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# Snow Leopards (*Panthera uncia*) in Nepal—Home Range and Movements

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Five snow leopards were trapped and fitted with radio-collars in the Langu Valley in west Nepal; their subsequent movements were monitored for periods of four to 18 months. Average daily distances traveled by males ( $n=3$ ) were ~1.3 km compared with 1.0 km for females ( $n=2$ ), but the difference was not significant. Snow leopards were crepuscular, bedding in different places each day unless on a kill. Home-range size varied widely among individuals, from ~12 to 39 km<sup>2</sup> but not significantly. Ranges of the five animals overlapped almost entirely, although use of a particular area was temporally separated. On average, individual snow leopards were separated by distances of 1.9 to 3.2 km, verifying the species' solitary social structure. Analysis of four tagged leopards indicated that 42 to 60% of home-range use occurred within only ~14 to 23% of the total home area. These individuals 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 very favorable for snow leopards. Due to the small sample and the uncertain breeding or social status of tagged males, the authors could not confirm whether adult males or females occupy exclusive ranges, or whether a male's range encompassed more than the range of one adult female. No evidence was found to indicate that snow leopards patrol home-range boundaries. Core areas were marked significantly more than non-core sites, suggesting that social marking plays an important role in spacing individual snow leopards.

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Secretive habits, low densities, sparse distribution, and difficult field logistics have long hindered study of the snow leopard in its remote mountain habitat. Until recent status surveys, information on the species had been primarily anecdotal (Guggisberg 1977). Incidental observations in India, