use is determined more by social factors, such as intraspecific marking and communication. Associated questions are whether the snow leopard's habitat use pattern differs between core and non-core areas, and if so, which habitat attributes or features could be most effectively used to predict core from non-core sites in the Langu Valley as well as other areas inhabited by this species? These questions are explored in the following sections.

7.3.1 Habitat Similarities and Differences

Core and non-core areas differ with respect to habitat condition. The average elevation, slope, aspect and the mean distance to selected landform types, habitat features and vegetation associations for random sites located in either the core or non-core portions of snow leopard home range areas are listed in Appendix A-8 (Parts 1 and 2). Based upon habitat preferences shown by snow leopards, these data suggest that the core area offers potentially more suitable habitat than that present within the non-core area. For example, random sites within the core are closer to the nearest landform or vegetation edge, significantly closer to linear landform features (262 m compared to 1,063 m), potential travel routes (388 versus 1,076 m), moderately broken areas (150 versus 237 m), very broken areas (191 versus 311 m), ridges (140 versus 258 m), a stream or river (460 versus 854 m), mixed shrubland (94 versus 862 m), and a tree vegetation type (204 versus 1,137 m). Conversely, core sites are located significantly further from subalpine shrubland (337 versus 260 m) and alpine grassland (860 versus 413 m). Mean elevations in the core area (3,147 m) are significantly lower than random sites sampled in the non-core areas (4,230 m). No differences were detected between core and non-core areas with respect to slope steepness and aspect, or the distance to the nearest cliff, major ridgeline or smooth terrain.

Widely applied landscape ecology indices suggest that core areas support higher relative richness, diversity and fragmentation of habitat, compared to the non-core area, with respect to both terrain and vegetation types (Appendix A-9). There is also greater diversity with respect to the number of landform and vegetation types within a three by three neighbourhood of cells 200 meters square in size (NDC index), as well as greater contrast between types (CVN index). The study area's complex juxtaposition and rich diversity of different terrain and vegetation types (Figures 2 and 3) is largely attributable to the high amount of edge and relatively small habitat patch size, as noted earlier (Appendix A-5). In terms of ecological scale, the study area is probably best described as being of the

Table 37: Observed and expected use of the nearest vegetation type by 5 snow leopards

Code	Nearest Vegetation Type	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
AG	Alpine grassland	0.191	16	113.1	0.027	-0.752	SD -
BA	Barren	0.351	244	208.3	0.411	+0.079	SD +
MS	Mixed Shrubland	0.152	217	90.4	0.366	+0.412	SD +
SA	Subalpine Shrubland	0.261	79	154.7	0.133	-0.324	SD -
TREE	Tree types	0.045	37	26.5	0.062	+0.165	NS

All Cats (593 locations): $\chi^2 = 308.19$; df = 4, $P < 0.0001$

- See Table 26 for explanation of availability, statistical significance and index of electivity

Table 38: Observed and expected use of distance to nearest vegetation edge for 5 snow leopards.

Class Code	Distance to vegetation edge (meters)	Expected proportion of usage	Observed usage	Expected usage	Observed proportion of usage (Pi)	Index of Electivity	Significance
1 & 2	≤ 50	0.497	429	294.9	0.723	0.185	SD +
3	>50 to ≤75	0.149	69	88.2	0.116	-0.122	NS
4	>75 to ≤ 100	0.106	52	62.8	0.088	-0.094	NS
5	>100 to ≤ 125	0.038	12	39.5	0.020	-0.534	SD -
6	>125 to ≤ 150	0.026	7	23.8	0.012	-0.546	SD -
7 - 16	>150	0.066	24	83.9	0.040	-0.555	SD -

All Cats (593 locations): $\chi^2 = 140.77$; df = 5, $P < 0.001$

- See Table 26 for explanation of availability, statistical significance and index of electivity

undivided heterogeneous type (Addicott et al. 1987). Note, however, that landscape indices may differ by 10% or less between each type of area, thus indicating that the study area as a whole has a high degree of terrain and vegetation diversity and juxtaposition.

7.3.2 Snow Leopard Utilization of Core and Non-Core Areas

A comparison of snow leopard bedding sites with respect to spatial measures for core and non-core locations indicates some significant differences in the utilization pattern which appears to reflect differences in availability between the two parts of the snow leopards home ranges (Table 39-a and 39-b). Core bedding sites were up to 250 m further from alpine grassland and subalpine shrubland, and a similar distance closer to linear features, mixed shrubland, and tree cover types (Table 39-a). Other differences were detected, but these generally involved distances of 30-50 m or less, which are unlikely to be biologically important.

Snow leopards tend to select bedding sites in areas with greater richness of landform and vegetation types, and sites that are more diverse and fragmented than those available by chance within the study area (Table 40). However, actual differences in mean values between snow leopard locations and random sites are relatively small, presumably supporting the contention that the Langu Valley offers prime habitat for snow leopard.

7.4 Habitat Classification Using Discriminate Function Analysis

Discriminant function analysis (DFA) was used to determine which habitat parameters could best be used to classify radio-located snow leopard sites into one of two groups, core or non-core locations. Discriminant analysis identified 9 factors from among the various habitat parameters investigated as the most effective predictors (significant at $P < 0.05$) of core/non-core area membership (Table 41). These were reduced to a model with 5 factors which most accurately and efficiently classified snow leopard sites according to core or non-core areas (Table 42). This model had a Wilk's Lambda of 0.459, with the variables elevation, distance to ridge and potential travel route, and the distance to smooth terrain contributing most significantly to site discrimination. Using a random subsample of 110 snow leopard locations (20% of the all locations), this model correctly classified 83% and 95% of core and non-core sites respectively (Table 43). These variables could easily be

Table 39-a: Comparison of selected habitat features for snow leopard core and non-core home range locations

Habitat Parameter [a]	Core Locations (n = 287)		Non-core Locations (n = 306)		Test Statistic [b]	
	Mean	Std. Error	Mean	Std. Error	t-value	U and χ^2
Landform:						
Dist to landform edge [c]	37.2	2.1	42.2	2.8	0.99 ns	
Dist to moderately broken terrain (LF-2) [c]	139.2	8.7	176.2	8.9	-2.95 **	
Dist to very broken terrain (LF-3)	166.7	8.4	179.1	10.5		U = 42710 ns χ^2 = 0.33
Dist to smooth terrain (LF-4) [c]	127.3	6.6	63.8	4.2	5.71 ***	
Dist to cliff (LF-5)	45.4	4.6	52.7	4.4	-1.16 ns	
Dist to linear feature	200.9	10.9	566.9	23.0		U = 70028.0 *** χ^2 = 156.93
Dist to DNOT2	167.2	9.5	203.5	9.2	-2.73 **	
Dist to DNOT3	185.4	8.6	209.2	11.3	0.50 ns	
Dist to DNOT4 [c]	152.8	6.9	88.3	4.9	6.11 ***	
Dist to DNOT5	90.4	7.4	88.7	6.1	-0.18 ns	
Dist to DNOTLIN	215.1	11.2	590.1	23.0		U = 64328.0 *** χ^2 = 168.15
Vegetation:						
Dist to vegetation edge	44.0	2.7	49.3	2.6	1.41 ns	
Dist to Barren type	40.5	4.2	37.9	3.8	0.46 ns	
Dist to Mixed Shrub	44.9	4.3	290.4	23.8		U = 63093.5 *** χ^2 = 86.69
Dist to Subalpine Shrub	402.4	16.9	196.2	12.9		U = 24794.0 *** χ^2 = 84.44
Dist to Alpine Grassland	1003.3	21.9	790.6	32.9		U = 32602.0 *** χ^2 = 29.42
Dist to Tree type	195.9	8.1	587.9	28.6		U = 68291.0 *** χ^2 = 136.76
Dist to DNOTBA	75.9	6.6	68.2	5.9	0.87 ns	
Dist to DNOTMS	70.2	5.9	371.8	28.3		U = 35026.0 *** χ^2 = 109.40
Dist to DNOTSA	435.9	16.8	260.4	14.8		U = 18887.0 *** χ^2 = 54.18
Dist to DNOTAG	1003.3	21.9	848.8	32.8		U = 32602.0 *** χ^2 = 17.62
Dist to DNOTREE	217.1	7.9	601.7	28.9		U = 59821.0 *** χ^2 = 123.42

Table 39-b: Comparison of selected habitat features for snow leopard core and non-core home range locations (continued)

Habitat Parameter [a]	Core Locations (n = 287)		Non-core Locations (n = 306)		Test Statistic [b]	
	Mean	Std. Error	Mean	Std. Error	t-value	U and χ^2
Elevation (m) (ELEV) [c]	3310.6	18.1	3714.8	25.5		U = 67118.0 *** χ^2 = 125.47
Slope (degrees) (SLOP)	43.8	0.7	42.6	0.7	1.23 ns	
Aspect (degrees) (ASP)	160.4	50.8	154.2	51.1		U = 45586.0 ns χ^2 = 0.64
Dist to ridge (RIDIS) [c]	118.9	6.1	200.8	9.4	5.57 ***	
Dist to major ridge (RMAJDIS) [c]	312.4	16.4	763.6	34.4	8.78 ***	
Dist to minor ridge (RMINDIS) [c]	604.9	18.1	814.5	22.9	5.84 ***	
Dist to linear landform feature (LINDIS)	202.6	10.8	568.1	22.9		70376.0 *** χ^2 = 161.11
Dist to travel lane (TDIS) [c]	328.2	12.9	1063.8	33.3	22.76 ***	
Dist to bluff (BLUFDIS) [c]	938.7	26.1	1106.1	43.6	1.41 ns	
Distance to river or stream (RIVDIS)	379.9	15.3	802.3	27.6	11.26 ***	
Dist to confluence (CONDIS) [c]	1977.3	80.8	1713.3	71.1	-2.88 **	

[a] Dist = distance to nearest specified feature in meters. DNOT = distance to specified type when located within the same type

[b] Two sample t-test value, unequal sample size; Mann-Whitney U statistic and χ^2 approximation

* = $P \leq 0.05$, ** = $P \leq 0.001$, *** = $P \leq 0.0001$, ns = not significant

[c] Variable transformed to meet homogeneity of variance requirement

Table 40: Landscape ecology indices for snow leopard and random locations

Landscape Index [a]	Snow Leopard Locations (n = 593)		Random Locations (n = 1096)		Test statistic [b]	
	Landform	Veg	Landform	Veg	Landform	Vegetation
Relative Richness Index	0.59	0.57	0.50	0.50	-11.43 ***	-8.34 ***
Diversity Index	0.63	0.55	0.53	0.48	-11.32 ***	-8.36 ***
Dominance Index	0.36	0.35	0.40	0.37	U = 300460 *	-1.49 ns
Fragmentation Index	0.52	0.46	0.42	0.39	-11.05 ***	U = 389488.5 ***
NDC Index	0.51	0.57	0.44	0.50	-10.07 ***	-8.33 ***
CVN Index	0.65	0.54	0.56	0.49	U = 391847.5 ***	U = 369701.0 ***
BCM Index	0.75	0.66	0.65	0.59	U = 424287.0 ***	U = 397516.5 ***

[a] All indices are standardized according to the scale 0 (low) to 1.0 (high). See Appendix A-9 for formulae

[b] Two-sample t-test value, unequal sample size (pooled variances, df = 1094); Mann-Whitney U statistic provided when variables remain non-normally distributed after transformation

$^{*} = P \leq 0.05$, $^{**} = P \leq 0.01$, $^{***} = P \leq 0.0001$, ns = not significant

applied to other areas within snow leopard range in an effort to identify potential core zones for other populations. This model violates the assumption of multicollinearity, as indicated by the fact that the travel lane variable coefficient value exceeds 0.7, indicating autocorrelation with one or more of the other model variables. In this case, it is probably correlated with the variable "distance to the nearest ridge", a component of travel lanes along with stream and riverbeds, riverine bluffs, and other linear landscape features. The ridge variable is retained in the model because the limits (width) of a travel lane may be difficult to apply consistently between different observers. Capen et al. (1986)

Table 41: Habitat site factors that best discriminate between core and non-core areas of snow leopards in the Langu Valley

Habitat Variable	Coefficient	F Value	Significance
Elevation	-59.426	6.316	0.012
Distance nearest river or stream	6.478	6.035	0.014
Distance to nearest ridge	-6.705	36.277	0.0001
Distance to nearest potential travel lane	-31.832	356.975	0.0001
Distance nearest confluence	0.002	5.688	0.017
Distance nearest moderately broken terrain	-0.022	5.963	0.015
Distance nearest subalpine shrub	1.794	4.956	0.026
Distance nearest alpine grassland	4.421	13.245	0.0001
Distance nearest tree vegetation type	-5.913	33.752	0.0001
$R^2 = 0.598$			

demonstrated the best approach is to validate models with independent data which vary in time, space and along habitat dimensions. A final word of caution: discriminant function analysis is better used for exploration than as an inferential tool (Williams 1983). Williams et al. (1990) reported strong bias in classification rates when group sample sizes were small and overlap among groups was high. For this reason, I ensured that the total number of samples per group was at least twice the number of variables measured.

Table 42: Discriminate function model for classifying between core and non-core areas

Habitat Site Factor	Function 1	Function 2	Pooled within-group correlation	F value	Significance
Elevation	761.268	752.412	0.496	139.064	0.0001
Distance to ridge	17.262	16.561	0.202	23.043	0.0001
Distance to Travel Lane	0.545	-2.115	0.834	393.627	0.0001
Distance to major confluence	14.802	15.286	-0.085	4.091	0.044
Distance to smooth terrain	6.314	6.399	-0.216	26.390	0.0001

Wilk's Lambda = 0.459; F-statistic = 112.24; df 5,477; Probability = 0.0001

Table 43: Number of resting sites classified as core and non-core habitat for snow leopard using discriminant function analysis

	Predicted Group		Total
Actual Group	Core	Non-Core	
Core	50 (83.3)	10 (16.7)	60
Non-Core	3 (6.0)	47 (94.0)	50

Note: Figures in parenthesis indicate percent sites which classified correctly and incorrectly

7.5 Discussion

I examined daytime habitat use as opposed to that used across the full 24-hour period (Beyer and Haufler 1994). Emphasis is thus on day beds and loafing sites, rather than habitat directly associated with hunting or travelling, although snow leopards may rest close to hunting areas or the travel lanes used to move between different parts of their home range. Different utilization and preference patterns may be associated with other behavioural activities. To this end, Harris et al. (1990) recommended that active fixes only be used to analyze an animal's movement pattern or habitat utilization when foraging. Interestingly, most snow leopard kills were associated with smooth-surfaced terrain and alpine grassland or subalpine shrub -- sites shown as being significantly under-utilized for daytime bedding. Radio-tagged snow leopards showed a strong preference for bedding on cliffs or in steep broken and rocky terrain, often close to ridgelines, stream-beds and other linear features used for travelling about their home areas. A third or more of all daytime locations were situated within a potential travel lane, and monitored snow leopards showed a strong preference for being close to a landform or vegetation edge. Maehr and Cox (1995) reported that 96% of Florida panther locations (N = 14,548) they tallied over a 5-year period were located within 90 m of a preferred cover type. Movement is often easier along the crest of a ridge than the base of a cliff and along the edge between shrubland and grassland. In the study area, ridges provided the primary means for moving rapidly through terrain heavily dissected by cliffs, gorges and ravines. Since there was no elevational difference in bedding sites between the seasons studied, it is unlikely that habitat use varies seasonally, at least for this snow leopard population.

The preference for steep-sloped, rocky areas for bedding is similar to that reported for bobcats studied by Anderson (1990), who used discriminant function analysis to correctly classify 88% of day-time sites into loafing and random sites. What benefits might accrue to those snow leopards which regularly utilize steeply broken terrain or cliffs for diurnal loafing? The snow leopard's protective coloration makes it extremely difficult to distinguish when standing motionless against a rocky background; such well-developed camouflage must increase the cats' stalking ability, while escaping the attention of humans who might otherwise kill it. Although definitive data are lacking, mortality due to poaching and human retribution probably far exceeds that of other natural or unnatural causes of death. Given the potential for serious injury in the event of physical encounters between two males, for example, it would be advantageous for individuals to have early warning of the approach of others. Cliffs may be selected for the excellent visibility they provide in at least one direction.

McCord (1974) considered that rocky areas provided important physical and physiological cover for bobcats, and this may hold for snow leopard as well. He also speculated that cliffs were important areas for reproductive and other social interaction. While F1 selected a cliff for her natal den-site, little information has been published on the reproductive habitat requirements of snow leopard, except that dens appear to be located in rocky areas (Heptner and Sludskii 1992, Guggisberg 1975). Maehr et al. (1990) considered day beds and den sites as important habitat features in the management of the Florida panther (*Puma concolor coryi*). Natal dens were maintained for about 60 days while kittens were incapable of independent travel. No information is available for how long snow leopard cubs are kept in their birth den before being shifted to a new site, but it is likely to be at least two weeks. Females need an area with abundant supply of prey that is also secure from human intrusion if they are to successfully raise their offspring. This situation is more likely to occur in places where broken and smooth-surfaced landforms are well interspersed. By contrast, heavily broken areas tend to be prey-poor, while expansive open areas are lacking in nearby escape cover for ungulates (see discussion section of Chapter 9 for more information).

Many of the mountain ranges within the snow leopard's range are not lacking in terms of cliff or broken terrain, so that its availability per se may not be the most significant factor in snow leopard distribution and survival. However, the juxtaposition of such habitats with alpine bowls, plateaus and less broken areas may be critical, for the latter provide foraging habitat for large ungulates, whose density may be directly related to habitat quality (Wegge 1976, Schaller 1977). Without rocky and broken cover, snow leopards (particularly females with small cubs) would be far more vulnerable to predation from both humans and wolves, the latter being primarily associated with rolling plains and uplands (i.e., smooth terrain landforms). Large parts of the Tibetan Plateau, including the Changtang region to the northwest, are mostly unsuitable for snow leopard due to a low blue sheep population, in part the result of high baseline elevation and associated low plant productivity (Schaller pers. comm.).

The few studies of habitat use and preference undertaken to date in other parts of snow leopard range seem to confirm my findings. Chundawat (1990a) found that the radio-tagged male he monitored during late winter used aspect in proportion to its availability, with 37 percent of locations having a northerly aspect, compared to 2.7 percent in my study. This individual also showed a very strong preference for using broken terrain with slopes in excess of 40°. Chundawat considered the top of a cliff or ridge as the ideal snow leopard resting site, especially if it gave the cat a good view of the valley or the mountain slopes opposite. More than 32 and 57 percent of locations were within 20 m of broken and very broken terrain respectively, with only 10 percent being located more than 100 m from a broken area. Working in the same area, but using sign as an indicator of habitat use, Fox et al. (1988) found greater utilization of westerly slopes and an avoidance of sites with an easterly aspect. Fifty percent of all track sites were located within 5 m of a sharp break in the terrain, such as a cliff or riverine terrace bluff. This substantiates my finding that snow leopard use terrain edges as orienting features for travelling about their home range.

The overlapping core area used by snow leopard in the Langu Valley contained habitat features that conformed more closely with those "preferred" by snow leopard, compared to the non-core area (Table 23 and Appendix A-8). Randomly-sampled sites within the core area were significantly closer to an edge, ridge, potential travel lane, linear feature and moderately broken terrain than other sites sampled within the home ranges. From a landscape ecology viewpoint, core areas were richer, more diverse and fragmented than non-core areas. The core area abutted a large patch of subalpine shrub and alpine grassland which contained the densest blue sheep numbers in the area (Figure 20, Chapter 9). Herds of more than 20 animals were not uncommon, and one herd of 85 individuals was recorded. Herd size in other parts of Nepal averages less than 10-12 individuals (Schaller 1973; Wegge 1977; Wilson 1984). As noted several times before, it is apparent that the Langu Valley constitutes prime habitat for snow leopard, given the favourable interspersion of cliffs with smooth and less broken terrain, the abundance of large prey, the complete absence of livestock and a low level of human disturbance.

Resource selection occurs in a hierarchical fashion from the geographic range of a species, to individual ranges within a geographic range, to use of general features or habitats within the home range, to the selection of a particular element (e.g., food) within the general features (e.g., feeding site). Criteria for selection may thus vary between levels (Johnson

1980), so that study design and sampling protocol must be carefully evaluated and examined for potential sources of bias. Habitat selection may occur among discrete categories (such as landform terrain types) or across a continuum of attributes, such as vegetation cover and density, elevation, slope and aspect, and the distance to selected habitat features, such as vegetation or landform edges, ridgelines and other topographic features, and proximity to escape cover. Many factors, such as population density, intra- and interspecific competition, prey availability and foraging conditions, natural selection, heredity and predation, contribute to resource selection (Peek 1986). Many theories and models have been proposed to help explain resource selection, including optimal foraging theory and habitat selection models.

A review of my data indicates several potentially important sources of bias. Firstly, the snow leopard locations were found to be time dependent (see Chapter 6), and habitat assessment was subject to potential bias resulting from pseudo-replication. My study design followed the second category (Design II) specified by Manley et al. (1993). With this design, individuals are identified and the use of resources is measured for each study animal, but resource availability is measured at the population level. Thus, variation between observations in one animal assumes greater precedence over variation between individuals, so inferences are model-based rather than designed-based (Manley et al. 1993). Secondly, the assumption that all snow leopards had unrestricted access to the full range and distribution of resource units sampled may not necessarily have been valid. For example, social avoidance and marking priorities could have modified movement and thus visitation rates to selected resource sites, irrespective of the other functions these sites may have provided. This could especially have been the case in individuals whose residency status had not been firmly established at the time of study (Bailey 1993). Manley et. al. (1993:67) note that "changes in the density of animals or in the availability of resource units may change the underlying selection strategies and the selection indices". Therefore, statistical inferences noted in this study are only made with respect to the specific conditions present in the study area over the time of interest. Finally, it is important to recognize that the reasons why a particular resource is selected or avoided is not directly revealed by the estimation of the amount of use or avoidance: controlled experimentation is the only means for establishing whether a particular food or habitat type is unattractive or simply rarely used.

Spatial differences between cat and random locations, or between core and non-core locations, may not necessarily infer biological importance, despite means which differ statistically. Geographic information systems and computers offer a precision that can be both misleading and illusionary. For example, the mean distance to an area with broken or very broken terrain differed by less than 37 m for the core and non-core area; from the viewpoint of the snow leopard, the additional energy expended in travelling this distance is very likely to be negligible. Furthermore, combining individuals due to small sample size may have obscured individual differences in the proportion of land-cover types (Maehr and Cox 1995).

Another and related problem area concerns potential sources of error and bias. For example, error may result from inaccurate habitat or landform mapping, generalized geographical projection, and from imprecise animal locations due to signal deflection or human reading error (White and Garrott 1990). As noted in the methods section on habitat utilization (Chapter 3), I chose to lump individuals wherever possible due to a small sample size. Use-availability analyses are closely dependent upon how one defines what is deemed as being available to the study population. I introduced some bias by considering all habitat located within the study area (see Figures 2 and 3) as being available to each of the 5 snow leopards studied, rather than basing this analysis upon that available within each individual home range: sample size precluded this except possibly for M2 and F4. Thus, small sample size precluded comparisons between individuals, while it was necessary to lump several habitat types into a single category for chi-square analysis (Byers et al. 1984; Neu et al. 1974). The pooling of data (Schooley 1994) may have obscured differences between individuals or sexes, although the animals studied utilized the same area over each of the two or three years monitored. Shifts might have occurred during the summer months, which are under-represented in my data-set. For example, one would expect snow leopards to make greater use of the higher elevation areas during summer months, and most high elevation habitat was located outside the home ranges described in Chapter 6. However, incidental observations indicated little evidence for a noticeable seasonal elevational shift in the Langu Valley's blue sheep population, probably because habitat loss due to winter snow accumulation was limited by the steep, southwesterly facing topography of the study area. Similarly, blue sheep were not subject to disturbance by humans or their livestock, and could thus remain in the more productive low or medium elevation areas.

Porter and Church (1987) investigated the effects of environmental pattern upon habitat preference analysis and concluded significant effect due to landscapes with aggregated patterns (i.e., areas where habitat types and boundaries tend to occur in relatively large and contiguous strips or patches). Significantly less error was detected using regularly distributed or small habitat patches, with cell size being the critical component. Precise locations are especially important when habitats have a patchy distribution in relation to locational error (Nams 1989). Samuel and Kenow (1992) recommended subsampling a minimum of 50 random points from the error distribution of each animal's location to reduce variability associated with habitat misclassification. However, this is impractical unless one has a large data-set and access to sophisticated computer programming capabilities. White and Garrott (1986) demonstrated that the power of the Chi-square goodness-of-fit test to detect habitat selectivity decreased with increased habitat complexity (i.e. heterogeneity of habitat), reduced precision of triangulation bearing and lowered sampling effort. Since the power of the Chi-square test can be improved by increasing the number of locations, data from all individual snow leopards were lumped, whenever justified. However, this obscures any difference between individuals or sex. In addition, error polygons for most snow leopard locations were delineated in the field, concurrent with bearing measurement. Location sites (and consequently their topographic configuration) were almost always visible, so that more realistic geographically delimited signal polygon error boundaries could be drawn, and the geographical center taken as the animal's most likely location.

A potentially more important factor involves the graininess of the habitat and landscape components examined (Schulz and Joyce 1992), particularly in light of the close association between snow leopard locations and distance to the nearest edge. Thus, more than 74 percent of daytime locations were located within 50 m of a landform edge, and a similar proportion (72%) were within the same distance of a vegetation edge -- indicating a high potential for habitat misclassification resulting from imprecision associated with fixing locations of the study animals. A sensitivity analysis indicated that misclassification error due to graininess increased substantially at cell sizes of 100 m or more (Figure 17). Thus, locational classification errors are about 6 percent for a grain cell size of 15 m x 15 m, increasing to 18 and 20 percent for cell sizes of 75-100 m on a side. Additional graininess dramatically increases the error rate, until it is 38 percent (vegetation) and 46 percent (landform) for a 250 m x 250 m cell size. Recommendations for grain size relative to the home range size of three target species (spotted owl, *Strix occidentalis*; marten *Martes americana*; and Douglas squirrel, *Tamiasciurus douglasi*) range from 1 - 25% (Laymon and Barrett 1986, Laymon and Reid 1986), but few spatial evaluations of the effect of grain size on habitat have been undertaken (Schulz and Joyce 1992). In my study the smallest habitat polygon mapped was 3.2 ha. The snow leopard radio-location error polygons averaged 6.17 ± 0.264 SE (N = 582) hectares in size, a value within the one percent limit (25 ha) recommended for the spotted owl, a species with a smaller home range and differing foraging or ecological requirements than the snow leopard.

Nams (1989) reported on the effects of radiotelemetry error on sample size, bias and distortion when testing for habitat selection, noting that when telemetry error exceeded 1.5 times average habitat size, the required sample size increased immensely. He (1989:1633) wrote, "Furthermore, if different habitat types have different sizes, or if habitats are not distributed randomly, then the bias is not the same for each habitat. Therefore, if efficiency is low, one cannot test for selection of individual habitats, or compare various habitats, unless the bias is removed." In my study, vegetation polygons averaged 31.8 ha (minimum = 0.61; maximum = 1,858.7; N = 220) in size, while landform types averaged areas of 19.4 ha (minimum = 0.15; maximum = 703.4; N = 360). Thus, landform and vegetation polygons were, on average, 3 to 5 as large as radio-location error polygons -- beyond the critical value Nams found to adversely bias chi-square test efficiency. However, while he noted that habitat dispersion had generally little effect on the Chi-square test efficiency, he concluded that special problems arose whenever animals used edges like snow leopards. Nams offered two solutions to this problem: (1) either remove all records whose error ellipse encompasses more than one habitat type; or (2) use a special habitat designation for any location within a certain distance from a habitat boundary. Neither solution is practical nor appropriate to the objectives of my study, since field observations consistently confirmed the snow leopard to be an "edge species". Given the extremely fragmented nature of both landform and vegetation in the study area, such classification error should have been reasonably random across the entire data-set.

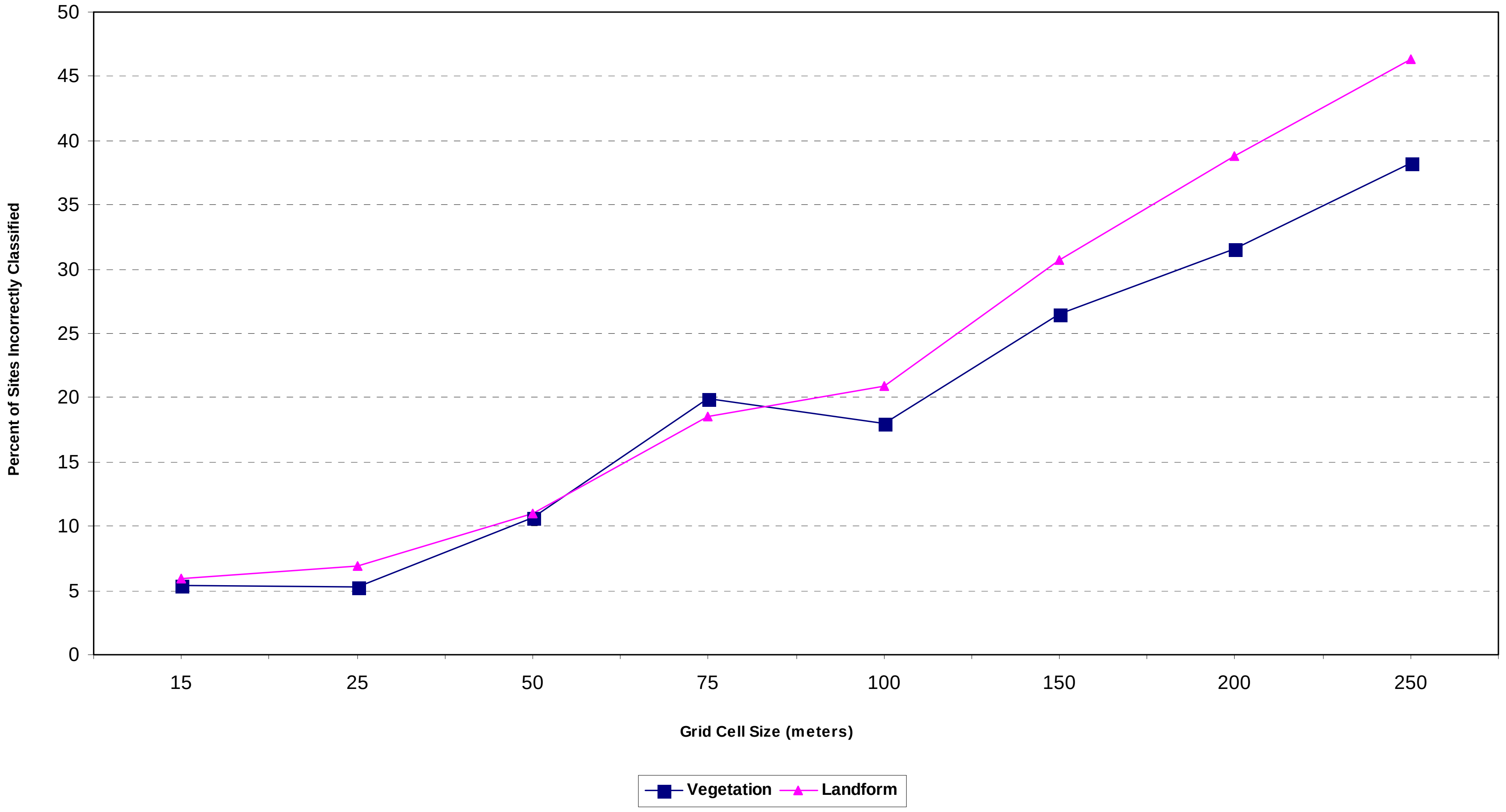
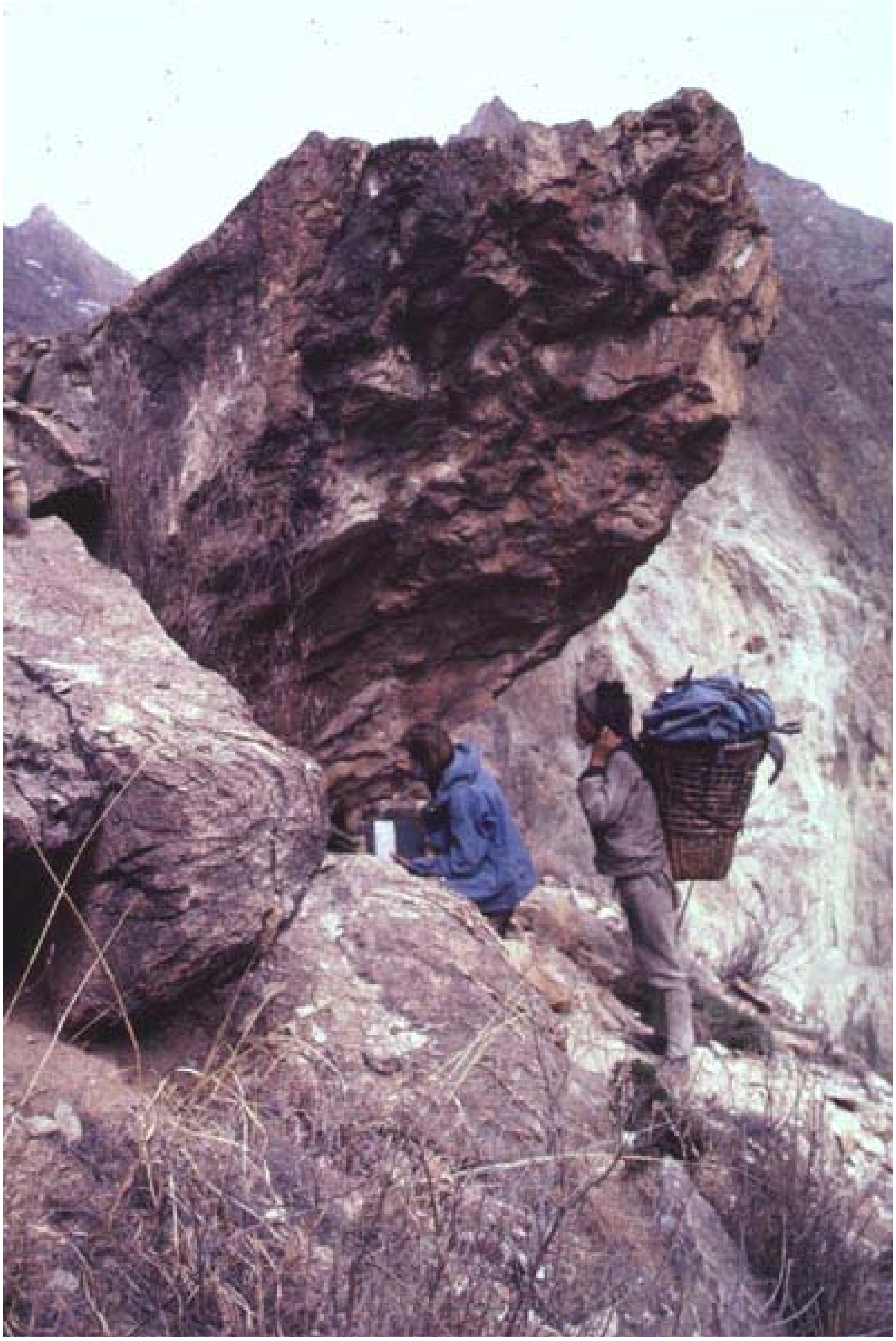


Figure 17: Effect of grain cell size on accuracy of habitat classification



Checking a frequently visited rock-scent along a permanent sign transect

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CHAPTER 8 SOCIAL INTERACTION PATTERNS AND COMMUNICATION

8.1 Sociality and Land Tenure Pattern

Although the radio-tagged snow leopards utilized a common space, they were separated temporally, thus confirming the species' essentially solitary social structure. Linear distances between snow leopards on the same day averaged between 1.9 and 3.2 km (Table 44), with a majority of snow leopard locations being within 2 km of another individual (Figure 18). No significant difference was detected in distance between the same or different sex (Kruskal-Wallis = 203.00; df 198; P > 0.389). Male to male distances are based largely on data gathered prior to the capture of F1 and F2; female to male distances primarily represent (a) interactions between M2 and F1 after the mating season, while F1 was pregnant or raising cubs, and (b) interactions between M2 and F2, during the period that F2 achieved her independence, but prior to her reaching adulthood. Only a few same-day records of M3 were tallied before I lost radio-contact with him. The female to female records represent the first 14 or so months of F2's independence and a period during which F1 was raising her cubs (i.e., less than one month of age, and then ages 5.5 - 12 months). The slightly larger distances between males and females compared to male to male or female to female may therefore reflect the maternal status of F1; like other solitary felids she might have been intentionally avoiding close contact with male snow leopards. In addition, males M2 and M3 could have been siblings and may therefore have been highly tolerant of one another.

The only association observed between the radio-tagged cats involved F1 and her presumed daughter F2: they travelled together for four days, starting on 14 May 1984. I have no evidence to indicate that they were travelling together when I first captured F1 45 days earlier. During their 4-day association, they travelled about 3.5 km (straight-line distance only), resting within 200 m of one another during the daytime. I did not record them together for the remainder of the study, with the closest location between this pair being about 300 m. Thus, if related F2 became fully independent in late May 1984, at an age of about 22 months. A month later her presumed mother (F1) gave birth.

Table 44: Linear distance between locations of radio-tagged snow leopards on the same day

Cat Number	Sample Size	Mean Distance ± Standard Error (kilometers)	Minimum Distance (km)	Maximum Distance (km)
M2 : M3	45	1.93 ± 0.18	0.31	5.51
M2/M3 : F1/F2	55	3.16 ± 0.29	0.31	7.03
F1 : F2	109	2.18 ± 0.17	0.02	7.88

Sample Size = number of times individuals were located on the same day

The only prolonged social contact in snow leopard is that of a female and her dependant offspring. We observed no known socialization at a kill, but cannot exclude this possibility. Neither were instances of siblings associating or of mating pairs recorded, although this undoubtedly occurs. Of 20 sightings, 18 involved solitary individuals, one a female with 12-month old cubs (F1) and one of a female accompanied by a large juvenile.

While no evidence was found to substantiate territoriality in snow leopard, home range tenure appeared to be in a state of flux through at least part of the study period, as noted earlier. Some evidence was found to suggest that fully grown males tend toward home range exclusivity with regard to other adult males presumed to be of breeding age.

Little is known about the age at independence: F2 was judged to be about 22 months of age when she left her presumed mother. M2 and M3 were already independent at first capture, and their age was judged at about 2.5 years.

8.2 Marking Behaviour: a summary

Since little was known about the marking patterns of wild snow leopards (Schaller 1977, Mallon 1984), we designed a study to: (1) Define the basic marking pattern shown by snow leopard; (2) Determine the extent to which snow leopard select specific locations and habitat

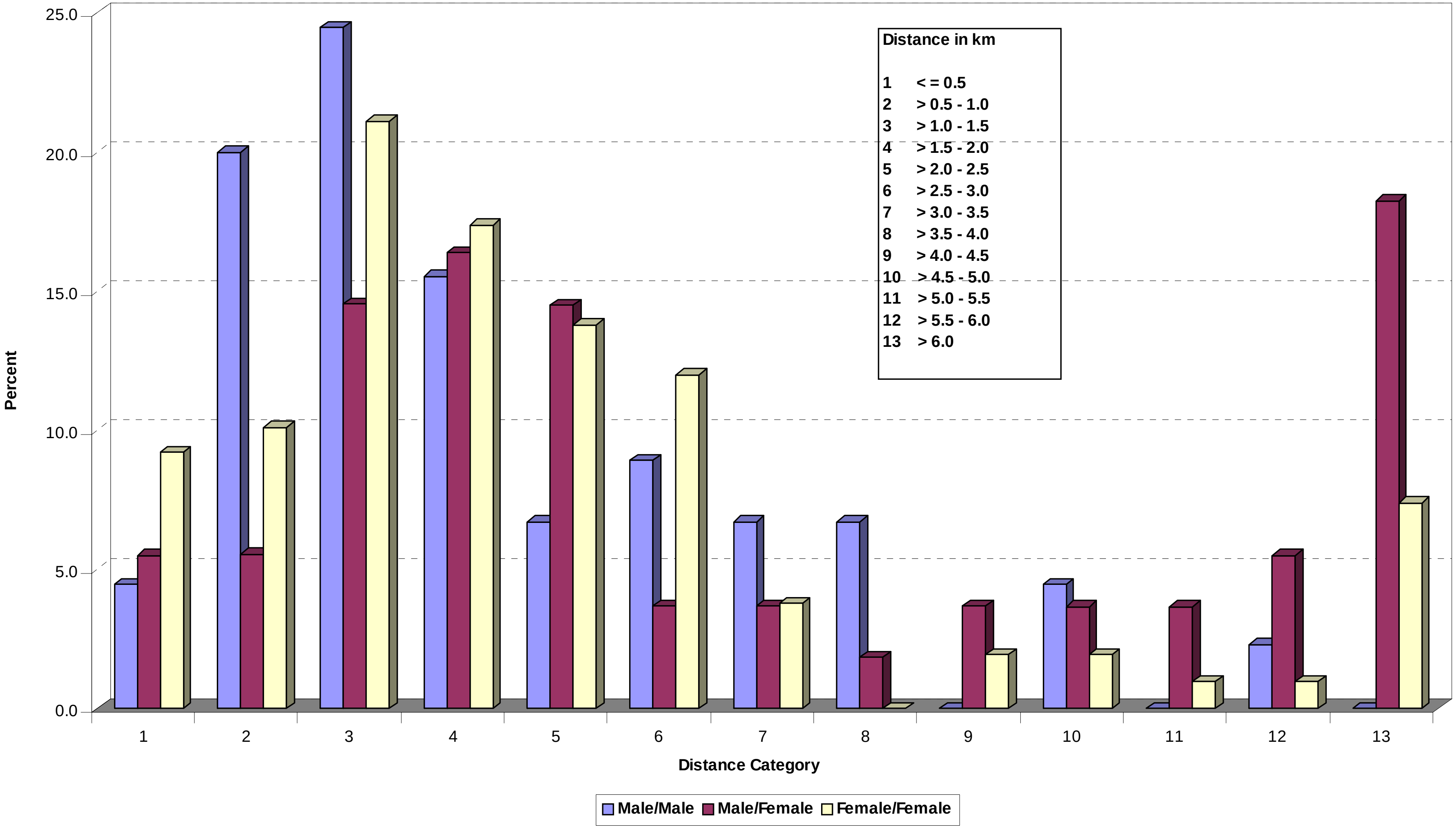

Figure 18: Frequency distribution of linear distances between male and female snow leopards on the same day

features to mark at; (3) Determine if marking occurs at a constant frequency with respect to time; and (4) Examine the degree to which individuals mark in response to each other. Results of the marking studies have been reported by Ahlborn and Jackson (1988), and are summarized in the following paragraphs.

Snow leopard markings consisted of scrapes, feces, urine and/or anal scent (often deposited on or adjacent to scrapes), scent-sprayed rock-faces, and claw-raked tree trunks. Snow leopard scrapes averaged 24.5 ± 0.28 cm (Std. Error) in length (range 13-38; N = 524) and 20.42 ± 0.22 cm in width (range 9-38). No differences in size were found for scrapes made in sand, gravel, rocky soils, snow, or those occasionally made entirely within vegetation, in this case primarily grass (ANOVA, $P > 0.05$).

Eighty-eight sprayed sites were found in the study area; of a sample comprising 78, the maximum number of spray-marks found at one site was 7, but most sites (81%) had only 1 or 2 scent-spray marks present. Boulders or rock outcrops comprised nearly 86 percent of the feature marked, with the base of a cliff face the remaining 14 percent. Approximately 40 percent of sites occurred along riverbeds or riverine terraces. Solitary (46%) or grouped (54%) scrape sites were found at 73 percent of the scented rocks characterized. Snow leopard hair was found on 41 of 130 (32%) marks and the odour at about 38 percent of these were classified as strong to very strong. We were able to distinguish scents by their odour, even after more than 60 days following spraying (during the dry season), indicating that longevity for snow leopards must be substantially longer. Snow leopards typically selected overhanging rock faces, orienting scent-marks toward northerly aspects, a behaviour that enhances sign longevity by sheltering scent from the prevailing weather (Ahlborn and Jackson 1988).

Dimensions of rocks scent-sprayed by snow leopards varied considerably, making it difficult to describe a "typical" site on the basis of sign size or placement alone. Seventy-five percent of the marked features stood less than 3 m in height (6.8 m ± 14.7 Std. Dev.; range 0.9 - 75; N = 76), and 51 percent were less than 3.5 m in width (18.7 m ± 41.4 Std. Dev.; range 0.5 - 175; N = 78). Measurement of the rock face actually sprayed varied less widely, and the average height of the sprayed rock face was 1.5 ± 1.1 m (N = 121), with an average width of 2.0 ± 2.3 m (N = 119). The height of the spray mark above ground level averaged 78.7 ± 12.5 cm (N = 132), while the length and width of the spray-mark averaged 16.6 ± 1.0 cm and 9.8 ± 7.5 cm respectively. When a rock was sprayed in more than one place, the average distance between separate spray-marks was 28.2 ± 15.6 cm (N = 82).

Observations of sign and marking activity along the four permanent transects which bisected the core study area (Figure 19) suggested that a snow leopard marked in response to sign left by another individual (Ahlborn and Jackson 1988). Scraping (including new scrapes and rescraping of existing marks) was the most abundant form of marking behaviour, constituting 77 percent of the change in all types of sign observed along the 4.9 km repeatable transect. About 55 percent of all sites were found to be remarked during the first six months of observation. While sites with solitary scrapes were more common, only 15 percent of the 1,134 scrapes catalogued occurred singly (Ahlborn and Jackson 1988). On average, the typical site contained 2.8 scrapes, with a range of 1-24. While a total of 235 scrapes per kilometer was tallied along a riverine bluff transect, the average scrape density was 28/km along transects sampled "one-time" and 72/km along repeated transects which bisected the core area.

Forty-three percent of all scrapes observed along the repeated transects resulted from the rescraping of a pre-existing scrape; furthermore, most scraping occurred at sites that appeared to have been repeatedly used over long periods of time by snow leopard. Approximately 55 percent of all sites were remarked at least once or more times over the 6 month period that they were monitored during the first year of sampling. Rescraping occurred most often at the more visible -- typically new or fresh scrapes -- further suggesting that animals were attempting to "overmark" existing sign with that of their own. The relative visibility, and thus age of scrapes, appeared to be an important factor in the selection of marks for rescraping ($\chi^2 = 49.79$, df = 4, $P < 0.05$). Scrapes in the more visible classes (3 and 4) were rescraped significantly more ($P < 0.05$) than those in low visibility classes, while the oldest scrapes were avoided ($P < 0.05$). Since high visibility scrapes are also the freshest (i.e. those made most recently), they are presumably more likely to contain viable chemical information (Muller-Schwarze and Silverstein 1979; Brown and MacDonald 1985). Measurements of both new and remarked scrapes were recorded over two years. The greatest length and width of remarked scrapes (N = 176) was significantly greater than that of new scrapes (N = 187) ($t = 3.29$; $P < 0.001$ and $t = 2.81$; $P < 0.005$, respectively). However, the difference between the two scrape mean dimensions amounted to about 1 centimeter and thus appears to be of no practical or biological significance.

Scraping occurred on about 86 percent of the occasions that a snow leopard was known to have visited a particular transect. During a typical visit, approximately 2.8 new scrapes and 2.1 rescrapes were recorded. New sites were established on 50 percent of the times that a cat was known to have visited a transect, for a marking rate of about 0.8 sites/visit. Of the sites which were revisited and marked, 73 percent were classified as relic, 17 percent as non-relic and 9 percent were sites established during the monitoring period. The overall decline of scraping activity during spring and early summer resulted in a corresponding deterioration of scrapes (and sites) in the higher visibility classes.

The density of feces along the repeated transects averaged nearly 16 per km, with 84 percent occurring at a scrape site, and most of these (74%) were associated with a relic or repeatedly utilized site. Four percent of all feces were deposited in a scrape depression or on its mound, while another 3 percent of scrapes were marked with "token" feces, defined as small feces containing much less than the normal amount of fecal material (Schaller 1967, Sunquist 1981). The pattern of feces accumulated along transects indicated a strong tendency for snow leopards to deposit fecal material at scrape sites rather than randomly along their travel route. Urine and/or anal gland marking of scrapes was detected at 33 of 181 scrapes (18%). Because the presence of urine was difficult to detect at many scrapes, it is probably more common than these data would suggest.

Use-availability analysis indicated a significant preference among snow leopard for scraping atop promontories or at the base of cliffs, along riverine bluffs, on knife-edge ridges, and in moderately to distinctly broken terrain. Areas with poorly defined terrain or lacking in topographic edges were significantly under-utilized. The disproportionate use of vegetation types for scraping seems to reflect their association with a particular landform condition. Thus, alpine grassland and subalpine shrub (most often associated with a smooth slope) were marked significantly less than expected by chance alone, while barren areas (like a cliff) or riparian areas (stream-bed or riverine bluff) were used significantly more than expected ($\chi^2 = 89.4$, df 4, $P < 0.001$).

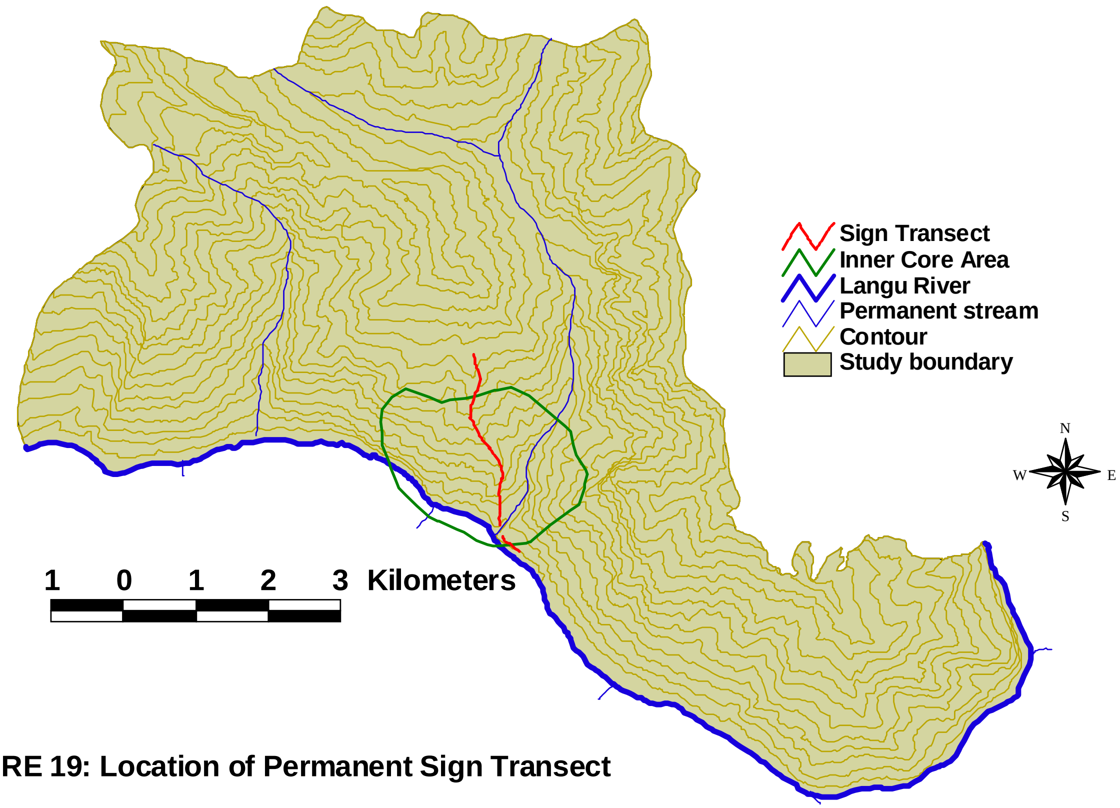

FIGURE 19: Location of Permanent Sign Transect

The amount of sign differed significantly (Kruskal-Wallis = 26.8, $P < 0.001$) between transects classified as confluence, major ridge, ridge or another type. Confluence transects (i.e., ridge-lines adjoining a well-defined stream and river confluence) had the highest density of sign, followed progressively by a major ridge, other ridges and transects along a poorly defined landform edge. The differences were significant ($P < 0.05$) for all categories except between a ridge and other transect types. Sign transects at major drainage confluences consistently supported more sign than non-confluence locations.

Finally, transects located within the overlapping inner core area contained significantly more sign than those transects located in similar terrain, but within a non-core area (Mann-Whitney U = 151, $P < 0.002$). Typically, the core area transects supported about 4 times as much sign (scrapes, feces, and scent-sprays) as found along transects elsewhere in the snow leopards' home ranges.

8.3 Discussion

Sociality and Land-tenure: Radio-tracking confirmed that snow leopards have an essentially solitary social structure, as first suggested by Schaller (1977). In this regard they are similar to common leopard (Bailey 1993, Schaller 1972) and puma (Hornocker 1969; Seidensticker et al. 1973). Same day distances between male snow leopards averaged 1.9 km, compared to 2.2 km between females and 3.6 km between the sexes. Although spatially overlapping to a large degree, use of the core area by the snow leopards studied tended to be temporally separated. Sweanor (1990) reported similar temporal separation among puma with overlapping areas. Bailey also found that common leopards with adjacent overlapping home ranges were seldom located closer than 1 km to each other, regardless of sex, social status or season of the year. In addition, males were generally spaced further apart ($\bar{X} = 5.4$ km) than adult females ($\bar{X} = 2.6$ km), and males and females were spaced further apart ($\bar{X} = 4.0$ km) than females. Spacing increased during the wet season when impala, the main prey species dispersed away from permanent water-holes.

Despite extensive range and core area overlap, associations between different individual snow leopards outside of mating and females with cubs are obviously quite rare. The only other association observed during this study involved a single occasion when two females (F1 and F2) spent four days together. They may possibly have been sharing a kill. Groups of up to 5 "adult-sized" snow leopards have occasionally been reported from Ladakh by local people (Chundawat pers. comm.); these probably also represent temporary associations of a female, her nearly or recently independent cubs, and possibly a resident adult male. It would be interesting to know if such groupings were associated with a kill or not. Heptner and Sludskii (1990) describe an incident in which five snow leopards belonging to a single family group attacked a wild pig. No specific information was gathered on adult male and female interactions during my study, but judging by the paucity of pairs of adult-sized pugmarks observed, such associations are likely short-lived. Bailey (1993) found that most associations in common leopard lasted only one day, although one resident pair remained together for a 5 day period.

Conclusions regarding both home-range and land-tenure in snow leopard are clearly compounded by my small sample, the uncertain breeding or social status of the radio-collared males, and the relatively long time that they used a common area. All tagged leopards met with the residency criteria assigned by Hemker et al. (1984) to the puma population they studied. Dispersal usually occurs soon after the offspring have become independent of their mother, estimated at around 18-22 months of age in snow leopard (this study), but earlier in common leopard (Bailey 1993; Sunquist 1983). Male M2 used a well-defined range until he was about 4 years old, when he lost his radio-collar. This snow leopard showed some evidence of becoming reproductively active during the period he was studied. Male M3 resided in the same area until he was over 3 years old, when I lost contact with him. The land tenure system of snow leopard must remain somewhat unclear, given my small and potentially biased sample. More research is needed to determine if males maintain more exclusive ranges in areas with less abundant prey or areas which are not as spatially broken by cliffs and other rocky terrain.

Several factors may explain the high degree of overlap between males and the lengthy residence observed among this young male snow leopard cohort, including the possible death of a resident male or high prey abundance in the study area, which may have permitted offspring to remain within their mother's range for an extended period before dispersing. Studies of tiger in Nepal's Royal Chitwan National Park have clearly indicated that land-tenure is in a state of constant flux (Smith 1984 & 1993; Smith et al. 1989; Sunquist 1981); the same situation may exist in snow leopards, but the species' precise land-tenure pattern will remain uncertain until a long-term study has been conducted. Little information on the subject is even available for the common leopard, a far more widely distributed and studied species. Norton and Henley (1987) estimated range overlaps of 10-

57 percent, but home ranges for the 3 adult male common leopards studied appeared to be unstable and undergoing change, with the apparent displacement of the oldest individual. A combination of exclusive home ranges, mutual avoidance and scent-marking has lead several investigators to suggest territoriality exists in male common leopards (e.g., Schaller 1972, Hamilton 1976, Bertram 1982), but this may better be termed a form of breeding territoriality in which resident males have exclusive rights to breed with one to six resident females (Bailey 1993). The latter researcher offered valuable insight into the land-tenure system of *Panthera pardus*, concluding that vacancies in the home range mosaic of resident leopards are quickly filled by either subadults already in the area or by animals migrating into the area from elsewhere. Male land tenure appeared to be based on prior use, while access to high-quality and prey-rich habitat needed to successfully rear young influenced the female land-tenure pattern.

Two common features in the spatial relationships of resident male common leopards were reported by Bailey (1993): firstly, home ranges were not maintained to the total exclusion of neighbouring resident males, and secondly, older resident males shared a greater proportion of their home ranges with younger (subadult) resident male leopards. Noting that male adult leopards never appeared to associate with other adult males, Bailey (1993:250) wrote, "Knowledge of each other's home range boundaries and core areas of intensive use probably contributes to a stable, peaceful society of solitary leopards. The spatial and temporal relationships among leopards can thus provide valuable insight into their social organization." Vacancies in the mosaic of home ranges in his two study areas were quickly filled by other individuals. Thus, land tenure among the common leopard apparently insures certain rights, including offering resident males exclusive breeding rights, for no known subadult or transient males associated with females long enough for them to breed with her. Bailey concluded that only resident and older males associated with females often and long enough to breed. Successful occupancy of an area and the social status apparently needed to maintain that occupancy ensured the owner's right to breed. Land tenure in males appeared to be based on prior use. Thus, the primary right associated with land tenure among male leopards appeared to be access to, and successful breeding with, resident adult female leopards. The area occupied by resident males was much larger than that needed to obtain sufficient prey and encompassed the home ranges of as many as six females. I was not able to determine how much of F1's home range overlapped with that of another adult female and her single cub whose pugmarks were occasionally sighted in the same area. Bailey found that resident adult female home ranges overlapped considerably with each other.

Emlen and Oring (1977) first suggested that female reproductive patterns, especially receptivity, were important for appreciating the extent of male competition over access to females. They theorized that there is little potential for individual males to monopolize multiple females if those females are sexually receptive in unison, as is the case for snow leopard (Rieger 1984). After reviewing the literature, Caro (1994:77) concluded, "The period over which females are receptive and how they are distributed in space therefore affects many aspects of male competition, including body size, weaponry, social relations and ranging behaviour." Variations in social systems would be expected to occur as a result of differences in the dispersion of critical resources, the availability of mates, or other ecological constraints. Lynx is another species that shows a strongly seasonal estrous and resulting narrow period of sexual receptivity (Ognev 1935; Sunquist, pers comm.). Studies have indicated that males may either hold an exclusive territory or move and mate over a wide area shared with other males (Bailey et al. 1986). Heptner and Sludskii (1992) report instances of a receptive female being accompanied by as many as five or more male lynx.

Time sharing of common space has also been shown in puma (Hemker et al. 1984), bobcats, *Lynx rufus* (Kitchings and Story 1984), and jaguar (Rabinowitz and Nottingham 1986) among other solitary felids. Anderson (1988) monitored bobcat home ranges before, during, and following the removal of a resident male. An adjacent male occupied the home range of another male after it had been removed; he continued to use his newly occupied range although its size shrunk and his activities were centered upon suboptimal habitat following the re-introduction of the same male several weeks later. Anderson therefore concluded that the size and location of home ranges and habitat use patterns in adult male bobcat were likely influenced by the presence of adjacent and overlapping males. He postulated that home ranges were maintained by prior rights, with animals only moving into areas after they had been vacated.

Intraspecific communication probably serves several functions: first, it may allow individuals to avoid each other and thus separate themselves spatially and temporally (Ahlborn and Jackson 1988; Bailey 1993; Ewer 1973; Kitchener 1991; Smith et al. 1989). Second, it enables individuals of different sexes to attract each other, which is especially critical during the brief courtship and breeding of the species. As explained below, snow leopards evidently use subtle modes of communication to distinguish each other by individual, sex, social status and reproductive condition.

Marking Behaviour: As first reported by Schaller (1977), snow leopards of both sex (including subadults of about 1.5 years in age) mark intensively, leaving sign such as scrapes, feces, urine and scent-spray in prominent locations. Scraping and the scent-spraying of overhanging rock-faces was the most prevalent form of communication observed during this study. Favored snow leopard marking sites are promontories, bluff edges and rocky outcrops or knolls along sharply defined ridges, particularly in areas of maximum overlap between different individuals and near major stream confluences. Given the snow leopard's preference for travelling along well defined terrain edges (such as the crest or base of a cliff, river-bluff or distinct ridgeline), it is not surprising that sign marking is concentrated in places where movement is channelled, impeded or directed by a physical barrier. Most of these "natural edges" offer an unobstructed field-of-view in at least one direction. Koshkarev (1984) suggested that the primary advantage of such a travel pattern lay in the greater potential for successful detection and approach of prey.

The snow leopard's mode of communication is well adapted to its social structure and the environmental conditions at hand. Most marking occurs during the breeding season and in late winter, after the peak snowfall, rather than during the summer when rainfall would quickly obliterate scrapes or scent-sprays. Marking during the mating season enables males (especially residents) to locate a receptive female during the short period that it is in oestrus (1-16 days, see Chapter 4), while marking at other times of year allows for temporal and spatial spacing of individual animals. Scrapes, in particular, tend to be very long-lived in protected places and areas where there is no disturbance from livestock. Thus, scrapes made beneath a protective, overhanging boulder could be discerned two years later. Clearly, most sign deteriorates far more rapidly due to natural weathering, and may last less than two months, even where it is not trampled by domestic livestock.

Beside seeking to place them in a prominent place, a snow leopard may enhance its scrape by depositing feces within the scrape or immediately adjacent to it. Snow leopards usually use overhanging, protected faces of boulders, rock outcrops and cliff ledges or bases to scent-spray. Marking is strongly concentrated in areas where a snow leopard spends a majority of its time and where the relative snow leopard density is greatest (i.e., the overlapping preferred use or core area). In the study area, these places were located at or near the confluence of a major drainage. Mallon (1984) presumably encountered a similar situation in Ladakh, for he noted that the greatest concentration of sign occurred in the bottoms of deep gorges, along the dry streambed. These observations appear to conform with Gosling's prediction that social marking would be most effective if it maximized the probability of encounter by conspecifics. Gosling (1982) concluded that the likelihood of sign being inspected by conspecifics could be increased by clumping sign at specific locations, by ensuring it is placed adjacent to a prominent object or feature, by increasing the amount of sign deposited at each site, and by advertizing its presence and making it as conspicuous as possible.

Common leopard social marking is described by Bailey (1993), who found they frequently scent-marked by urine spraying the base of trees, bushes and grass as they walked along trails, roads and dry river-beds. Scrapes often accompanied scent marks, but remarking of existing scrapes, so conspicuous in snow leopard, was not documented by Bailey. However, nearly 80 percent of scrapes were located at conspicuous places along travel routes frequented by different leopards, with more sign being located near a trail intersection than elsewhere. Bailey concluded that fecal material left by leopards along such travel routes represented another form of social marking, although he felt that such behaviour was more closely associated with an extremely dry environment.

Our data is not adequate to establish whether resident animals mark more than non-resident transients. Bailey (1993) found marking in common leopards occurred primarily in resident males, being far more limited among the transient male cohort. This could offer several potential advantages to the population at large, including allowing transients and other newcomers to determine if an area is already occupied by a resident animal, to provide the site specific information needed by a transient to avoid a resident, to allow the sharing of space, and to enable a resident to direct communication primarily toward its neighbour, thus better maintaining each individual's territorial boundary.

Rescraping is uncommon in other solitary felids as well, or possibly its frequency has been underestimated for various reasons. In any event, snow leopards appear to scrape mark far more intensively than common leopard, puma, jaguar or tiger (Ahlborn and Jackson 1988, Bailey 1993, Smith et al. 1989). Schaller and Crawshaw (1980) noted that jaguars in their study area in Brazil vocalized and left less visual or olfactory sign than snow leopard. Seidensticker et al. (1973) estimated that puma reused only 12.8 percent of 86 scrape sites in his study area, while Sweanor (1990:121) observed that "Scrapes were usually, but not always, freshened by the same male." This investigator found that few female puma scraped.

In my study scraping was found to be 4 times as intensive within the shared core area as elsewhere, including along the periphery of the snow leopard home ranges (Ahlborn and Jackson 1988). Other solitary cat species also tend to concentrate sign in certain places. Puma studied by Seidensticker et al. (1973) marked most frequently along the edges of their territories or in regions of overlap rather than toward the home range centers, but Sweanor (1990) found males scraped throughout their respective home ranges, not just along home area boundaries. She determined that 23-39 percent of scrape sites were shared by different males and reported that scrapes were commonly found at kills, along drainage bottoms, beside prominent trees, in the saddles of ridges, along ridgelines, near water and in rocky alcoves. Jaguar sign was also concentrated within the overlapping use areas (Rabinowitz and Nottingham 1986). Smith et al. (1989) reported that tigers in the Chitwan National Park marked recurrently along their travel routes, by leaving scrapes and selectively urine-spraying certain trees. Such scent-marking was 5 times higher at territorial boundaries than in the middle of tiger territories. In the Kruger National Park, Bailey (1993) observed that most marking occurred "at the periphery of leopard home ranges rather than deep within them", although there were fewer marks along roads bordering a natural barrier like a large river. Bailey thought this could be due to the reduced likelihood of common leopards encountering a conspecifics in such a situation. In the case of the Langu snow leopards, such barriers appeared to funnel movements and to contribute to the high intensity of marks observed at or near a stream or river confluence. Thus, it appears that most of the marking observed in the felids mentioned above occurs within areas of common use or the area of greatest overlap.

In males, marking may also play an important role in reducing the likelihood of a close encounter, thereby minimizing the likelihood for a fight which could result in serious injury or even possibly death to those involved. Sweanor (1990) documented high mortality from direct associations: thus, 40 percent of male-male and 12 percent of male-female puma contact resulted in mortality. Smith et al. (1989) presented a model for tigers where an odour field signals the risk of encountering a conspecific, thus allowing animals to compare the cost of possible encounter with the benefits of using a given area. They concluded that concentrating marking in mutually used areas, where the probability of encountering a conspecific is greatest, makes good sense with respect to communication. The potential for transfer of information among individuals is maximized, while the effort invested by an individual in transferring information is minimized. Ahlborn and Jackson (1988:44) suggested that such a marking pattern may constitute "an important prerequisite for the development and maintenance of an extensively overlapping land-tenure system, as observed for snow leopards in the Langu Valley." In areas with a lower snow leopard density or where there is less home range overlap, Ahlborn and Jackson (1988) predicted that the density of sign within concentration areas would be less and that the distance between marked sites greater.

Adult male blue sheep, the primary prey species of snow leopard in the Langu Valley as well as across most of its geographic range in the Himalaya and Tibet

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CHAPTER 9 FOOD HABITS AND PREY SPECIES DISTRIBUTION PATTERN

9.1 Food Habits, Hunting Behaviour and Prey Consumption

Diet: Preliminary analysis of a subsample of 78 scats from the core study area indicate blue sheep are the primary prey item, with small rodents (voles, *Alticola stoliczkanus*; murids, probably *Apodemus* spp.) and pikas (*Ochotona roylei*) constituting important supplementary prey (Table 45). The presence of other small rodents is interesting given the absence of marmot (*Marmota* spp.) from the study area. Further study is required to determine if there are any seasonal dietary differences in this snow leopard population. A large percentage of prey items could not be definitively identified, possibly due to deterioration of scats or substantial variation in hair characteristics. Although blue sheep are the primary prey, Himalayan tahr are also an important part of the Langu Valley's snow leopards food base. Field observations confirmed that subadult leopards, weighing an estimated 20 - 25 kg, can kill a fully grown male blue sheep weighing over 58 kg, indicating that the species is able to subdue prey 3 times its own weight.

Kill Frequency, Hunting Behaviour and Feeding Site Characteristics: Stationary consecutive-day locations of the radio-collared animals suggest that snow leopards kill large prey once every 12.1 ± 1.46 days (standard error, N = 30), with the interval between suspected kills ranging from about 3 to 29 days. The mean number of days spent at a suspected kill site was estimated at 2.7 ± 0.15 days (standard error, range 2 - 8 days). Since animals were not always located daily, kills may have been made more frequently, because of some incidents passing undetected. On the other hand, the assumption that all stationary locations (with the exception of females with immobile cubs) are associated with large prey kills may not necessarily be valid.

Only four snow leopard hunts were observed during the four years of my field study, all of which ended unsuccessfully. All but one of the instances occurred during late morning or early afternoon. In one instance, two snow leopards stalked to within 10 m of a widely-scattered herd of 41 tahr, when one rushed toward a tahr and chased the herd downslope. The pair gave up soon thereafter (Shah 1989). The second instance involved an adult male

Table 45: Frequency and percent occurrence of food items in snow leopard feces

Prey Item	Frequency of Occurrence	Percent Occurrence
Large mammals:		
Blue sheep	35	34.0
Himalayan tahr	11	10.7
Unidentified	12	11.6
Small mammals:		
Cricetid	9	8.7
Murid	9	8.7
Pika	1	1.0
Unidentified	7	6.8
Birds	2	1.9
Plant material	17	16.5
Totals:	103	100.0

snow leopard which stalked a fully-grown male blue sheep from above, then rushed and chased it at full-speed down a 15° slope in alpine grassland, before the blue sheep veered sharply to the right -- a manoeuver that the cat was unable to match and the blue sheep thus escaped (Ahlborn, personal observation). In the third incident, an adult snow leopard was observed for over 30 minutes as it lay in ambush on a small ridge in slightly rolling terrain as a herd of 8 blue sheep grazed some 150 m away, slowly moving toward the crouched leopard. With the grass shorter than 10-20 cm in height, the cat lacked cover to move any closer. The sheep moved downslope when about 100 m from the ridge and darkness precluded continued observation, although no kill was observed there the following day. The final incident involved an adult male snow leopard which approached a group of 5 blue sheep (2 females each with a lamb and a subadult male) from upslope. One female and her lamb were resting on a large rocky promontory about 30 m high, while the other three blue sheep grazed just below, beside a deep gully, but hidden from the leopard's view. The snow leopard walked quickly toward the resting female, which saw the predator when it was about 20 m away; she leapt up and ran off with her lamb, followed by the other sheep. The snow leopard made no attempt to rush or pursue the sheep, who stopped 50 - 100 m away to look back briefly, before quickly leaving the area. The snow leopard stood on the promontory and watched as they disappeared into a gully leading toward a series of cliffs.

Little data was collected on the sex and age composition of snow leopard kills. Twelve fresh, confirmed kills were examined, including 5 involving Himalayan tahr and 7 involving blue sheep. All but three of the animals killed (all tahr) were adults, and of a sample of ten animals, 6 (60%) consisted of males and the rest were females (40%). Forty-five percent of the kills were made in relatively cover-poor, even terrain, with the remainder about evenly distributed between cliff, moderately broken terrain and linear landform types (river-bed and riverine terrace). All blue sheep and tahr kills I investigated indicated the victims had been killed with a throat bite. After eviscerating the prey, the snow leopards started to feed, usually at the rump. While an adult blue sheep provides sufficient food to keep a single cat occupied for 2 - 5 days or more, F1 and her 2 cubs fully consumed an adult female blue sheep in less than 48 hours. No evidence for caching of kills, such as occurs in the common leopard (Bailey 1993), was discovered. Neither were kill remains covered, as reported for puma (Anderson 1983).

There is circumstantial evidence to suggest that blue sheep are more easily approached from above and that bachelor male herds are less wary than those containing females and young. Not only is the snow leopards' camouflage superb, but they are remarkably adept at concealing themselves despite poor cover. Given their short, muscular limbs, it is reasonable to presume that they must have to approach relatively closely before launching their final attack, if they are to be successful.

Kill sites were highly clumped, with over 60 percent (37) of the 61 known or suspected kill sites occurring within the inner common core area (Figure 20). Over 75 percent of these sites, as determined from radio-telemetry, were located in a barren area or mixed shrubland, and 1.6 percent were in open alpine grassland cover type -- suggesting that most kills are made in or a near cover-rich place (Table 46). Although barren sites are largely devoid of vegetation, rocks and terrain features usually offer ample stalking cover. In general, snow leopard appeared to utilize sites in proportion to their availability. In terms

Table 46: Habitat characteristics of known or suspected kill sites, based on radio-telemetry locations

Habitat Feature & Class	Percent Occurrence (n = 61 locations)				
Vegetation	*Barren*	*Mixed Shrub*	*Subalpine Shrub*	*Alpine Grassland*	*Tree Types*
Site	39.3	36.1	18.0	1.6	4.9
Nearest Type	52.5	34.4	8.2	1.6	3.3
Landform	*Smooth*	*Broken*	*Very Broken*	*Cliff*	*Linear Types*
Site	23.0	21.3	13.1	39.3	3.3
Nearest Type	21.3	26.2	11.5	27.9	13.1

of terrain, the majority of sites were classified as cliffs (39.3%), with only 3 percent of suspected kill/feeding sites being located in a river-bed, landslide or other linear landform type. The nearest other landform type tended to be moderately broken (26.2%), a cliff (27.9%) or smooth-surfaced (21.3%). No significant differences between site use and availability were detected, except that areas more than 125 m from a cliff were significantly under-represented as kill or feeding areas ($\chi^2 = 27.117$, df 4, $P < 0.002$). Sites with a northerly aspect were also significantly under-utilized ($\chi^2 = 10.482$, df 5, $P < 0.03$), and fewer kills than expected were made at distances of more than 400 m from a travel corridor ($\chi^2 = 10.375$, df 4, $P < 0.03$).

9.2 Prey Species Abundance and Distribution

Attempts at censusing large prey were severely hampered by poor visibility due to the extremely rugged and broken terrain, as well as the densely covered brushy slopes. Sign abundance was used to identify relative blue sheep density according to each major landform and vegetation type present. Pellet group abundance and distribution differed with respect to type of landform ($\chi^2 = 22.243$, df 3, $P < 0.001$), suggesting that terrain is an important factor in habitat selection by blue sheep. Moderately broken and smooth terrain

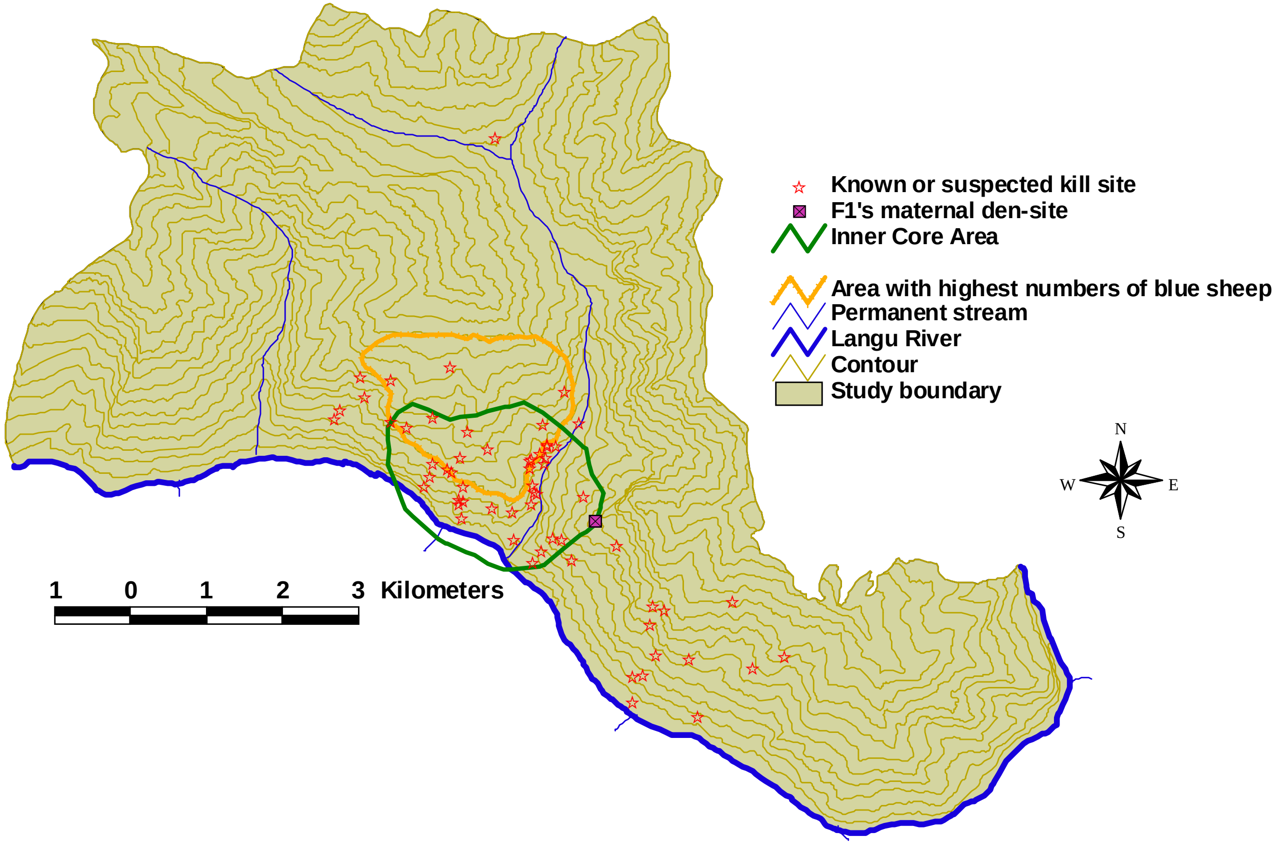


FIGURE 20: Kill Sites in Relation to Common Inner Core Area

sites contained higher mean pellet group densities than occurred on cliffs or in very broken areas (Table 47). Very broken areas contained the least amount of blue sheep sign,including pellets, beds and tracks. No differences in pellet group number or distribution were detected with respect to aspect. Pellet density tended to decrease with increasing slope steepness. Thus, slopes steeper than 40° had significantly fewer pellet groups than slopes under 20°. The mean number of beds was greatest on smooth terrain and slopes of 30-40°(1.2 and 1.4 beds/site respectively), as well as slopes greater than 50°(i.e., cliffs; 1.2 beds/site), supporting observations that these sites are used for daytime foraging and night-time bedding respectively. Actual bed densities on cliffs are probably higher than indicated, since their detectibility is reduced by the rocky substrate. Few beds (0.2/site) were detected on slopes less than 20° in steepness, indicating gentle slopes were generally avoided by blue sheep, at least for purposes of bedding.

Pellet group analysis indicated that habitat utilization differed with respect to the type of vegetation present ($\chi^2 = 11.421$, df 3, $P < 0.0097$), with mixed shrub sites containing significantly more pellet groups ($\overline{X} = 1.96$) than barren sites ($\overline{X} = 1.07$) (Table 48). Although some difference may be attributable to the steeper gradient associated with barren sites (i.e. places having a greater likelihood for gravity-induced dispersal of pellets), these areas are used by blue sheep more for bedding rather than foraging.

Increases and decreases in the relative abundance of pellet groups and beds respectively, were noted as the vegetation canopy coverage increased, but such differences were not statistically significant except when sites with less than 10% canopy cover were compared to sites with 26-50% canopy cover. Presumably, blue sheep are attracted to cover-rich sites when foraging, but cover-poor sites when bedding. Pellet-group abundance differed slightly with respect to the proportion of grass present ($\chi^2 = 8.856$, df 4, $P < 0.0648$). Thus, the pellet-group frequency increased with increasing grass composition, with those sites supporting less than 10% grass composition containing significantly fewer pellets than sites with 11-50% grass cover by composition. Blue sheep pellet sign was least abundant at sites with 10 percent or less shrub composition and most abundant in sites with 51-75% shrub coverage ($\chi^2 = 11.184$, df 4, $P < 0.0246$).

These data suggest that the most suitable foraging cover for blue sheep consists of a mixture of shrubs and grass, such as occurs in the mixed shrub and subalpine shrub types, while

Table 47: Blue sheep sign in relation to selected landform types

Parameter	Landform Type			
	Smooth LF = 4	Moderately Broken LF = 2	Heavily Broken LF = 3	Cliff LF = 5
Blue sheep Pellet Groups				
Frequency	40.0	36.4	20.7	9.6
Number ± S.E.	2.53 ± 0.34	1.81 ± 0.28	1.24 ± 0.26	0.6 ± 0.18
Other Ungulate Sign				
Number of beds	1.20 ± 0.24	0.93 ± 0.32	0.97 ± 0.20	1.14 ± 0.22
No sign types	1.98 ± 0.15	1.76 ± 0.15	1.59 ± 0.21	1.29 ± 0.20

Table 48: Blue sheep sign in relation to selected vegetation types

Parameter	Vegetation Type			
	Barren	Mixed Shrub	Subalpine Shrub	Alpine Grassland
Blue sheep Pellet Groups				
Frequency	18.0	35.2	39.1	35.7
Number ± S.E.	1.07 ± 0.17	1.97 ± 0.81	2.37 ± 0.61	2.57 ± 1.19
Other Ungulate Sign				
Number of beds	1.32 ± 0.23	0.66 ± 0.13	1.37 ± 0,42	1.14 ± 0.74
No sign types	1.56 ± 0.14	1.76 ± 0.14	1.81 ± 0.23	1.86 ± 0.40

cliffs offer the most secure escape and resting cover. These apparent preferences were used to construct a simple habitat suitability model for blue sheep (Figure 21). Cliffs and areas of subalpine shrubland (grass-rich compared to mixed shrub) were buffered out to a distance of 200 m, and then overlain to create a mosaic of polygons adjacent and further from required foraging and resting habitat. Areas containing both cover and foraging habitat were rated as high, while medium suitability sites were located within 200 m of either food or cover, but not both. Low suitability areas were those sites which were located further than 200 m from food and cover, or are situated at elevations above 4,572 m (15,000 feet) where plant production is very limited.

Blue sheep densities within the core study area were estimated at 4 to 8 or more animals/km^2 (unpub. data). The rolling grassy slopes bordering the bands of cliffs of Tillisha Mountain, and abutting the snow leopard's core area supported the highest number of blue sheep, with post-rut densities estimated at 15 - 20 animals/km^2 (Figure 20). Surveys indicated that fewer than a dozen Himalayan tahr roamed within the area primarily utilized by the radio-collared snow leopards, placing the density of this species at 0.25 animals per kilometer square or less (unpub. data). By contrast, some of the substantially more heavily forested slopes of the south-side of the Langu Gorge supported up to 10-15 tahr/km^2 (K.B. Shah, pers comm. and unpublished data).

9.3 Discussion

Food Habits: Food habits in snow leopard have been investigated in detail in Ladakh, India by Chundawat and Rawat (1994); in Nepal by Oli et. al. (1993), in Pakistan by Blumstein (pers. comm.), and in Qinghai, China by Schaller et al. (1988b). These and other reports indicate that snow leopards are primarily dependent upon large or medium-sized ungulates, such as blue sheep, Asiatic ibex (*Capra ibex*), markhor (*Capra falconeri*), and Himalayan tahr, as well as sciurid rodents like the Himalayan marmot (*Marmota himalayana*) and lagomorphs like the pika (*Ochotona* spp.).

Although the snow leopard's distributional range is vast, nearly everywhere they are dependent upon just a few large ungulates -- blue sheep, ibex and the occasional argali (*Ovis ammon*), as well as domestic livestock (goat and sheep, cattle, subadult yak and

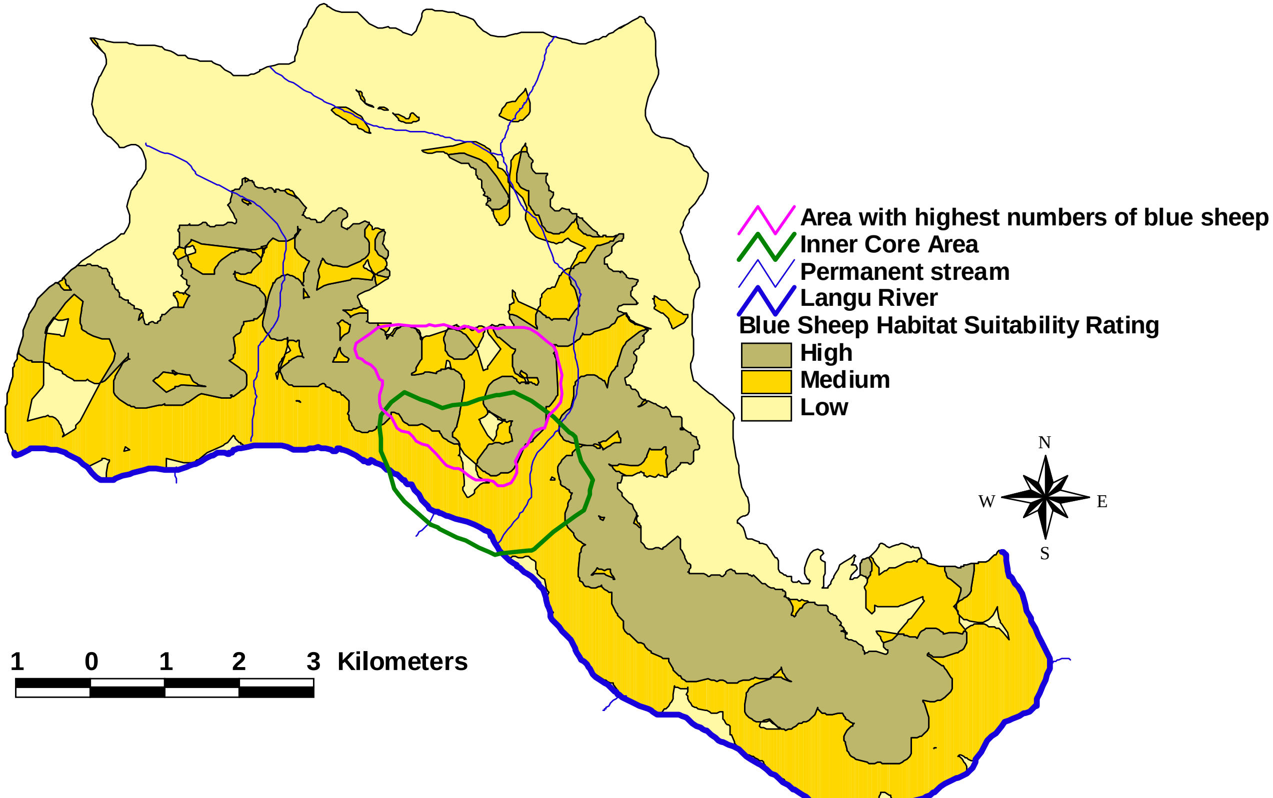


FIGURE 21: Relative Habitat Suitability for Blue Sheep

horse). The ranges of ibex and blue sheep, in particular, closely define the limits of known snow leopard distribution (Wang and Hoffmann 1987). Thus, blue sheep are the principal prey item of snow leopard in northwestern India (Chundawat and Rawat 1994), Nepal (Oli et al. 1993, Schaller 1977; this study) and parts of Tibet (Jackson et al. 1994a; Schaller pers. comm.). Schaller (1977) considered most wild high-altitude ungulates except adult Asiatic wild ass (*Equus hemonius* and *E. kiang*), takin (*Budorcas taxicolor*) or yak (*Bos grunniens*) represented potential prey for the snow leopard. Information from other parts of the snow leopard's range indicate the following medium- and large-sized prey species in addition to those mentioned above: Tibetan gazelle (*Procapra picticaudata*), goitered gazelle (*Gazella subguttorosa*), Tibetan antelope (*Pantholops hodgsoni*), serow (*Capricornis sumatraensis*), goral (*Nemorhaedus goral*), wild boar (*Sus scrofa*), musk deer (*Moschus chrysogaster* and *M. sifanicus*), roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), white-lipped deer (*C. albirostris*), and the young of wild camel (*Camelus bactrianus*) (Fox 1989; Heptner and Sludskii 1992; Mallon 1984b; Schaller et al. 1994; Zhirjakov 1990; Zhirnov and Ilyinsky 1986). A two-year old brown bear (*Ursus arctos isabellinus*) was killed and partially eaten by a snow leopard in Kazahkstan, but this must be quite unusual (Heptner and Sludskii 1992).

One would assume that the snow leopard's diet and annual prey requirements, like that of common leopard, would be influenced by prey size, abundance and availability, the latter depending upon prey population density, behaviour and habitat preferences (Bailey 1993). Using the estimated kill frequency derived from successive stationery locations (see Section 9.1), an adult male snow leopard (or female without dependent young) would be expected to kill about 30 adult blue sheep annually. Assuming an average consumable weight of 37 kg for an adult blue sheep (Schaller 1977), a snow leopard would be expected to consume as much as 1200 kg of large prey (including meat and inedible body parts, estimated at about 30%) per annum, or 1.5 - 2.5 kg of meat per day (Jackson and Ahlborn 1984; Wemmer and Sunquist 1988). However, given the relatively large occurrence of small rodent items (over 20%) in the diet of snow leopards from the Langu Valley, per annum kill rates of 20 to 25 large ungulates appear to be more realistic. By way of comparison, Beier et al. (1995) reported that adult puma inhabiting a comparable latitude to that of my study area, consumed some 48 large and 58 small mammals (medium-sized rodents) per year. They fed for an average of 2.9 days on a single large mammal, a very similar period to the snow leopards investigated.

Snow leopard are reputed to kill larger prey relative to their body weight than all other felids, except for some puma which prey heavily upon elk (*Cervus canadensis*) (Packer 1986). Even accounting for small prey remains being naturally over-represented in scats (Floyd et al. 1978), it is curious that these snow leopards devoted so much effort to preying upon small prey like mice and voles (Table 45). Skeletal remains confirmed consumption of cricetid and murid prey; with a notable scarcity of red fox (*Vulpes vulpes*) in the study area, and the complete absence of marmot, this snow leopard population may simply have been exploiting the most available alternative and locally abundant small food source present. The significance of marmot (*Marmota* spp.) and domestic livestock as supplemental items in the snow leopard's summer diet has been clearly documented. Schaller et al. (1987) found that 29 percent of snow leopard scats collected in the Taxkorgan Reserve contained the remains of marmot. In another part of China, Schaller et al. (1988b:190) reported that "marmots (*Marmota himalayana*) were a staple prey as important as, and in some places more important than, ungulates". Importance in this context relates to the frequency of marmot items found in snow leopard scats collected during summer. Finally, in the Annapurna region of Nepal, Oli et al. (1993) found that snow leopards relied heavily upon Himalayan marmot (*Marmota himalayana*) during spring and summer, with livestock and Royle's pika (*Ochotona roylei*) constituting a substantial portion of their winter diet when marmots were hibernating and therefore unavailable. Besides other marmot species, small prey items include voles and mice (*Alticola* and *Pitymys* spp.), and hares (primarily *Lepus oiostolus* and *L. capensis tolai*). Snow leopards also prey upon game birds like the snowcock (*Tetraogallus tibetanus, T. altaicus* and *T. himalayensis*), chukor (*Alectoris chukor*) and snow partridge (*Lerwa lerwa)* (Heptner and Sludskii 1992; Mallon 1984b; Schaller 1977), as well as the occasional mustelid (Oli et al. 1993).

Similar diet flexibility has been reported for the African and Asiatic common leopard (Bailey 1993; Johnson et al. 1993). Thus, small mammals ranked second in importance to ungulates in the common leopard's diet from several parts of Africa where the diversity of medium-sized ungulates is high (Bailey 1993; Hamilton 1976; Grobler and Wilson 1972). Johnson et al. (1993) found that Asiatic leopard (*Panthera pardus fusca*) consume a wide variety of small, medium and large-sized prey, from pheasants, pika and bamboo rats (*Rhizomys sinense*) to takin and sambar deer (*Cervus unicolor*).

Hunting Behaviour: Very few hunting attempts were witnessed and consequently, I gathered almost no information on this aspect of snow leopard behaviour. Therefore, it cannot be confirmed if snow leopards are opportunistic predators like the common leopard or tiger, taking the most abundant or easily captured prey. Stalking and ambushing appeared to be the common leopard's most frequent hunting strategy (Bailey 1993), and this probably also holds for snow leopard. However, there is no evidence to suggest that this species caches its kills like the common leopard, instead remaining at the kill site and completing all of the meat. Rock-piles could easily substitute for trees as cache sites, and the ambient temperatures are lower and would thus preserve meat for a much longer time than under the climatic conditions associated with tropical or subtropical areas. However, tree-caching appears to be an anti-scavenger strategy rather than an attempt to store prey for future use (Bailey 1993), and prime snow leopard habitat harbors few, if any, scavengers capable of constituting a threat. The Langu leopards stayed on a kill for 2.7 days (range 2-8) on average, compared to 2.4 days (range 1-6) for common leopards studied by Bailey. The snow leopard's crepuscular activity pattern would suggest that most kills are made in the late afternoon or early morning. By contrast, common leopards are thought to kill mostly at night or late in the evening (Bailey 1993). Presumably, any benefit accruing from hunting under the cover of darkness would be offset by the danger of stalking on cliffs and other precipitous places -- which blue sheep tend to select for nighttime bedding.

Our data are clearly inadequate to assess whether snow leopard kill more adult males than the other sex or age classes available to them, as suggested by Schaller (1977) or Heptner and Sludskii (1992). The latter investigators noted that male ibex were most vulnerable during winters with heavy snowfall. Circumstantial evidence suggests that snow leopards may more easily approach male blue sheep groups than herds with females, who are especially vigilant when they have lambs present (unpublished data and Paul Wilson, pers. comm.). However, whether a particular sex or age class is selected may be more a matter of chance, since snow leopards hunt like a tiger. Usually hunting alone, tigers rely upon concealment, a slow stalk and a final but short rush, thus making animals in prime health equally vulnerable to those which are less healthy or younger (Sunquist 1981). While no data exists on hunting success, Heptner and Sludskii (1992), Schaller (1977) and Fox and Chundawat (1988) have described hunting methods used by snow leopard. Fox and Chundawat observed several domestic sheep kills and concluded that the snow leopard's stalking and killing was essentially consistent with other accounts of the species' use of steep cliffs as cover in stalking. Like other felids, snow leopards probably rely primarily upon sight to detect prey. Both of the hunting strategies described by Kitchener (1991) for small cats also apply to snow leopard (Heptner and Sludskii 1992). In the mobile method, the predator patrols its home range until a potential prey animal is encountered, which it slowly stalks until it is near the intended prey, at which time it rushes forward to attempt a kill. If the intended prey is not caught within a short distance the cat will desist from chasing it further. The stationary or ambush method involves a predator lying in wait on a cliff or among rocks along a trail leading to water, a salt lick or other place visited frequently by large ungulates. By resting within in a rocky outcrop containing pika, a snow leopard would be offered the opportunity to feed upon this diurnal species. Blue sheep are perhaps more likely to be detected from above, such as may occur when a snow leopard is bedded on a cliff or other rocky elevated site near a suitable foraging area.

Hunting success is no doubt influenced by many factors, among the most important of which are likely to be the availability of suitable stalking cover (Sunquist and Sunquist 1989, Schaller 1972). Most of the study area offered excellent cover in the form of rocky terrain, shrubby vegetation or both. On the other hand, the presence of other kills indicated that snow leopards were quite capable of successfully hunting in open, smooth-sloped alpine grassland areas, with little or no vertical cover of any consequence. The tendency of snow leopards to travel along ridges, and other landform or vegetation edges aids the predator in its attempts at concealment. Fox and Chundawat (1988) cite an incident of a snow leopard moving along a cliff-top near a village, from where it could follow the movements of domestic sheep and goats upon which they frequently preyed. After tying a goat out as bait, they observed and described how a male snow leopard carefully approached from above, until it was about 40 m away when it walked quickly toward its prey, then running at it when 25 m away.

Schaller (1977) and Fox and Chundawat (1988) found that domestic goats were killed with a suffocating throat bite. This was noted for the blue sheep or tahr kills found during this study. Snow leopard are capable of easily killing prey over twice their body weight (Jackson and Ahlborn 1988). Packer (1986) refuted large prey size as the only cause for sociality in carnivora, citing the preference shown by cougar, leopards and snow leopards (all confirmed solitary species) for prey items even larger relative to their own body weight than found in lions, by far the most social of the large felids. Packer (1986) placed the modal ratio of prey size to female weight for snow leopard at 1.26, but a figure of 1.45 is more realistic (given the ability of an adult female to kill fully grown male blue sheep weighing an 50 kg or more). Modal prey size in felids is most strongly correlated with prey availability and vulnerability according to Sunquist and Sunquist (1989).

Telemetry data suggested that the tagged snow leopards killed large prey about once every 12 days, a rate comparable to that of puma (Ackerman et al. 1986, Hornocker 1970, Shaw 1977). Bailey (1993) found that African leopards averaged a kill once every 7.1 days and 6.8 days in the dry and wet seasons respectively. He suspected, however, that kill rates varied considerably with season and between individual, with younger leopards killing more smaller mammals and fewer impala than older leopards. Assuming 30 percent wastage, Bailey estimated male and female leopards required between 5.4 and 4.3 kg/day of large prey respectively; this is nearly twice the consumption rate of snow leopard although they live in a colder climate and are not significantly smaller than their common cousin. The figure of 1.5 - 2.5 kg/day for snow leopard cited by Wemmer and Sunquist (1988) also fits with estimates for consumption rates in puma. For example, Gunson et al. (1993) found that a solitary female puma consumed 2.5 kg/day over a three-month period.

After making a kill, a snow leopard usually moves the carcass into vegetative or rocky cover, where it will remain feeding and resting until all meat has been consumed, unless it is disturbed or chased away. One kill site in relatively dense shrubland had numerous trails 5 to 20 m in length worn between the carcass and the 5 resting places used by the adult female leopard which had killed the fully grown blue sheep. She remained at her kill for 3 days in all, shifting her resting place in response to the sun's movement, as well as chasing avian scavengers away.

Snow leopards commence to feed on the groin and thigh or rump area in a pattern similar to that described by Bailey (1993) for the common leopard. It is not clear if the prey is intentionally eviscerated, or whether this occurs accidentally as suggested by Bailey for common leopard. While intestine and associated viscera are consumed, the rumen content is not eaten. Fox and Chundawat (1988) describe one cat consuming the viscera of a domestic goat left out as bait for it. Observations indicated the Langu snow leopards were able to almost completely consume their kills, provided these were guarded from scavengers like the red fox (*Vulpes vulpes*), ravens (*Corvus corax*) or Himalayan griffon vultures (*Gyps himalayensis*). Heptner and Sludskii (1992:306) considered it rare for a snow leopard to remain near its kill and chase vultures away, noting, "the remains of a kill are usually left behind, and are consumed by vultures, bears, or wolves." In other parts of their range, animals may be interrupted or chased away from their meal by humans, in search of retribution or simply exploiting an opportunity to have fresh meat (Fox and Chundawat 1988; Oli et al. 1994). The tendency of snow leopards to predate upon domestic stock, to eat slowly and stay at their kills for five days or more, and the ease with which they can be dispatched (even by people whose only weapon are stones) no doubts contributes to its reputed population decline and the species endangered status. There are many instances of surplus killing of domestic goats and sheep by snow leopards in the literature (for example, see Fox 1989; Heptner and Sludskii 1992; Jackson et al. 1994 a & b; Mallon 1987; Schaller 1977), a phenomenon also noted in common leopard (Stuart 1986). Usually this occurs after a snow leopard has entered an enclosed livestock pen during the nighttime. Such events lead to concerted attempts at retribution by herders who may lose 5-30 or more of their livestock. Fox and Chundawat (1988) suggested that those snow leopards killed in retribution for stock thefts may be old or physically incapacitated individuals who are unable to catch wild prey.

Prey Species Distribution and Density: A review of the literature indicates densities of 2.6 blue sheep/km^2 in a population under substantially greater pressure from humans than my study area (Wilson 1981). Winter concentrations of 8.8 to 10.0/km^2 were reported by Schaller (1977) at Shey, which is located close to the Langu study site. However, the Shey animals inhabit more barren habitat, and must also compete with livestock for forage. As noted, domestic herbivores are completely absent from my study area. Although blue sheep density varies widely from 4 to 20 animals per km^2 within different parts, it is apparent that the Langu Valley provides prime habitat for this caprid (Jackson and Ahlborn 1989). I roughly estimated blue sheep biomass at 350 kg/km^2, compared to less than 95 kg/km^2 for the Himalayan tahr (unpublished data), for a total ungulate biomass of about 445 kg/km^2. Given a snow leopard biomass of between 3.1 and 4.5 kg/km^2, the predator/prey ratio ranges between 1:98-143. Jackson and Ahlborn (1984) judged that 150-230 blue sheep would be required to support a single adult snow leopard in the Langu Valley, given the area's blue sheep age and sex composition and an overall harvesting rate of 13 percent of the standing crop. Under this regime, an adult snow leopard could be assumed to require 20-30 blue sheep annually. Assuming there are about 1,000 blue sheep in the study area, it should therefore be capable of supporting 4-6 adult snow leopards at a 13 percent harvesting rate.

Oli (1994) estimated similar year-round densities for blue sheep (6.6-10.2 per km^2) and snow leopard (4.8-6.7 per 100 km^2) in his study area in the Annapurna Conservation Area of Nepal. This amounts to a snow leopard/blue sheep ratio of 1:114-1:159 on a weight basis. Livestock contributed 34 percent of the Annapurna area leopard's diet, compared to 66 percent for wild prey (primarily blue sheep, marmot and pika). Livestock biomass in this area ranged as high as 1,700 kg per km^2 (i.e. over five times as much as that of blue sheep), suggesting that domestic stock is more abundant but probably not as available as blue sheep (Jackson et al. 1994b). Even when large-bodied adult yak and cross-bred cattle (36 percent of the total domestic herd) are removed from consideration, the biomass of livestock in Annapurna exceeds that of blue sheep by 200 percent or more.

Prey populations are ultimately controlled by forage quality, quantity and availability. Blue sheep are primarily grazers, preferring various grasses and forbs throughout the year (Schaller 1977, Wegge 1976, Wilson 1981). Shrubs may provide an essential food source in areas heavily grazed by livestock (Schaller 1977) or during winter (Roberts 1977, Wegge 1976) when snow accumulation precludes or limits access to grasses or low herbaceous vegetation. Snow cover reduces forage availability, impedes movement, mobility and habitat selection, increases energy expenditures, and may cause crowding and the subsequent overuse of critical winter range. The generally warmer temperatures and increased solar radiation of southerly slopes reduce heat losses and increase snow-melt, thereby minimizing thermoregulatory stresses and maximizing access to forage. This may be one reason why blue sheep prefer foraging areas with a southern exposure and gradual to moderately steep slopes (<35 degrees) during winter and early spring (Wegge 1976, Wilson 1981). Blue sheep tend to utilize the middle slopes of mountain ranges, thus avoiding exposure to the colder temperatures that prevail at higher elevations, on ridge-tops and in the valley bottoms (Schaller 1977, Wegge 1976, Wilson 1981, this study).

Escape, resting, bedding and thermal cover is critical for maintaining prey populations. Blue sheep rely almost exclusively on steep, broken, rocky terrain as cover to bed, to lamb, to escape predators, and to help maintain homoiothermy (Schaller 1977, Wegge 1976, Wilson 1981). In Ladakh, Fox et al. (1988) found that 63 percent of all blue sheep herds within 50 m of a cliff, while 84 percent of herds sighted were located within 150 m of this feature. The mean distance to a cliff was 62 m. Wegge (1979) reported herd size decreased as terrain became increasingly broken and the habitat structurally more "closed". He found that, while larger herds and the greatest number of individuals foraged in uniform terrain with gradual slopes (< 20°), smaller herds were generally restricted to moderately broken (i.e., structurally diverse) or steep (≤ 35°) terrain. Wegge concluded that this was due to the selective pressure of predation and the adaptive characteristics of social behaviour (Estes 1974, Geist 1974, Jarman 1974). While steeper, more broken terrain may offer less productive habitat for blue sheep, such areas may well be very important to their overall maintenance and distribution, especially during winter.

Females usually lead herds in their retreat from known or potential threat (Wilson, 1981, Schaller, 1977, Roberts 1977, this study). The blue sheep's alarm call, a high-pitched "chiret", attracts the immediate attention of all other sheep within hearing distance. In terms of vulnerability to predators, small herds are likely more at risk than large herds. Incidental field observations suggest that all-male herds are less vigilant than herds with adult females and young, which are also more likely to flee upon an alarm call. This leads to speculation that snow leopard would likely be more successful hunting male herds, especially in broken terrain with abundant rock or vegetative cover. Presumably, large herds feeding in open grassland are least available to snow leopard.

Scant data is available to assess what constitutes optimal interspersion between forage and escape cover for blue sheep. However, conclusions from several studies (Schaller 1977, Wegge 1976 and 1979, Wilson 1981) and systematic observations of prey occurrence and relative abundance in relation to vegetation and topography (this study) indicate that blue sheep movements are characteristically restricted to relatively small areas and that both food and cover are obtained within a short distance of the forage-cover interface. (Wegge 1976:20) noted that "extensive grassy meadows which at first may look like prime sheep ranges, receive little use as the animals are reluctant to move further than 100-150 yards away from rocky outcrops or steep bluffs". Movements by blue sheep in winter are typically restricted to less than 1 km (Schaller 1977, Wegge 1976). Blue sheep forage in moderately xeric vegetation communities with relatively low productivity. During winter, forage production for a given area decreases while metabolic demands increase. A key anti-predator strategy of blue sheep is to stay near cliffs or other precipitous cliffs to which they can run if threatened (unpub. data).

A snow leopard habitat suitability model developed by Jackson and Ahlborn (1984) relied upon blue sheep habitat indicators. These investigators considered optimal winter blue sheep foraging habitat as those areas consisting of grassland with 30 percent or more canopy cover, shrubland with 30 percent or more canopy cover and 25 percent or greater grass and forb composition, areas with a distinct southerly or westerly exposure (average aspect from 160° to 200°), generally uniform terrain, and areas with an average slope of 30° or less. These conditions are most closely associated with the smooth terrain type found in the study area. By contrast, optimum winter cover is provided by rocky terrain broken by gullies, scree chutes, ravines, ridges and scattered promontories, with steep slopes. Substantially less snow accumulates on precipitous or steep slopes in excess of 35 degrees. The increased structural diversity provided by broken rocky areas also tends to mitigate for the effects of extremes in ambient air temperature, thermal and solar radiation and wind speed. Jackson and Ahlborn's model assumed that high and medium forage areas were located within 200 m of suitable cover, and that 75 percent or more of the foraging areas available contained high quality forage.

Tracks of a snow leopard at 5,100 m crossing from Tillisha basin into the main Langu Gorge

CHAPTER 10 DISCUSSION

10.1 Observations on Spacing and Habitat Use in a Dense Snow Leopard Population

I examined activity, movements, home range and habitat utilization patterns of a dense snow leopard population in western Nepal. Snow leopards were crepuscular in their activity pattern, and although highly mobile, nearly 90% of consecutive daily movements involved a straight-line distance of 2 km or less (Chapter 5). Home ranges showed a high degree of spatial overlap, both within and between sex. However, the land-tenure system of the snow leopard population I studied remains unclear due to a small and biased sample. Analysis of locations for four radio-tagged snow leopards showed that 47 to 55% of home range use occurred within only 6 to 15% of the animal's total home range area (Chapter 6). Individuals shared a common core-use area, which was located near a major stream confluence (Figure 15). An examination of the locations of radio-tagged animals indicated a strong preference for bedding on cliffs, and in steep, broken terrain close to linear landform features, ridges and travel corridors (Chapter 7). In terms of habitat, the core area is closer to a landform or vegetation edge, moderately and very broken terrain, mixed shrubland, a ridge, a travel lane or a major stream confluence, than the typical non-core site. Snow leopards used common range areas at different times; thus the use of core areas was staggered temporally, with the different individuals being separated by an average distance of at least one kilometer on the same day (Chapter 8). No seasonal differences in movement or home range were detected. Blue sheep, pika and small rodents are the principal prey for the Langu Valley snow leopards, and the core use area may have contained more blue sheep kill sites than the non-core area (Chapter 9). Like other solitary cats, individual spacing in snow leopard is maintained through scent marking and possibly the occasional non-fatal fight. Ahlborn and Jackson (1988) suggested that the high degree of spatial overlap observed is permitted through social marking, mutual avoidance and the use of common travel routes or lanes. Such spatial dynamics may also serve to limit density in a particular area.

Home Range, Land-Tenure and Habitat Utilization Patterns: Under the typical land-tenure system shown by large solitary felids, males occupy larger, exclusive ranges which encompass several female ranges (that in turn may or may not overlap with those of other females) (for example, Anderson 1983; Bailey 1993; Rabinowitz and Nottingham 1986). Subadult males utilize habitat within or near their parental range for a relatively short time only, unless they are successful in occupying the area vacated by the death of a resident male. Most young males disperse to become widely-ranging transients, not all of whom are successful in establishing their own range. Females appear to be more tolerant of sharing habitat and space with one or more of their daughters. Home ranges are stable unless influenced by the death of another resident, and resident males have reproductive access to all females using the same area (Anderson 1983; Bailey 1993; Packer 1986; Seidensticker et al. 1973; Smith 1984; Sunquist and Sunquist 1989). While solitary felids maintain home ranges which provide for all of their needs over the course of a year, these may differ between the sexes. Female ranges are usually smaller, but capable of providing sufficient food for rearing successive litters, even during lean years. The function of a male's range is to provide an area where he can successfully mate with as many females as possible, without interference from surrounding males. By mating with more than one female, a male seeks to maximize his number of progeny; females also seek to maximize progeny by protecting their young, especially from infanticide by intruding males during times of land-tenure, social and resident animal change. Theoretically, such predictable land-tenure systems promote social stability and maximize the reproductive success of both females and males (Kitchener 1991; Sunquist and Sunquist 1989).

Before examining factors that help explain snow leopard home range and habitat utilization patterns revealed by this study, it is worth briefly reviewing current theory on resource utilization. Several theories have been propounded in an effort to explain and understand how a predator determines where and when it is profitable to hunt. Because it is unprofitable for a predator to spend excessive time in areas with few prey, it must discover the most productive way of allocating its hunting time and identify which prey species are the most productive to hunt (Sih 1993). Optimum foraging is a strategy which efficiently balances energy expended in search of an optimal diet (efficient prey size in terms of handling and net energy return), without placing the predator at undue risk (Stephens and Krebs 1986). Optimal foraging predicts that a predator will hunt and pursue prey where it is most "available", that an optimal diet includes those prey items which offer the greatest return in terms of energy expended, and that foraging efficiency leads to hunting activities being concentrated in the most profitable parts of an animal's home range, where preferred prey items are most abundant. Greatest foraging efficiency is projected for home ranges which have well defined sites offering a predictable food supply for its owner. This in turn, depends upon resource distribution and habitat quality, as well as habitat patch size and heterogeneity (Morrison et al. 1992). The importance of heterogeneity at the landscape level is being increasingly recognized, in large part due to the emerging science of conservation biology. As Meffe and Carroll (1994:197) note, "Individuals of the same species living in relatively close proximity to one another may experience quite different physical and biotic environments, even to the extent that some may not be able to survive and reproduce while others do very well. At spatial scales substantially larger than what one individual encounters, the landscape experienced by a population represents a mosaic of good and bad places for the species. The growth, or lack thereof, of the population is determined not only by the quality of the individual microsites occupied, but also by the spatial and temporal distribution of suitable and unsuitable microsites or patches of habitat."

Spatial diversity is especially conspicuous in mountain ecosystems. However, high mountain areas like the Himalaya are usually viewed as offering a harsh environment with severely limited resources, compared to the more productive, adjacent lowland and subtropical habitat (Bishop 1990). Animals inhabiting mountain environments must adapt to a vicissitude of formidable climatic and physical elements. Diurnal and seasonal temperature ranges are extreme, while precipitation varies substantially with respect to both local and regional topography. Considerable snowfall may accumulate in some areas, although large parts of the snow leopard's range either receive little snow or it melts off rapidly. Snow leopards have extremely long, luxuriant fur and a long bushy tail that can be used to keep it warm while resting, although it probably better serves as a means for maintaining balance while jumping among the boulders and cliff ledges so prevalent in their habitat (Heptner and Sludskii 1992; Hemmer 1972; Kitchener 1991). It is popularly believed that the snow leopard's large forepaw serves as an adaptation for walking across deep snow, but it is probably more useful for travelling across steep, loose rocky slopes. The periodic severe snowstorms which occur every 10-15 years are more influential in decimating wildlife: many animals may die from hyperthermia and exposure, or hunger due to their inability to break through the snow or ice to reach forage (Schaller 1977; Schaller and Junrang 1988). Herbivores must contend with a short growing season, which severely limits primary production, and predators must adapt to extremely variable prey distribution and abundance.

On the other hand, this sharply defined elevational and topographic gradient creates spatially diverse and complex habitat conditions with associated opportunities for wildlife, although resource availability is strongly influenced by land-use and human activity. Resources are rarely continuously distributed, rather occurring in small or isolated patches, clumped irregularly in places or sites with a gentle slope, deeper soil and a more favorable exposure to the sun. Over the centuries, the local human cultures have also adapted to these environmental conditions with varying success (e.g, Bishop 1990; Brower 1991), but pastoralism is the dominant land-use found across snow leopard habitat. In fact, at higher elevation, except for tourism and mountaineering, the only human use consists of seasonal (generally summer and fall) grazing of livestock. As a result, humans usually exert strong negative pressures, such as direct retribution for depredated livestock, decimation of the prey base through hunting and poaching, and the displacement of wild ungulates from critical breeding and wintering habitat (Jackson et al. 1994b; Miller and Jackson 1994; Oli et al. 1994). Given this complex environmental milieu, it is important that appropriate habitat parameters be measured for one to fully appreciate the snow leopard's habitat utilization pattern.

Ford (1983) used optimal foraging theory to model home ranges in a patchy environment. He constructed a model which predicted (among other factors) that (1) home range size should be inversely related to maximum resource density and resource renewal rate; (2) the optimal shape should tend to be elongate rather than circular (a length/breadth ratio of 2:1); and (3) animals should concentrate their activity in a particular subregion, the degree to which depends upon resource density. He measured the latter tendency as the ratio of the area which contained 65% of animal occurrences to the area required to contain 95% of the occurrences (analogous to the 65% harmonic mean measure isopleth and core use areas described in Chapter 6). Home ranges of the four snow leopards modelled appear to conform with some of these predictions. Thus, the home range length-width ratio ranged from 1.7:1 to 3.3:1 (Table 6.1, Chapter 6), no doubt due to the elongate nature of habitat resulting from precipitous slopes, gorge topography, and relatively high baseline elevations. Core area use is even more concentrated than that predicted by Ford's model: 47-54% of overall home range use was located within the 30% harmonic isopleth or inner core area (Table 6.5).

Resource density and renewal was not adequately measured in this study to assess its relationship to home range size. In fact, identifying which habitat and behavioural parameters should be measured is a complex undertaking, because one must focus upon those aspects of the environment that an animal perceives as being most relevant to fulfilling its different needs. Morrison et al. (1992) emphasized the importance of being well-grounded in the species' biology, and recommended that selected variables should be (1) measurable to the desired level of precision; (2) biologically meaningful; and (3) relevant to the species involved. Habitat structure, foraging location, and prey consumption all determine the utilized area or habitat of an individual or species. Habitat selection may be influenced by evolutionary factors (which confer reproductive fitness and survival values) and behavioural factors, which provide the mechanism by which animals select habitat from that available to them (Morrison et al. 1992; Stephens and Krebs 1986). The relationship between density and habitat quality is often misunderstood, for animals may be occupying "marginal" habitat because optimal areas are already at carrying capacity (Van Horne 1983). This augurs for the need to examine second and third order habitat selection (Johnson 1980) and to establish baseline conditions in an optimal area like the Langu Valley, where livestock are entirely absent and human influence minimal compared to the more typical situation prevailing across most of the snow leopard's range. In assessing the utilization pattern of snow leopards in a dense population, I have relied upon home range models which provide output that can be geographically referenced -- thus enabling GIS-based analyses of habitat utilization and related landscape-level processes. There is evidence to suggest that the harmonic mean measure and its related utilization distribution oversimplify reality, and fail to measure how coarse-grained an individual perceives its habitat is within a local area and given period of time (Gautestad and Mysterud, In Prep). There is also a real danger of GIS-derived data assuming greater precision than it merits, simply because of the sophisticated algorithms or computing power of the software used (see discussion section of Chapter 7).

Snow leopard home range sizes observed in this study conform with predicted home range size based on body size (Gittleman and Harvey 1982). These investigators examined the relationship between home-range size, metabolic needs and ecology across different carnivore species and concluded that home-range size increased with metabolic need, regardless of taxonomic affinity. If the effects of metabolic need were removed, other ecological variables such as activity pattern, habitat, diet and ecological zonation showed a significant influence on home-range size. Lindstedt et al. (1986) reconsidered the relationship between home range and body size and suggested that animals select their home range areas to meet metabolic needs over biologically critical periods; however, relationships between body mass and home range size were confounded by differences in habitat productivity, methods of home range locations, latitude and social organization. Buskirk and McDonald (1989) concluded that between-site differences in home range size in marten emphasizes the need for identifying ecological factors that may explain such variability. In the case of martens (*Martes americana*), resource abundance appeared to exert the greatest influence on home range size (Thompson and Colgan 1987).   Similarly, Litvaitis et al. (1986) found metabolic home range size in bobcat to be inversely correlated with stem cover density and estimated snowshoe hare (*Lepus americanus*) density.

Whether prey are evenly distributed (almost never), randomly distributed (even more unusual), or clumped (typical pattern), influences a predator's search time and has important energetic, spatial and social consequences (Sunquist and Sunquist 1989). Seasonal movement of prey clearly contributes to a larger home range size and differential use (through the presence of seasonal ranges), such as occurs in puma which have larger summer home ranges compared to winter use areas, in which prey is more concentrated (Seidensticker et al. 1973). The snow leopard is an opportunistic predator, but with a few large prey species like blue sheep, ibex, markhor and Himalayan tahr constituting its dietary mainstay. Observations from widely-separated areas indicate it utilizes alternative prey such as marmot during the summer or livestock during the winter. In the Hemis National Park, blue sheep tended to move into open areas at higher elevation during summer, a time that snow leopards resorted to alternate prey like marmot, Woolly hare and pika. Chundawat and Rawat (1994) felt that the presence of livestock in the Hemis National Park enables a predator prey ratio of one snow leopard to 45 blue sheep, lower than the 1:100 ratio typical for large predators (Schaller 1972). Blue sheep are extremely sedentary in the Langu Valley, and none of the radio-collared snow leopards shifted their use areas to any degree seasonally. The lack of seasonal deer migration was attributed by Sweanor (1990) as the main reason some puma use the same range year-round. Incidental observations suggest seasonal movement in snow leopards occurs where the prey species move distances of 10-20 kilometers or more, such as the Tien Shan (E. Koshkarev, pers. comm.) and parts of Pakistan (Roberts 1977). However, radio-telemetry studies are needed to quantify the extent of summer and winter home ranges in such populations.

Land-tenure systems of medium and large-size felids are unquestionably more flexible than previously suspected (Sunquist and Sunquist 1989), as shown for common leopard, jaguar and puma. These species are able to share common habitat while avoiding intraspecific fights by remaining separated in time, space or both. For example, Neal et al. (1987) observed varying degrees of range overlap within both male and female puma in California, while Rabinowitz and Nottingham (1986) found overlapping male ranges in a jaguar population with a high turnover of males. Maehr et al. (1991) documented extensive home range overlap among normally exclusive adult female puma in an area where prey was more abundant. These and other recent studies reveal wide variability in home range size and overlap between different individuals and sexes among the solitary Felidae, especially where numbers of resident adult, subadult and transient animals are high. Although our understanding of causal factors affecting home range size in solitary felids is still rudimentary, key underlying factors include differences between areas and habitat with respect to prey availability, hunting cover, breeding sites, human disturbance, social or other factors. In discussing land tenure flexibility, Sunquist (1981:52) stated, "...in general, correlates can be drawn between the social system and various ecological factors such as habitat structure, prey size, distribution and density. These factors influence the social interactions and movement patterns of individuals and hence shape the overall social organization of the population." He suggested that the major factor influencing variability is the seasonal distribution and abundance of prey, as well as the cost of "defending" home-range boundaries from intrusions by conspecifics. Sociality in felids and other carnivores is associated with habitat openness (Packer 1986), where conditions usually make it more difficult to protect kills from scavenging by conspecifics or other animals.

Sunquist and Sunquist (1989:285) submit that "sedentary, predictable prey resources are often associated with small, exclusive predator ranges or territories." Rabinowitz and Nottingham (1986:156) noted that, "if density and distribution of prey are favorable, it is reasonable that large solitary felids can share limited areas...", provided there is some mechanism to facilitate mutual avoidance. The Langu Valley snow leopards spent much of their time in or near a relatively small central core area, which supported more blue sheep. Bobcats also concentrated their activities in more prey-rich habitat, although these may constitute only a small portion of their total home range (Heller and Fendley 1986). Seidensticker et al. (1990) attributed the small (6-13 km^2) home ranges of common leopards living along the edge of the Chitwan National Park in Nepal to an abundant nearby food source in the form of wild and domestic ungulates. However, scarce resources can modify land-tenure patterns as well. For example, male and female leopards in the Wilpatti National Park of Sri Lanka overlapped completely, with each pair claiming a 8-10 square km area centered about a permanent water-hole and its attendant prey (Muckenhirn and Eisenberg 1973).

Sandell (1989) suggested that home range size in solitary female carnivores is determined mainly by food abundance, while male spatial organization is influenced by a combination of food outside of the mating season and the presence of receptive females during the mating period. Sandell hypothesized that (1) solitary female carnivore home range size should be correlated with food abundance, especially during the most critical time of year; (2) exclusive ranges should be expected when food resources are stable and evenly distributed, whereas temporal and spatial variation in food availability should tend toward a system of overlapping ranges; and that (3) exclusive ranges should be relatively smaller than overlapping ranges. Unfortunately, the difficulty of measuring and comparing resource abundance, distribution and availability between different study areas makes testing of such hypotheses highly problematic.

Sweanor (1990) concluded that puma in the San Andres Mountains are ultimately limited by food resources, one of the reasons behind the high level of intraspecific aggression that she observed. Reduced female overlap in this population was considered to be related to the type of environment (a desert) and the low prey density present. Interestingly, overlap between male home ranges was more extensive than overlap between female ranges, thus contrasting with many other temperate puma populations intensively studied to date. However, Sweanor found that adult core use areas were used almost exclusively of other puma of the same sex, in sharp contrast to the substantial intrasexual overlap noted among the Langu Valley's snow leopards. Habitat differences led Bailey (1993) to speculate that female common leopards selected higher quality habitat than males: thus, female ranges tended to contain more prey-rich vegetation types than those of males occupying the same area. Female ranges were centered along permanent rivers to which prey is attracted during the dry season and which offers suitable cover for hunting, feeding and the raising of cubs. Bailey found that the amount of overlap between home ranges of common leopard varied with the abundance and distribution of prey and cover, and home range size. Increased overlap was observed in prey-rich areas with an abundance of cover, breeding sites and dry-season habitat. Such a land tenure system allowed young leopards to remain in the same area used by their parents as long as food was abundant and they did not compete reproductively with their parents or other resident leopards. The pressure to disperse intensified when they matured sexually or encountered scarce resources. Dispersal of subadult male leopards from their natal ranges and their influx into surrounding areas appears to depend upon leopard population density and the availability of prey (Bailey 1993). A similar situation appears to pertain to my study area, which is best described as a prey rich, heterogenous habitat in which parents and offspring are able to share the same space for an extended period of time before young animals must disperse or establish themselves as residents with full rights to the area. M3 may be an example of a late disperser, while M2 may have established itself as a permanent resident.

Prey abundance is generally considered the most important factor in the selection of habitat types in bobcat, followed by such factors as protection from severe weather, the availability of resting and denning sites, dense cover for hunting and escape, and freedom from disturbance (Bailey 1974; Litvaitis et al. 1986). Behavioural factors, including hunting, travelling and social interaction appear to dictate the temporal and spatial use of habitat types (this study, McCord 1974). Bailey (1974) suggested that female bobcats utilize better quality habitat than males because they require more prey from a smaller area, especially during the physiologically demanding period of raising offspring. Mutual tolerance, especially among males, reaches its zenith in grizzly bear (*Ursus arctos*) in Alaska, when they are concentrated at seasonal salmon feeding sites (Stirling 1993). However, this high degree of tolerance is short-lived, waning with the end of salmon spawning.   Still, localized abundant or super-abundant food resources can permit more individuals to occupy smaller and overlapping home ranges than is the norm for the species. Davies and Houston (1984) considered the sharing of a common area to be an economically efficient strategy in situations of resource abundance. In areas where essential resources, especially food, are in short supply, home ranges are expected to be larger, with zones of overlap further apart and/or more poorly defined.

While a key factor, food availability may not be the only factor in home range selection. Thus, Anderson et al. (1992) found that female resident puma tended to occupy home ranges in low deer-elk density areas, while resident males appeared to select for high deer density areas. They speculated that females with dependent young may have been attempting to avoid cannibalistic males by occupying areas less frequently utilized by resident males. During periods of food scarcity, mutual avoidance may cease to function as a spacing mechanism in lynx (Tumlinson 1987). Seidensticker et al. (1973) concluded that food abundance was not ultimately controlling the puma population he studied, for an apparent increase in ungulate prey was not followed by a similar response in the puma population. He felt that some other requirement within the vegetative-topographic complex determined population size, possibly social factors.

The snow leopards' preference for broken terrain with cliffs is well substantiated in the literature (Fox 1989; Heptner and Sludskii 1992; Jackson and Ahlborn 1984; Mallon 1984, 1987; Schaller et al. 1987, 1988b). By bedding on a cliff, a snow leopard is more likely to place itself closer to large prey, since blue sheep tend to utilize the same landform feature during the nighttime. During daytime, blue sheep are also more likely to be close to a cliff, broken terrain or similar landform offering suitable escape cover from predators (Wegge 1976, 1979; Schaller 1977). Chundawat (1990a) found snow leopard and blue sheep habitat use patterns were very similar, except that blue sheep preferred open, smooth terrain for foraging and tended to avoid very broken areas, a pattern remarkably similar to that existing in the Langu Valley. Cliffs are used by other key snow leopard prey species, including ibex (Fox et al. 1988). In rugged terrain, snow leopards are able to increase their search area by seeking ridges, the tops of cliffs and rock outcrops from which to scan the surrounding land for potential prey. This strategy is greatly facilitated by the snow leopards' preference for bedding and travelling along cliffs, ridges and other terrain edges. Other solitary felids like leopard, puma and bobcat also take advantage of rocky terrain. For example, Seidensticker et al. (1973) found that puma preferred timbered, rocky broken areas. Puma in Utah preferred habitats that offered good cover for hunting (Logan and Irwin 1985). Rugged terrain and dense vegetation may also limit the number of escape routes available to prey, while providing excellent cover and enabling the predator to approach its prey more easily. Hunting success may be enhanced on steep slopes, since these have more limited visibilities (especially in the upslope direction), thus facilitating a closer stalk; fleeing animals may find it difficult to run fast, giving a non-courser like the snow leopard the advantage it needs to successfully catch and subdue its victim. Increased vulnerability to predators may explain why extremely cover-rich areas, such as those afforded by heavily broken terrain and sites with more than 75 percent vegetation canopy cover, were generally avoided by blue sheep (this study).

Rocky terrain provides other potential benefits as well. The adaptive coloration of snow leopards enables them to blend into the background remarkably well, and numerous authors have commented on how difficult it is to detect a snow leopard hiding or stalking among rocks. By utilizing snow-free, steeply-sloped areas and sites with southerly exposures, snow leopards avoid the need to break new trails in deep snow. Heptner and Sludskii (1992) observed that snow leopards are poorly adapted to moving over deep, loose snow, and in these situations utilized "beaten trails", such as occur along the windward side of mountain crests or cliffs. Snow leopard attacks upon domestic stock appear to occur more frequently during severe winters with deep snow, when animals are forced to lower elevations near human settlements. It is possible that wild ungulates are harder to hunt under such circumstances.

Sixty-one percent of all stationary locations at which a snow leopard remained for two days or more (and may therefore have been on a kill), were located within the overlapping core use area (Figure 20). In terms of landform type, these sites consisted of a cliff followed by smooth and moderately broken terrain. Areas more than 125 m from a cliff or further than 400 m from a travel route were significantly under-represented in the sample of known or suspected kill sites. This would suggest that the radio-tagged snow leopards made a significant proportion of their kills while moving along a cliff or travel lane. The suspected kill sites tended to be located within 1 km of prime blue sheep habitat on Tillisha Mountain which supported in excess of 15 - 20 animals/km^2 (Figure 21). Much of the area mapped as prime blue sheep habitat consisted of smooth-sloped and rolling alpine grassland or subalpine shrub, preferred foraging habitat for blue sheep. At night, blue sheep moved onto cliffs or broken terrain along the periphery of these foraging areas; if disturbed by predators, they sought refuge on the steep slopes bordering the Langu River and Tillisha gorge. Hornocker (1970) concluded that prey are less vulnerable in an area that has been recently hunted. If this holds true for blue sheep, I would expect fewer successful kills in or close to a frequently visited area, such as the common core area with its high density of potential travel lanes. This does not appear not to be the case in the Langu Valley, for more kill sites were apparently situated within the well-travelled the core area.

Considerably more ridges and other potential travel routes intersect the common core area than the nearby high-density blue sheep area (Figure 16); thus disturbance of prey by non-hunting cats should be minimized, in contrast to potentially intensified interference when blue sheep are on or close to nighttime bedding or escape habitat. Hunting sites are not necessarily located in those parts of the predator's home range with the highest prey densities (Anderson et al. 1992); rather, good cover enabling a close approach may ultimately be more important to success than the presence of large herds of ungulates, which are usually harder for a predator to approach undetected. By placing themselves on or near cliffs and along the edge between blue sheep escape and foraging cover, snow leopards may be maximizing their chances for successfully locating and killing prey. This is speculative, for behavioral studies quantifying hunting patterns and success have yet to be undertaken in the snow leopard, a secretive and especially difficult felid to study.

Presumably, reproductive success in female snow leopards is closely linked to the availability of secluded denning habitat, in close proximity to areas where prey availability and abundance is dependable. Reproduction is very expensive energetically, given the relatively long period of lactation and training involved; reproductive advantage likely accrues to those females selecting inaccessible den-sites within reach of prey rich sites. Thus, they must secure a site where they can hide their cubs from other predators and humans for an extended period, especially during the first three months of life, yet obtain sufficient food without investing excessive energy searching for prey. Snow leopard F1 selected a maternal den within her core-use area (Figure 12). Located at 3,960 m in a cave near the top of a cliff, it offered ample cover and a good vista of the surrounding terrain. The den was within 30 m of a small birch forest where moderately broken terrain was juxtapositioned with a large smooth slope, vegetated with mixed and subalpine shrub. The smooth grass-rich slope was regularly utilized by blue sheep that sought refuge on the nearby cliffs at night. Blue sheep densities in the general area were estimated at about 10 animals per km^2 (unpub. data). In prey-poor areas, females have to spend more time away from their cubs, thus exposing them to danger for a longer period, especially if habitat in the form of strongly broken terrain and cliffs is lacking. These threats are particularly great where livestock is grazed during the summer, or where poaching of prey species is pervasive. Most shepherds will catch or kill any snow leopard cub they find, especially if there are persistent reports of livestock depredation or ample opportunity for locating a female and her cubs.

To what extent can the snow leopard's habitat preferences be used to predict which sites are most at risk to livestock depredation? Jackson et al. (1994b) characterized 70 kill sites in the Annapurna Conservation Area of Nepal where livestock were known or suspected of having been killed by snow leopard. These authors concluded that "depredation hotspots" were most likely to be located in moderately broken terrain, within 100 m of a cliff, near a vegetation edge, or close to a heavily broken area (especially if a human settlement is located nearby). Snow leopard were responsible for annual predation rates of 7.1 (*yak-chauri*), 0.3 (cattle), 2.4 (sheep and goat) and 6.5 (horse) percent, which amounted to an overall depredation rate of 2.8 percent (Jackson et al. 1994b). This study indicated that depredation hotspots are not necessarily only associated with areas supporting a low density of natural prey species: surveys confirmed the livestock biomass to be as high as 1,700 kg/km^2, or nearly three times that of blue sheep (304 kg/km^2, reported by Oli, 1994). Oli estimated the snow leopard/blue sheep ratio at between 1:114-159. Livestock are easily killed, for only sheep and goats are guarded to any significant degree. Oli et al. (1993) found that domestic prey constituted 34% of the biomass of the diet of these snow leopards. Livestock is an important component of the snow leopard's diet in other parts of its range as well. For example, Chundawat (1992) determined that 39% of the snow leopard's diet, on the basis of biomass, consisted of domestic stock during the summer months and 34% during the winter; Schaller et al. (1987, 1988b) also reported high domestic stock losses from snow leopard range in China. Depletion of native ungulates like ibex and blue sheep probably results in increased predation upon marmot (summer) and livestock (year-round), and may result in increased dispersal of snow leopard from a particular area or population center with an inadequate food base.

Social and Marking Behaviour: The functional significance of social marking in mammals has received special interest since review papers were published on the topic in the early 1970's (for example, Johnson 1973; Ralls 1971; Wemmer and Scow 1977). Social marking patterns in mammals are reviewed by Brown and MacDonald (1985), Gosling (1982) and Gorman and Trowbridge (1989). Based on current knowledge, Bailey (1993) identified four primary functions for scent-marking in the common leopard: (1) to delineate their home ranges; (2) to communicate specific information about their social and reproductive status; (3) to prevent or enhance encounters among leopards, especially along common travel routes; and (4) to identify places of special interest such as kill sites or encounter sites between leopards and other predators. Smith et al. (1989) concluded that scent-marking served as the primary means for shaping and maintaining tiger territories and that tigers must learn to use and scent an area frequently in order to establish a strong claim to it.

These observations appear to be applicable to the snow leopard population I studied which exhibited a particularly sophisticated system of social contact for a species that normally avoids direct contact (except during breeding), and yet shares remarkably small and confined common use areas, without any evidence for territoriality or direct conflict.

Assuming that snow leopards are capable of using olfactory cues for determining an individual's gender (Gorman and Trowbridge 1989), scent-spraying rocks and scrapes provides the species' with an efficient means for locating mates and spacing themselves within shared use areas. Temporal information contained in such sign may allow individuals to avoid using areas currently or recently occupied by other snow leopards. Besides reducing the chance for a direct encounter with another snow leopard, this may help animals to better space themselves with respect to their prey. For example, it would tend to limit the amount of time spent in an area where prey species may have been disturbed and thus are more wary. Olfactory communication may serve to supplement visual or auditory forms of communication such as scraping and yowling. Odors can be deposited in the environment as scent marks and thus provide a spatial and historical record of an individual's movement and behaviour. Leyhausen and Wolff (1959) suggested that "marking might act like ‘ railway signals’ to minimize encounters between individuals by signalling how recently an animal has passed". Snow leopards are well-endowed with odoriferous glands and possess a complex behavioural repertoire for communicating with conspecifics. All home ranges of the Langu snow leopards contained a network of interlinked trails and travel corridors, including cliffs, ridges, riverine bluffs and streambeds, where individual snow leopards could leave (or not leave) sign like scrapes, scent-marks and feces. While residents may only make slight changes in their movements in response to scent marks left by other cats, transients and animals of like sex may react more drastically by avoiding an area with fresh sign. Both resident and transient leopards used the same system to travel through the rugged, broken terrain, circumnavigate impassable obstacles such as vertical cliffs, or simply to rapidly reach another part of their home range. As noted by Gorman and Trowbridge (1989), social odours, whether feces, urine or glandular secretions, are a limited resource, and the tendency of snow leopard to mark selectively with respect to terrain features and to concentrate sign to relatively few places within the home range appears to be both adaptive and efficient.

Scent-marking appears to be strongly related to sexual activity and may be due, in large part, to increased frequency of female spraying (Rieger 1978). Ahlborn and Jackson (1988) concluded that seasonal differences in marking within the core-use area were apparently related to increased marking intensity rather than differential visitation by snow leopards. Thus, the intensity of marking (amount of marking per visit) among the Langu Valley snow leopards during pre-oestrus and oestrus periods (December through March) far exceeded that found during post-oestrus months. While Ahlborn and Jackson (1988) were unable to measure snow leopard marking rates according to sex, female tigers have been reported to mark intensively just prior to oestrus (Smith et al. 1989). Studies of captive felids have indicated that urine is a potentially rich source of information concerning reproductive state: estrogen levels increase markedly as the female becomes more receptive, but detection in the field would be extremely difficult (David Wildt, pers. comm.).

It is behaviourally and energetically advantageous for solitary animals sharing a common space to mark at or near the same places. Snow leopard scrapes and scent-sprays are distributed in ways that maximize their chance of being discovered by other individuals for whom they appear to be intended (Jackson and Ahlborn 1988). In this regard, Gorman and Trowbridge (1989:65) commented, "a recurring feature of object marking is that scent marks are placed not at random within the environment, but instead at visually conspicuous, often elevated, and traditionally used landmarks". This certainly seems to be the case for snow leopard, which remark existing sign and leave new sign more intensively than any other large solitary felid. Although overmarking has been demonstrated in the brown hyena (Mills et al. 1980), it has not been widely reported among the solitary Felidae. Gorman and Mills (1984) suggest that as territory size increases, so it becomes more difficult for an animal to mark and maintain its respective area, with 'hinterland marking’ providing an alternative, safer strategy. In many ways, this strategy is comparable to the pattern of core area marking noted in my study, although no evidence was found for territoriality in snow leopard. Common leopard scrapes are more long-lived during the dry than the wet season, and Bailey (1993) suggested that they scrape more often in areas of low precipitation than in areas with a high rainfall. The high incidence of scraping in snow leopards compared to other species may result from the fact that this species' range largely encompasses areas of limited snowfall and/or accumulation, as well as sparse rainfall.

It is reasonable to assume that snow leopards, like all vertebrates, remember the location of a favourable bedding site, a productive hunting area or some secure escape cover within the limits of their home range. Even if these resources are heterogeneous and patchy, animals can "home in" on such areas if they have appropriate behavioral mechanisms for identifying and locating specific resources, and if the habitat follows a reasonably predictable pattern. Landform edges may serve as one cue for snow leopards, aiding them to move about their home range in search of food or mates. By using ridges and other easily recognizable terrain features, and by leaving scrapes and other markings, so snow leopards are able to live a solitary yet "social" life. Behaviourally, the snow leopard needs to balance the energy expended in locating, pursuing and killing prey, with that expended in avoiding or accommodating conspecifics using the same area.

The sharing of a common space also minimizes the daily distance an animal has to travel (Kitchener 1991), thus further conserving its energy -- a potentially important consideration given the steep and rugged terrain prevailing within much of the snow leopards' range. Reduced cost of movement is a potentially important benefit associated with compact home ranges and well-defined core use areas. The act of locomotion in such precipitous and broken terrain as the Langu valley must involve relatively large energetic cost: it was hardly surprising that the mean daily distance moved by snow leopard was only slightly over a kilometer. The ability of a cat to protect its home range from unwanted intruders is contingent upon its capability to visit and regularly sign mark all areas subject to visitation by conspecifics. Only by continually updating its scent marks can an individual "remind potential intruders who is at home" (Kitchener 1991:163). A strategy aimed at maintaining exclusive male ranges or territories in rugged, mountainous terrain may therefore be energetically prohibitive in permitting regular remarking of widely dispersed sites. By advertizing its presence within a smaller core area, located in close proximity to a food-rich area, snow leopards appear to have the best of two worlds.

Ahlborn and Jackson (1988) emphasized that the disproportionate use of different topographic elements for marking should be viewed as a fourth-order selection. They argued that a considerable number of prior selections have already been made by the individual as it leaves sign along its travel route, in various habitats, within its home range. Site selectivity by snow leopards for marking thus becomes a question of where an individual should mark along its travel route to most efficiently and effectively communicate with conspecifics. Radio-tracking indicated that travel routes were far more extensive than suggested by sign alone (see Chapter 7, Figure 16). For example, river beds were used extensively for travel, but marking was far more likely to occur at or near a confluence than elsewhere. Furthermore, sign was almost always deposited in the most "obvious" place. Even in smooth terrain generally devoid of prominent features, almost without exception the only locations marked were rocky outcrops. Other solitary felids also deposit their sign in prominent sites. For example, Seidensticker et al. (1973:47) observed that puma tended to scrape in areas where " the lay of the land dictated easy passage", such as the mouths of canyons, in draws, and on ridges. Reused sites were in situations where topography "moulded a convenient runway or pass."

In light of these considerations, are the Langu Valley snow leopards using a common core area because it better satisfies their basic ecological needs like food provisioning, diurnal bedding, and the raising of young -- or does it serve more of a social function, enabling regular interaction between individuals sharing a common space, through the frequent deposition of sign? This question is not easily answered, as I used multivariate analysis more for exploratory purposes than for confirmatory analysis (Morrison et al. 1992). Other factors such as the relatively young age of males and possible filial relatedness among the cohort studied complicates matters, for carnivores may be more willing to share use areas if those involved are related and not perceived as being potential competitors. For several reasons, I suspect that both prey and social spacing requirements were satisfied within the overlapping snow leopard core area delineated by the spatial analysis I conducted. First, habitat parameters in the core area tend to more closely match those shown to be preferred by snow leopard, and second, the core area is located at the intersection of numerous travel lanes and contained as much as four times the sign found elsewhere within the snow leopards' home ranges. Although snow leopards were able to spend a substantial amount of time within the core area, social marking better assured that such use was temporally separated. The data also suggest that more snow leopard kills were made in or near the common core area, which abuts and encompasses a significant portion of the area with the greatest blue sheep density (Figure 20). Hunting places and opportunities appear to be more favorable here, at least on the basis of snow leopard habitat preferences with regard to parameters like distance to a cliff, the nearest edge, and a potential travel lane. This situation may offer the best of combinations, for Kruuk (1986) observed that hunting areas and other aspects of prey availability may be at least partly independent of actual numbers and biomass of prey.

In summarizing, the Langu Gorge is characterized by a heterogenous habitat, an abundant and reliable food source in the form of blue sheep, the absence of any other large competing predator, and a snow leopard population that shares a common core area. Tagged snow leopards exhibited a strong preference for broken terrain, mixed shrubland, and bedding sites close to edges, linear features and ridgelines or other travel lanes. Core use areas overlapped extensively, but their use was temporally separated. The shared core area partially overlapped a shoulder of Tillisha Mountain, which supported the most extensive grassland and obviously productive blue sheep habitat in the study area. Jackson and Ahlborn (1989) speculated that the well-developed social marking system of snow leopard permits temporal spacing within a relatively small area, so all animals residing there can share the area's resources with minimal intraspecific strife. Mutual avoidance appears to be facilitated by scent-marking, scraping, and deposition of other sign, which presumably identifies the particular snow leopard, its sex, relative age, and reproductive status, and thereby possibly conferring some home-area "ownership right" over periods of time (Bailey 1993; Kitchener 1991; Smith et al. 1989). The incidence of marking within the core area was four times greater than non-core sites (Ahlborn and Jackson 1988). Significantly more sign-marking was found along linear topographic features, such as major ridge-lines forming the juncture of large stream confluences, along the knife-edged sections of ridges that separated drainages, and along the base of prominent cliffs. These terrain features are well represented in the core area. Judging by the intensity of use of core areas, the large amount of overlap among individuals, and the relatively small total home areas, it is remarkable that the tagged cats managed to remain on average more than two kilometers apart. These observations imply that the Langu snow leopards were actively avoiding one another, while sharing the same area. Presumably this sophisticated communication system permits coexistence among an extremely solitary species, enabling individuals to better exploit an unequally distributed food resource, especially in areas with a high density of snow leopard.

These conclusions may not be applicable to other snow leopard populations. The primary constraint of my study lies in the small sample of individuals captured, instrumented and successfully monitored, as well as its relatively short duration (3.5 years). As noted above the high degree of home range overlap observed could be related to several factors, and is clearly complicated by the social status and ages of the individuals sampled. Thus, the snow leopards may have shared a common area because some grew up together in the same vicinity, were related or had not yet dispersed. The subject of land-tenure in snow leopard must therefore remain somewhat obscure, and neither is any information available on related topics like dispersal, intraspecific infanticide or the extent to which resident males achieve matings versus those made by non-residents. However, my study provides a good starting point for urgently needed long-term investigations of snow leopard and its high-altitude ecosystem. Different patterns of home-range, land-tenure and social marking are likely to be found in less favorable habitat where there are fewer snow leopards or where man and wildlife coexist precariously. Conversely, it may prove that a strongly overlapping land-tenure system is pervasive in the species, and an adaptation for better accommodating immigration in highly fragmented and insular mountain ranges, such as those found in China's Tien Shan and Mongolia's Gobi regions. The puma of the southwestern United States inhabit similar terrain, and Sweanor (1990) felt that animals immigrating from other areas may choose to stay in a localized area that is already supporting residents rather than risk travelling across large desert basins in search of more suitable sites. With critical information lacking on dispersal in snow leopard, I urge future research efforts to focus upon snow leopard populations in marginal habitat, in order to better understand important ecological relationships. Such knowledge is vital for the effective protection of snow leopard and sustained utilization of its fragile mountain habitat across Central Asia.

10.2 Comparisons with Other Solitary Felids

While snow leopards share many ecological and behavioural characteristics with other large solitary felids like common leopard, tiger and jaguar, it is closely associated with mountain habitat like the puma (Table 49). However, puma generally occupy larger home ranges, tend toward range exclusivity in males, and are found across a greater diversity of habitat types. Partial or full range exclusivity is characteristic of all other solitary felids, especially in males. This may also prove to be the case in snow leopard for I do not know how typical the population I studied is. Snow leopard and common leopard ranges overlap in a few places, along the Himalaya and mountains of south-east Tibet where low-lying river valleys penetrate into the uplands of central Asia. Usually, common leopards are found in

Table 49: Ecological and behavioural characteristics of some large solitary felids

Feature	Snow Leopard	Common Leopard	Tiger (Bengal)	Jaguar	Puma	Eurasian Lynx
Ecological						
Primary habitat(s)	mountains, alpine zone	brushlands, forests	forest, woodlands & floodplain	rainforest, swamps	forest, shrublands, desert	forest & shrubland
Principal Prey	sheep, goats, livestock & rodents	antelope, hyrax & small prey	large or medium-sized deer & pig	peccary, capybara, armadillo, small prey	deer, elk, peccary, & small prey	deer, hares & rodents
Home range size (km^2) (range):						
Male	10 - 21	9 - 388	60 - 105	28 - 152	42 - 826	14 - 210
Female	18 - 36	6 - 487	16 - 39	10 - 168	32 - 685	10 - 26
Land tenure	♂ = O ♀ = O	♂ = E ♀ = O	♂ = E ♀ = E	♂ = E ♀ = O	♂ = E ♀ = O	♂ = O ♀ = E
Density No/100 km^2	0.3 - 12.0	0.6 - 16.4	2.3 - 4.7	1.6 - 6.6	0.4 - 4.4	0.9 - 10.0
Behavioural						
Scent-marking	urine/scrapes/feces	urine/scrapes/feces	urine/scrapes/feces	scrapes	scrapes	urine/scrapes
Spacing vocalization	yowling ?	rasping call	roaring	pulsed roar	none ?	none
Fighting common	no ?	no	no	no ?	sometimes	sometimes ?
Differential marking	yes (core area)	yes (periphery)	yes (periphery)	occasional	periphery	unknown
Sharing of core areas	yes	occasional	occasional	occasional ?	occasional ?	unknown
Seasonality of Mating	very restricted (winter-spring)	year-round (peak July-Sept)	year-round (peak Nov- May)	year-round (mid-late wet season)	year-round, several peaks	very restricted (spring)

Sources: Kitchener 1991; Guggisberg 1975; *Snow Leopard*: this study; Fox 1989; Schaller 1977; Schaller et al. 1994; *Common Leopard*: Bailey 1993;Schaller 1972; *Tiger*: Sunquist 1981; Schaller 1967; *Jaguar*: Rabinowitz and Nottingham 1986; Schaller and Crawshaw 1980; *Puma*: Anderson 1983; Seidensticker et al. 1973; Hornocker 1970; *Lynx*:Tumlinson 1987

E = Exclusive range; O = Overlapping range more densely vegetated lower valley slopes, with snow leopards inhabiting the more open alpine and subalpine zones. Common leopard seems to subsist more upon wild goats and domestic livestock, while the favorite prey of snow leopards are blue sheep and ibex (Schaller 1977). As the more aggressive of the two species, the common leopard is likely the more dominant in areas where both overlap. Common leopard utilize different sized prey and center their activities in different sites where they overlap with a considerably larger species, the tiger (Seidensticker 1976). Considerably more of the snow leopard's range is sympatric with that of the Eurasian lynx, *Lynx lynx*. Competition is minimized by differences in prey selection, with lynx largely subsisting upon much smaller prey, especially hares. As noted in Chapter 9, snow leopard are able to regularly hunt prey larger relative to their body size than other solitary felid, with the possible exception of the puma (Packer 1986). It is worth noting that small prey is important supplementary food in all felids, except possibly for tiger.

Snow leopard and lynx are the only two solitary felids in which all females are sexually receptive in unison, during a remarkably short time frame. Compared to other cats, there is very limited potential for an individual male to monopolize multiple females, and correspondingly, little incentive for a male to invest substantial energy in maintaining an exclusive range, at least on the basis of potential reproductive gain. Unfortunately information on land-tenure among the Eurasian lynx is very limited, but studies in Alaska indicate that males may either occupy exclusive ranges or share large areas with other males (Bailey et al. 1986). Heptner and Sludskii (1992) report instances of a receptive female being accompanied by as many as five or more male lynx.

Hornocker and Bailey (1986) compared natural population regulation in bobcat, puma and leopard, noting that the availability of food appeared to control leopard populations, with subadult and cub mortalities of 32 and 50 percent respectively. Socially mediated forms of mortality, such as intraspecific killing and male infanticide have been reported in a number of felids, including lion, tiger, puma, and leopard, but documentation in snow leopard must await further research (Bailey 1993; Kitchener 1991; Smith and McDougal 1990; Sweanor 1990). Dispersal may provide a significant population regulating mechanism in snow leopard, especially given its generally fragmented habitat (Greenwood 1980).

10.3 Implications for the Conservation and Management of Snow Leopards

The principal threat to snow leopard arises from poaching or hunting for its valuable pelt and bones, the killing of animals suspected of taking livestock, and depletion (through hunting, poisoning or habitat loss) of natural prey species, thereby increasing the snow leopard's dependence upon domestic stock. Although pelts may fetch from 50 to 500 US dollars or more, the international fur trade has declined significantly due to regulation, animal rights activism, and changes in western fashion, the primary market for fur coats (Nowell and Jackson 1995). However, snow leopards appear to face significant threat from the Chinese medicinal trade (Jackson et al. 1994a), which places high value on the bones of tiger and the larger felids. For example, local tribesmen in northern Nepal are trading snow leopard bones for domestic sheep along the border with Tibet to persons from as far away as Beijing. Medicinal products are marketed in Asia's wealthy cities like Hong Kong, Seoul, Taipei and Singapore, where demand greatly exceeds supply.

Although snow leopards have been extirpated from some parts of their former range, baseline information is lacking, and there are no reliable estimates of the total population. Fox (1989) reported that suitable habitat totalled 1,230,000 km^2, but this figure should be viewed as preliminary until the snow leopard's distribution pattern and overall range can be more accurately defined (Hunter and Jackson, In Press). Green (1988) estimated the world's population at 1,504 - 2,880, while Fox (1989) put the number at 3,350 - 4,050 individuals. During recent years, population estimates for several countries, notably China, Nepal and parts of the former USSR have been revised upward (Jackson and Ahlborn 1990; Schaller et al. 1988a, 1988b, Koshkarev 1989), suggesting that there may possibly be as many as 5,000 - 7,000 snow leopards remaining (Fox 1994). However, lack of information on population density and current distribution are significant constraints to establishing the total number present in each of the 12 countries supporting wild snow leopards. See Nowell and Jackson (1995) for information on the status and distribution of snow leopards.

From the conservation and biodiversity perspectives, the snow leopard can be viewed as an indicator or flagship species for motivating the general public and decision-makers to ensure that Asia's high mountain ecosystems are protected and well-managed *in-perpetuity*. Snow leopards exhibit some of the elements associated with an extinction prone species, including low population density, comparably large home range, and the need for a relatively pristine or undisturbed environment (Terborgh 1974). While the species also shows some features found in "keystone species" (Mills et al. 1993), snow leopards are better viewed as a "flagship or charismatic megafaunal species" about which to rally public support for the conservation of high-altitude areas. By protecting snow leopards, habitat for a wide-range of other alpine plants and animals is also protected. The International Snow Leopard Trust, a non-profit organization devoted to the protection of snow leopard and its habitat, advocates the species as an indicator for environmental equality, arguing that the environment is more productive and healthy where snow leopards occur in good numbers (Jackson and Hillard 1986).

Long-term conservation of the snow leopard requires an understanding of such life-history parameters as home range size and configuration, seasonal shifts in range, core areas, dispersal rates and patterns, and habitat fragmentation (Villarrubia and Jackson 1994). This information can be used, in concert with socio-economic baseline data and well-grounded understanding and appreciation of local people's aspirations, to design more effective conservation programs supported by the local residents (Miller and Jackson 1994; Schaller et al. 1987). Conservation plans should be prepared with the principles of conservation biology in mind (Meffe and Carroll 1994). Fortunately, conservationists are beginning to adopt the landscape perspective when designing such plans or when analyzing the environmental factors affecting a species of interest. Therefore, some of the key elements in the conservation and management of snow leopard are: (1) field surveys to determine its current status and distribution, using a standardized survey technique; (2) a country by country assessment of gaps in the protected areas coverage; (3) identification of key corridor and buffer areas linking adjacent protected areas or critical snow leopard habitat; and (4) habitat and species-specific management actions and strategies aimed at minimizing poaching and other human disturbance, reducing people-wildlife conflicts due to the predation of livestock, ensuring sufficient wild prey, and maximizing the biodiversity value of key areas, both within and outside of the existing protected areas network.

With the advent of GIS and increased availability of remotely-sensed data, basic principles of landscape ecology can be applied to snow leopard conservation on a regional basis. An early step in the process involves the use of "gap analysis" to map alpine habitat and biodiversity patterns, as a basis for ensuring all representative habitats and ecosystems are present within the existing or proposed protected areas network, buffer areas or other special management zones (Scott et al. 1993). While gap analysis is usually directed toward assessing multi-species (plant and animal) distribution patterns, it is equally applicable to assessing gaps in the distribution of a single species (provided it is based upon good information). In the case of snow leopard, a problem arises from the fact that it is not closely associated with a particular, definitive vegetation type that can be easily mapped. Rather, the species is found in arid and semi-arid shrubland, and grassland or barren habitats. Dense forest is avoided, although snow leopards occupy open coniferous forests in the Sayan Mountains of Russia and parts of the Tien Shan Range (Heptner and Sludskii 1992). According to these criteria, much of Central Asia would qualify as potential snow leopard habitat. Blue sheep and ibex are closely associated with snow leopard, and their presence can be used to delineate potential snow leopard habitat.

Land-surface ruggedness offers another means of mapping and classifying potential snow leopard habitat, especially if it can be combined with other factors such as human population density, or the density of settlements and roads. The close association between snow leopard and the presence of rocky, broken terrain (including cliffs) has been well documented by this and other studies. Findings from this telemetry study were used by Jackson and Ahlborn (1984) to develop a habitat suitability model (HSI) for snow leopard for application in areas like the Langu Valley. They later used a simplified version for assessing habitat suitability throughout the Nepal Himalaya on the basis of 1:250,000 topographic maps (Jackson and Ahlborn 1990), but neither models have been subject to field validation. Potential habitat can be identified and predicted using terrain or digital elevation models developed specifically from topographic contour maps or other sources (Hunter and Jackson, In Press). Since accurate maps are difficult to procure, aerial radar and improved resolution satellite stereo pair imagery offer an alternative to reliance upon militarily restricted topographic maps. Digital imagery has been used with varying success to identify ibex habitat in Italy (Wiersema and Schroder 1985), but there are many obstacles to overcome, not least of which is the high cost of developing digital terrain models (DEMs) (Hunter and Jackson, In Press). It is essential that HSI models be rigorously tested and refined if they are to serve as a reliable management tool. This will require systematic research in other parts of snow leopard range, under a variety of conditions, followed by an intensive period of model validation (Verner et al. 1986). Capen et al. (1986) listed some of the many potential problems in deriving single-species habitat models from multivariate analyses, including the difficulty of obtaining an adequate sample size, estimating habitat parameters within normally acceptable margins of error, and the fact that some biologically important components of a species' niche are not estimated at all.

While these techniques may aid in locating potential snow leopard habitat, there is no alternative to ground-based verification for establishing both the presence/absence and abundance of snow leopard. Unfortunately, field surveys are very expensive and time-consuming, and require trained and motivated personnel. The need for a standardized approach to surveying and mapping snow leopard range was recognized by the International Snow Leopard Trust in 1989, when it established the SLIMS (Snow Leopard Information Management System) protocol. This involves use of standardized sign transect survey techniques for detecting snow leopard presence and relative abundance, based upon sign abundance and the status of major prey species, derived by systematically censusing and extrapolating data from representative sample blocks (Jackson and Hunter 1995). A knowledge of marking preferences in snow leopards is vital to proper transect placement and the interpretation of field observations (Ahlborn and Jackson 1988). This study indicated the snow leopard's preference for utilizing ridgelines, riverbeds and other linear features as travel lanes, and confirmed that core use areas contained an abundance of these type of features (Chapter 7). A discriminant function model was developed to help predict and locate core use zones in other areas inhabited by snow leopard. This model suggests that distance to the nearest ridge, travel route or lane, and stream or river confluence may reliably predict the presence of a core area. Potential sites could be identified by examining topographic maps or aerial photographs, thus better prioritizing sites for field visitation and status validation.

More research is needed to establish snow leopard and large prey density and resultant predator/prey ratios in different parts of its range, under varying habitat conditions. The calibration of snow leopard densities with prey population estimates (numbers and biomass) for wild ungulates, livestock and rodents (primarily marmot), based upon systematic surveys, may help to determine the degree to which food abundance and availability influences population size in the species. Snow leopard densities in good habitat range as high as 10-12 residents, transients and juveniles per 100 km^2 (Jackson and Ahlborn 1989), with Chundawat (1992) estimating 8 individuals per 100 km^2 in a protected area in India which supports a good number of blue sheep and livestock. Oli (1994) judged that there were 4.8-6.7 leopards/100 km^2 in the Manang Valley in Nepal, another area with an abundance of blue sheep and domestic stock. The livestock biomass of this area is as high as 1,700 kg/km^2 (Jackson et al. 1994b), compared to an estimated blue sheep biomass of 304 kg/km^2 (Oli 1994). These figures compare favourably with those for puma, the ecological equivalent of snow leopard in North America. Thus, the maximum mean resident densities of puma are 3.3/100 km^2 (Hopkins 1989) and 3.0/100 km^2 (Neal et al. 1987) in two areas in California, protected for several years from trophy hunting. In one area studied by Neal and others, the adult puma density was estimated as high as 5.1/100 km^2. This contrasts with densities of 0.3-0.5 resident, transient and juvenile puma per 100 km^2 in Utah (Hemker et al. 1984) and 1.1/100 km^2 in Colorado (Anderson et al. 1992), both involving populations which were either hunted or occupied less productive habitat than that found in California. Sweanor (1990) reported densities of 1.7 - 2.3/100 km^2, or 0.9-1.1 adult residents per 100 km^2 in the San Andres Mountains of New Mexico, a relatively isolated desert mountain range. Seidensticker et al. (1973) placed the resident puma density at 1.7/100 km^2 in Idaho, while Logan et al. (1986) reported a density of 2.0/100 km^2 in Wyoming.

A knowledge of prey density and predator:prey ratios would help set limits for validating snow leopard numbers in a particular area: clearly, there must be sufficient prey to support the predicted predator population. Field studies are needed to better establish how many blue sheep or similar large prey animals are needed to sustain predation by snow leopard at varying densities, with or without the presence of a buffering species like marmot. No effort has been made to determine the extent to which hunting by humans is placing the snow leopard population at risk; Kenney et al. (1995) used a stochastic spatial model to demonstrate the long-term, negative impact of unabated poaching on tigers.

It may be reasonably assumed that snow leopards disperse outward from high density areas or high quality habitat (a source) into less favorable habitat (a sink). The importance of sources and sinks in preserving a species on a regional basis was first noted by Pulliam (1988), and later incorporated into land conservation planning strategies by others (Noss 1992; Noss and Cooperrider 1994). Source areas likely play a critical role in sustaining snow leopard populations, especially since its habitat is typically comprised of a fragmented, linear mountain range. The Langu Valley appears to offer a prime example of an area capable of sustaining a dense snow leopard population. Habitat profiles based upon my research could help identify prime habitat elsewhere in snow leopard range, while sign-based field surveys would locate potential refugial areas along mountain corridors between widely-separated national parks or reserves. At the landscape level, high density sites are likely to be widely and irregularly spaced, separated by large expanses of habitat where snow leopard density is low and their existence tenuous. Wide-ranging status surveys have not been undertaken, so that we have little insight into snow leopard distribution patterns except to note that such "hotspots" exist. These are essentially "islands in a sea of less suitable habitat" where conditions for the cat are optimal and hunting pressures minimal. Such areas are generally associated with rugged, broken terrain well interspersed with patches of smooth, grass or shrub-rich terrain capable of supporting in excess of 10 blue sheep (or an equivalent large ungulate prey species) per square kilometer -- a large ungulate biomass of at least 400 kg/km^2 (Jackson and Ahlborn 1984). The presence of ridges and other "travel lanes" with suitable cover is also desirable. Usually, prey availability is more limiting than the presence of suitable terrain, especially in the Himalayan region. Thus, land-use and human activity are factors of the greatest importance promoting the fragmentation of snow leopard habitat.

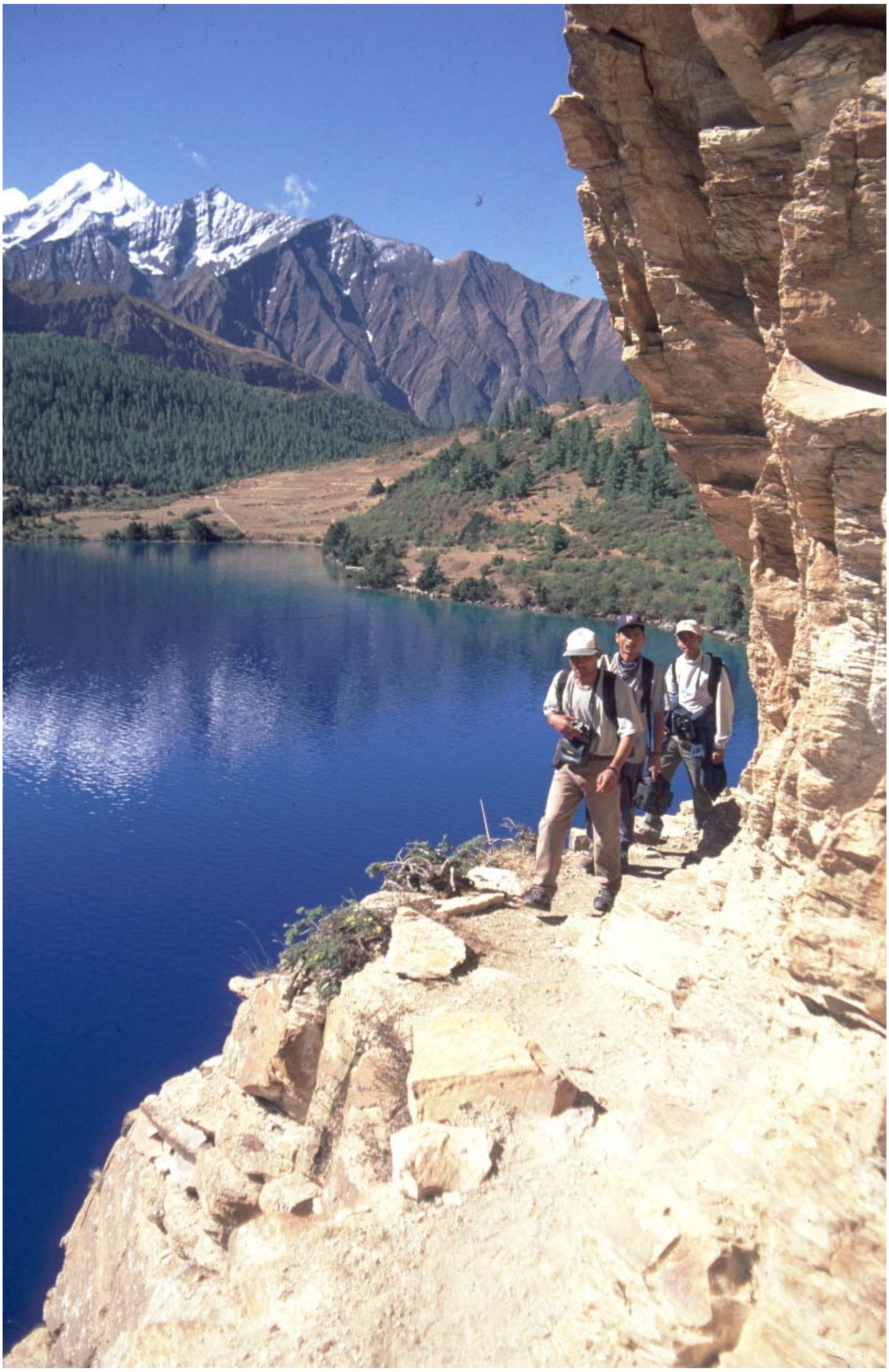
Jackson and Ahlborn (1990) concluded that non-protected areas harbored the bulk of Nepal's snow leopard population, and that corridors were critical to encouraging the regular dispersal and subsequent genetic exchange between otherwise isolated protected area populations. Such corridors become all the more critical as snow leopard habitat is further fragmented by new roads, increased livestock grazing, mining and other human activity (Fox 1994; Jackson and Hunter

1995). Indeed, the bulk of the world's snow leopard population is very probably located outside of existing protected areas, except possibly in Bhutan (Hunter and Jackson, In Press). The degree of population and habitat fragmentation is unknown, but given the insular nature of mountain ranges it is likely to be significant; no doubt, snow leopard population size and distribution reflects the status of sources and sinks, and the presence or absence of corridor linkages (Fox 1994; Pulliam 1988; Villarrubia and Jackson 1994). Virtually nothing is known about dispersal patterns in snow leopards, and even a rudimentary understanding of this process is vital to long-term conservation efforts and the avoidance of inbreeding depression. Dispersal capability is a critical element in determining how rapidly vacant habitats are occupied or depleted areas replenished. Recent work in Mongolia indicates that snow leopards are capable of crossing flat, cover-poor valleys as wide as 40 km in the sparsely populated Gobi Desert (T. McCarthy and personal observations). There is an urgent need to investigate snow leopard movement rates along linear, narrow mountain ranges with restrictive points and across areas interrupted with relatively dense human settlements or unfavorable terrain. As Gadgil (1971:253) has noted, "Dispersal is one of the most important and among the least understood factors of population biology". Such research would establish if dispersal of subadults occurs soon after independence and if males disperse further than females, as in the case of puma (Anderson et al. 1992; Hemker et al. 1984; Logan et al. 1986; Sweanor 1990). Sweanor speculated that dispersal may be an adaptive mechanism to obtain mates, driving subordinate males to disperse longer distances in search of areas with fewer dominant males, several mature females and sufficient food resources. From sign found at one isolated massif, dispersal is not without risk: a snow leopard carcass was found at an isolated Gobi desert mountain spring where it may have succumbed to heat and/or lack of prey (Zhirnov and Ilyinsky 1986).

Status surveys need to be followed up with regionally based conservation plans identifying key snow leopard areas, reserves and corridors permitting inter-refuge movement. The major requirements for the maintenance of a healthy snow leopard population include the provision of a patchwork of areas offering suitable habitat, the presence of corridors to accommodate dispersal, and security from poaching or unregulated hunting for an adequate population of breeding adults. Such as conservation strategy, although focussed on a single species, could also protect

functioning ecosystems because of the extensive ecological and spatial requirements of a large predator. This approach has been applied to tigers in India and proposed for jaguar conservation in Brazil (Quigley and Crawshaw 1992). Special management problems result from conflict with herders, which threatens to undermine snow leopard conservation unless addressed by resource managers and politicians (Jackson et al. 1994b; Miller and Jackson 1994; Oli et al. 1994). Quigley and Crawshaw (1992) postulated that unregulated hunting and the decimation of prey species affected jaguar predation of livestock, with cattle becoming the most abundant prey in many areas. Given the rapid depletion of prey populations through much of Central Asia, conservation initiatives must seek to ensure an adequate population of wild ungulates, especially blue sheep and ibex. Similarly, marmot, pika and small rodents help buffer domestic livestock from predation by snow leopard, and should not, therefore, be depleted through over-exploitation or widespread poisoning such as occurs in some parts of China and Mongolia.

Observations by Chundawat and Rawat (1994) that livestock are critical to the maintenance of snow leopards in some areas, including national parks, raises an interesting question: should local people be compensated for the ecological service (i.e., provision of a reliable food source) they are offering to this endangered species, in return for an agreement not to seek retribution for livestock predated by snow leopard? Compensation could be made in the form of cash or other incentives targeted at the entire community rather than one or two herders, so that as many people as possible benefit from the intervention (Western and Wright 1994). To date, very little research has been conducted on such people-wildlife conflict, despite that fact that it is becoming abundantly clear protected areas cannot survive without the full cooperation and support of local people (McNeely and Miller 1984; Wells and Brandon 1993). Conservation initiatives must also address the rapidly intensifying demand for snow leopard body parts used in traditional Chinese medicine. Profit from the sale and trade of snow leopard bones and organs is an almost irresistible attraction to any mountain dweller, especially those residing amid rampant poverty. Snow leopards need to be worth more alive than dead, but how this can be achieved is unclear; tourism may represent one option, but long-term subsidies for "biodiversity maintenance" may be necessary on the part of affluent urban residents or nations from outside the snow leopard's range. In any event, ensuring that local communities serve as effective stewards for snow leopards and other rare wildlife is critical to curbing the decline in their numbers, and is an essential pre-requisite to removing this beautiful cat from the endangered species list.



Training protected areas staff in snow leopard surveying techniques, Shey-Phoksundo National Park, Nepal, May 1999

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APPENDICES

APPENDIX A-1: Vegetation Types (percent frequency) associated with Landforms in the Langu Valley, as derived from GIS database tabulation

	Vegetation Type (code in parentheses)					
Landform Type (code in parentheses)	Barren (BA)	Mixed Shrub (MS)	Subalpine Shrub (SA)	Alpine Grassland (AG)	Tree Types (TREE)	Totals (N)
Smooth (4)	28.37	11.40	23.26	34.88	2.09	100 (430)
Moderately Broken (2)	37.86	32.86	19.29	7.14	2.86	100 (140)
Very Broken (3)	64.06	9.38	19.53	4.69	2.34	100 (128)
Cliff (5)	86.72	4.07	6.50	2.17	0.54	100 (369)
Linear Types (20)	24.14	10.34	0	0	65.52	100 (29)
						1096

APPENDIX A-2: Elevation, slope, aspect and spatial characteristics of major landform types found in the study area, based on random GIS locations

Habitat Parameter	Landform Type				
	Smooth LF = 4	Moderately Broken LF = 2	Heavily Broken LF = 3	Cliff LF = 5	Linear Types (LF = 20)
Elevation					
Sample Size	411	131	128	365	29
Mean ± S.E.	4289 ± 27.95	3877 ± 57.01	4280 ± 55.42	4165 ± 37.64	3089 ± 70.51
Minimum	2896	2896	3048	2896	2896
Maximum	4289	5335	5487	5640	3658
Slope					
Steepness	34 ± 0.58	38 ± 1.03	39 ± 1.05	44 ± 0.69	25 ± 5.13
Mean ± S.E.	5	5	5	5	5
Minimum	85	65	55	85	85
Maximum					
Mean Aspect ± S.E. (°)	166 ± 43.25	170 ± 48.53	136 ± 2.58	151 ± 47.49	24 ± 33.17
Distance to landform edge	94.6 ± 4.49	39.3 ± 2.98	37.4 ± 2.58	65.0 ± 4.18	41.8 ± 6.03
Distance to vegetation edge	81.8 ± 5.32	50.9 ± 4.13	88.8 ± 9.78	98.1 ± 6.43	32.9 ± 4.7
Distance to travel corridor	853.2 ± 37.06	564.9 ± 46.82	592.0 ± 60.05	592.5 ± 38.7	n/a
Distance to ridgeline	285.5 ± 9.68	281.4 ± 18.79	190.5 ± 13.47	210.2 ± 10.29	344.7 ± 39.32
Distance to major ridgeline	458.5 ± 18.56	455.6 ± 33.97	424.4 ± 35.79	561.0 ± 27.95	613.0 ± 113.02
Distance to minor ridgeline	943.2 ± 22.84	918.2 ± 42.11	659.7 ± 29.49	769.4 ± 22.63	1201.8 ± 76.64
Distance to bluff	2956.0 ± 70.32	1856.0 ± 105.21	2509.7 ± 130.99	2422.1 ± 88.11	560.4 ± 147.49
Distance to linear feature	1162.4 ± 36.50	695.4 ± 47.21	963.7 ± 51.26	1050.4 ± 43.72	22.5 ± 2.67
Distance to river	900.4 ± 30.65	752.8 ± 44.44	875.8 ± 40.36	816.5 ± 29.91	61.8 ± 13.17
Distance to stream confluence	2597.0 ± 68.34	2449.2 ± 123.46	2756.5 ± 143.96	2842.9 ± 85.08	2038.2 ± 405.13

All distances given in meters

APPENDIX A-3: Landforms Associated with Vegetation Types (percent frequency), as derived from GIS database tabulation

	Landform Type (code in parentheses)					
Vegetation Association (code in parentheses)	Smooth (LF 4)	Moderately Broken (LF 2)	Very Broken (LF 3)	Cliff (LF 5)	Linear Types (LF 20)	Total (N)
Barren (BA)	20.89	9.08	14.04	54.79	1.20	100.0 (584)
Mixed Shrub (MS)	39.80	36.80	9.60	12.00	2.40	100.0 (125)
Subalpine Shrub (SA)	56.82	15.34	14.20	3.45	8.11	100.0 (176)
Alpine Grassland (AG)	86.21	5.75	3.45	4.60	0	100.0 (174)
Tree Types (TREE)	24.32	10.81	8.11	5.41	51.35	100.0 (37)
						1,096

APPENDIX A-4: Elevation, slope, aspect and spatial characteristics of major vegetation associations found in the study area, based on random GIS locations.

Habitat Parameter	Vegetation Association				
	Barren (BA)	Mixed Shrub (MS)	Subalpine Shrub (SA)	Alpine Grassland (AG)	Tree Types (TREE)
Elevation (m)					
Sample Size	584	125	176	174	37
Mean ± S.E.	4283.3 ± 29.99	3378.8 ± 31.47	4230.8 ± 32.75	4450.6 ± 21.4	3452.2 ± 78.66
Minimum	2896	2896	3353	3658	2896
Maximum	5640	4573	5335	4450	3451
Slope (°)					
Mean ± S.E.	39.8 ± 0.58	40.0 ± 1.12	39.5 ± 0.76	31.9 ± 0.96	33.6 ± 4.18
Minimum	5	5	5	5	5
Maximum	85	65	65	85	85
Mean Aspect ± S.E.(°)	151.1 ± 46.03	172.8 ± 48.96	173.2 ± 48.65	142.4 ± 41.11	26.1 ± 45.00
Distance to landform edge	59.0 ± 2.77	51.2 ± 4.55	54.2 ± 3.84	138.9 ± 9.17	42.8 ± 5.67
Distance to vegetation edge	106.8 ± 5.61	45.2 ±3.96	45.2 ± 3.35	77.4 ± 5.38	37.9 ± 4.94
Distance to travel corridor	690.9 ± 34.33	539.4 ± 49.41	625.8 ± 45.10	871.8 ± 46.53	204.5 ± 58.45
Distance to ridgeline	221.2 ± 8.10	320.3 ± 19.81	220.7 ± 12.79	312.1 ± 15.55	318.4 ± 37.57
Distance to major ridgeline	479.5 ± 20.01	553.1 ± 43.45	497.3 ± 27.40	476.5 ± 31.57	553.6 ± 84.10
Distance to minor ridgeline	822.5 ± 19.11	974.2 ± 45.94	708.8 ± 31.79	971.1 ± 29.84	1121.5 ± 77.6
Distance to bluff	2731.3 ± 69.67	1121.9 ± 79.18	2367.6 ± 84.28	3296.1 ± 95.72	990.6 ± 140.96
Distance to linear feature	1142.1 ± 34.46	343.2 ± 25.48	1056.2 ± 40.07	1196.2 ± 51.18	130.5 ± 26.44
Distance to river	848.3 ± 23.63	431.9 ± 23.75	1084.6 ±41.45	923.7 ± 50.97	182.4 ± 36.28
Distance to stream confluence	2908.6 ± 67.81	2381.4 ± 164.62	2559.4 ± 7784	2320.2 ± 96.92	1894.6 ± 273.17

All distances given in meters with standard error

APPENDIX A-5: Size and Perimeter of Vegetation and Landform Polygons in the Langu Valley (derived from GIS analysis).

Landform Types	Item	Area (ha)	Perimeter (km)	Patton's "edge" Diversity Index
Moderately Broken				
(n = 140)	Mean ± Std. Error	32.78 ± 2.23	4.99 ± 0.35	3.72 ± 0.08
	Minimum	2.18	0.65	1.13
	Maximum	90.73	16.37	4.85
Heavily Broken	Mean ± Std. Error	32.28 ± 2.48	5.06 ± 0.32	2.46 ± 0.08
(n = 128)	Minimum	2.15	0.6	1.15
	Maximum	90.02	12.19	3.91
Cliff	Mean ± Std. Error	187.21 ± 6.96	24.75 ± 0.91	4.82 ± 0.11
(n = 369)	Minimum	0.93	0.62	1.18
	Maximum	398.99	49.76	7.03
Smooth	Mean ± Std. Error	281.86 ± 13.207	17.96 ± 4.49	2.90 ± 0.07
(n = 430)	Minimum	0.92	0.17	1.08
	Maximum	703.41	586.07	5.65
Linear	Mean ± Std. Error	109.53 ± 13.5	35.58 ± 4.39	8.42 ± 0.87
(n = 29)	Minimum	0.66	0.37	1.29
	Maximum	157.46	51.15	11.49
Vegetation Cover Types:				
Barren	Mean ± Std. Error	1791.61 ± 13.17	170.51 ± 1.28	11.24 ± 0.07
(n = 584)	Minimum	2.36	0.62	1.12
	Maximum	1858.69	183.34	11.99
Mixed Shrub	Mean ± Std. Error	45.61 ± 2.83	5.69 ± 0.29	2.38 ± 0.06
(n = 125)	Minimum	1.87	0.613	1.12
	Maximum	102.27	11.29	3.49
Subalpine Shrub	Mean ± Std. Error	45.59 ± 3.52	4.85 ± 0.29	2.05 ± 0.05
(n = 176)	Minimum	1.31	0.49	1.06
	Maximum	142.57	11.23	3.40
Alpine Grassland	Mean ± Std. Error	129.10 ± 9.13	10.13 ± 0.69	2.37 ± 0.08
(n = 174)	Minimum	1.95	0.61	1.10
	Maximum	297.95	23.69	3.87
Tree Type	Mean ± Std. Error	91.04 ± 11.10	30.48 ± 3.96	7.56 ± 0.84
(n = 37)	Minimum	1.15	0.411	1.08
	Maximum	145.93	50.09	11.69

APPENDIX A-6: Descriptive statistics for selected landform habitat parameters for male and female snow leopards, and random locations

Parameter / Variable Code	Sample Group	Sample Size	Mean ± Standard Error	Minimum	Maximum
Elevation (m) (ELEV)	♂♂	265	3479 ± 26.09	2896	4878
	♀♀	328	3551 ± 24.27	2896	4878
	Random	1049	4176 ± 20.49	2896	5640
Slope (degrees) (SLOP)	♂♂	265	42.1 ± 0.76	5	75
	♀♀	328	44.1 ± 0.63	5	75
	Random	1096	38.3 ± 0.42	5	85
Aspect (degrees) (ASP)	♂♂	265	156.8 ± 57.49	n/a	n/a
	♀♀	328	158.2 ± 58.17	n/a	n/a
	Random	1096	165.3 ± 54.82	n/a	n/a
Distance to nearest landform edge (LFDNE)	♂♂	265	38.3 ± 2.61	0.2	360.7
	♀♀	327	41.0 ± 2.52	0.3	431.9
	Random	1096	69.5 ± 2.41	0.2	733.7
Distance nearest Smooth (SMODIS)	♂♂	265	87.3 ± 6.3	0	417.7
	♀♀	327	100.5 ± 5.38	0	467.4
	Random	1096	83.7 ± 3.56	0	801.0
Dist nearest mod. broken (BROKDIS)	♂♂	265	153.9 ± 8.92	0	623.2
	♀♀	327	162.0 ± 8.84	0	696.79
	Random	1096	231.0 ± 7.75	0	1629.5
Dist nearest very broken (VBROKDIS)	♂♂	265	183.2 ± 9.91	0	848.8
	♀♀	327	164.7 ± 9.31	0	860.0
	Random	1096	303.4 ± 10.42	0	1969.2
Dist nearest cliff (CLIFDIS)	♂♂	265	58.2 ± 5.12	0	409.5
	♀♀	327	41.9 ± 3.97	0	431.9
	Random	1096	91.9 ± 3.81	0	658.1
DNOT Smooth [a] (DNOT4)	♂♂	196	118.1 ± 7.35	1.2	417.7
	♀♀	263	125.0 ± 5.75	1.2	467.4
	Random	666	137.7 ± 4.82	0.3	801.0
DNOT Cliff [a] (DNOT5)	♂♂	155	99.6 ± 7.08	0.2	409.5
	♀♀	171	80.3 ± 6.30	0.3	431.9
	Random	726	138.8 ± 4.91	0.2	658.1

DNOT Moderately Broken [a] (DNOT2)	♂♂	228	178.8 ± 9.37	1.2	623.9
	♀♀	275	192.7 ± 9.43	1.3	696.8
	Random	956	264.8 ± 8.34	0.2	1629.5
DNOT Very Broken [a] (DNOT3)	♂♂	233	208.3 ± 10.23	1.5	846.8
	♀♀	286	188.3 ± 9.88	1.1	860.1
	Random	968	343.6 ± 11.18	1.2	1969.2
DNOT Linear Type [a] (DNOTLIN)	♂♂	313	434.3 ± 22.83	1.9	1861.3
	♀♀	248	383.1 ± 19.38	0.4	1411.8
	Random	1067	1038.5 ± 23.26	1.1	3561.4

Notes:

[a] DNOT is the distance to the specified landform type when a snow leopard location or random point are not located within the same type.

All distances are in meters

APPENDIX A-7: Descriptive statistics for selected vegetation spatial habitat parameters

Parameter / Code	Sample Group	Sample Size	Mean ± Standard Error	Minimum	Maximum
Dist nearest vegetation edge (VDNE)	♂♂	265	45.4 ± 2.58	0.4	259.9
	♀♀	327	47.9 ± 2.68	0.8	299.9
	Random	1096	82.9 ± 3.29	0	1128.8
Dist nearest barren site (BADIS)	♂♂	265	46.3 ± 4.4	0	375.3
	♀♀	327	33.5 ± 3.61	0	391.4
	Random	1096	35.9 ± 2.09	0	542.0
Dist nearest mixed shrub site (MSDIS)	♂♂	265	131.8 ± 15.68	0	2631.0
	♀♀	327	204.4 ± 20.59	0	2671.7
	Random	1096	811.3 ± 25.79	0	3766.4
Dist nearest subalpine shrub site (SADIS)	♂♂	265	320.6 ± 17.95	0	1087.2
	♀♀	327	275.2 ± 14.48	0	1082.0
	Random	1096	265.5 ± 8.60	0	1390.6
Dist nearest alpine grassland site (AGDIS)	♂♂	265	865.8 ± 30.18	0	1977.2
	♀♀	327	914.2 ± 27.93	0	2099.3
	Random	1096	442.4 ± 13.68	0	2248.2
Dist nearest tree type (TREEDIS)	♂♂	265	292.9 ± 18.05	0	2508.2
	♀♀	327	484.2 ± 26.77	0	2822.2
	Random	1096	1075.4 ± 27.11	0	3895.5
DNOT Barren [a] (DNOTBA)	♂♂	156	78.6 ± 6.36	1.2	375.3
	♀♀	167	65.6 ± 6.12	1.0	391.4
	Random	512	76.9 ± 3.73	0.1	542.0
DNOT Mixed Shrub [a] (DNOTMS)	♂♂	181	192.9 ± 21.51	0.7	2631.0
	♀♀	241	277.3 ± 26.41	1.6	2671.7
	Random	971	915.8 ± 27.37	0.4	3766.3
DNOT Subalpine Shrub [a] (DNOTSA)	♂♂	221	384.5 ± 18.76	2.4	1087.2
	♀♀	274	328.5 ± 15.32	0.8	1082.0
	Random	920	316.2 ± 9.36	0.4	1390.6
DNOT Alpine Grassland [a] (DNOTAG)	♂♂	254	903.3 ± 29.28	9.9	1997.2
	♀♀	317	943.0 ± 27.28	3.2	2099.3
	Random	922	525.9 ± 14.73	0.1	2248.1
DNOT Tree [a] (DNOTREE)	♂♂	248	312.9 ± 18.61	0.4	2508.25
	♀♀	309	512.4 ± 27.49	2.9	2822.16
	Random	1059	1112.9 ± 27.23	0.4	3895.5

Note:
[a] DNOT is the distance to the specified vegetation type when the snow leopard or random point are not located within the same type

All distances are in meters

APPENDIX A-8: Comparison of Landform and Vegetation Features for Core and Non-Core Areas based on 1,096 GIS derived random locations

Habitat Parameter ^{a}	Core Area (n = 72) (Cincore)		Non-Core Area (n = 1024)		Test Statistic ^{b}	
	Mean	Std. Error	Mean	Std. Error	t-value	U and X^2
Landform:						
Dist to landform edge ^{c}	45.8	5.06	71.2	2.55	2.47 *	
Dist to moderately broken terrain (LF 2) ^{c}	150.1	16.83	236.7	8.18	1.50 *	
Dist to very broken terrain (LF 3) ^{c}	191.2	21.36	311.3	11.01	2.04 *	
Dist to smooth terrain (LF 4)	104.1	14.06	82.3	3.68	-1.52 ns	
Dist to cliff (LF 5) ^{c}	80.5	12.01	92.7	3.99	0.05 ns	
Dist to linear feature	262.5	25.33	1063.7	23.92		U = 586771.0 X^2 = 93.52 ***
Dist to DNOT2 ^{c}	174.3	17.71	271.1	8.79	2.36 *	
Dist to DNOT3 ^{c}	229.5	22.59	351.1	11.79	1.68 ns	
Dist DNOT4 ^{a}	169.8	16.63	145.2	5.16	-1.27 ns	
Dist DNOT5 $^{a\ c}$	123.1	15.09	148.9	5.30	-1.27 ns	
Dist to DNOTLIN ^{c}	286.4	25.67	1088.1	23.92	9.45 ***	
Vegetation:						
Dist nearest vegetation edge ^{c}	55.1	6.57	84.8	3.49	2.11 *	
Dist Barren type (BA) ^{c}	61.0	11.80	34.2	2.07	2.73 **	
Dist Mixed Shrub (MS)	94.3	14.44	861.7	26.89	9.73 ***	
Dist Subalpine Shrub (SA)	337.4	36.76	260.4	8.82	-2.22 *	
Dist Alpine Grassland (AG)	859.7	47.16	413.1	13.81	-8.33 ***	
Dist Tree type (TREE)	204.0	16.99	1136.6	28.01	8.75 ***	
DNOTBA	95.5	16.46	75.2	3.76		U = 10691.0 X^2 = 0.01 ns
DNOTMS ^{c}	144.4	18.33	955.0	28.14	8.45 ***	
DNOTSA	426.2	38.58	308.9	9.61	-3.034 **	
DNOTAG	859.7	47.16	497.6	15.08	-6.75 ***	
DNOTREE	222.6	16.75	1172.1	28.15		U = 57217.0 X^2 = 103.24 ***

[a] Dist = distance to nearest specified landform or vegetation type. All distances are measured in meters; LF = landform type; DNOT4 = distance nearest landform # 4 when not located in this type (n = 201 core, 422 non-core); DNOT5 = distance nearest landform # 5 when not located in LF 5 (n = 214 core, 471 non-core)

[b] Two-sample t-test value, unequal sample size (pooled variances, df = 1094) Mann-Whitney U statistic and X^2 approximation

* = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.000$, ns = not significant

[c] Variable transformed to meet homogeneity of variance requirement

APPENDIX A-8 (CONTINUED): Comparison of Selected Spatial Landscape Features between Snow Leopard Core and Non-Core Home Range Areas based on GIS derived 1,096 random locations

Habitat Parameter [a]	Core Area Random Locations (n = 72)		Non-Core Area Random Locations (n = 1024)		Test Statistic [b]	
	Mean	Std. Error	Mean	Std. Error	t-value	U and X^2
Elevation (m)	3147.7	38.34	4230.1	20.73		U = 57107.0 $X^2 = 92.17^{***}$
Slope (degrees)	40.4	1.67	38.2	0.43	1.30 ns	
Aspect (degrees)	156.1	45.00	166.7	45.00	1.12 ns	
Dist to ridge (RIDIS) [c]	140.3	12.64	257.8	6.41	4.28^{***}	
Dist to major ridge (RMAJDIS) [c]	365.1	33.69	501.7	14.55	1.31 ns	
Dist to minor ridge (RMINDIS) [c]	534.8	30.34	877.8	14.54	5.83^{***}	
Dist to linear landform feature (LINDIS) [c]	263.9	25.12	1064.2	23.89	9.78^{***}	
Dist to travel corridor (TDIS) [c]	387.9	25.77	1076.2	19.77	12.59^{***}	
Dist to bluff (BLUFDIS)	1088.5	48.68	2620.9	49.50		U = 59031.0 $X^2 = 72.90^{***}$
Distance nearest river or stream (RIVDIS) [c]	459.9	34.23	854.1	18.63	4.16^{***}	
Dist to confluence (CONDIS)	1307.2	56.28	2760.2	48.71		U = 61253.0 $X^2 = 88.25^{***}$

[a] Dist = distance to nearest specified feature. All distances in meters

[b] Two-sample t-test value, unequal sample size; Mann-Whitney U statistic and X^2 approximation

$^{*} = P \leq 0.05$, $^{**} = P \leq 0.01$, $^{***} = P \leq 0.000$, ns = not significant

[c] Variable transformed to meet homogeneity of variance requirement

Landscape Index [a]	Core (n = 72)		Non-Core (n = 1024)		Test statistic [i]	
	Landform	Vegetation	Landform	Vegetation	Landform	Vegetation
Relative Richness Index [b]	0.57	0.58	0.49	0.50	-3.93 ***	-4.61 ***
Diversity Index [c]	0.58	0.54	0.52	0.48	-2.42 *	-3.07 **
Dominance Index [d]	0.47	0.42	0.40	0.37	-2.24 *	-1.61 ns
Fragmentation Index [e]	0.49	0.47	0.41	0.38	-3.61 ***	-4.37 ***
NDC Index [f]	0.50	0.58	0.43	0.49	-4.04 ***	-4.62 ***
CVN Index [g]	0.59	0.50	0.55	0.49	-1.35 ns	-0.57 ns
BCM Index [h]	0.68	0.64	0.65	0.59	-1.45 ns	-2.08 *

[a] All indices are standardized according to the scale 0 (low) to 1.0 (high).

[b] Relative Richness (R = number types / maximum number types present *100)

[c] Diversity (h = -sum(p*pIn(p)) [where p = proportion of the footprint in each class, In = natural log]

[d] Dominance (D = Hmax-H) [where H = diversity; and Hmax = maximum diversity - In (n) where n = no different classes, In = natural log]

[e] Fragmentation (F = (n-1)/(c-1) [where n = no different classes present and c =no cells considered, always 9)]

[e] NDC or number of different classes in each 3x3 neighborhood (1-9)

[e] CVN or number of cells different from center in each 3x3 neighborhood (0-9)

[e] BCM or number of different pairs in each 3x3 neighborhood

[i] Two-sample t-test value, unequal sample size (pooled variances, df = 1094)
* = P $\leq$ 0.05, ** = P $\leq$ 0.01, *** = P $\leq$ 0.000, ns = not significant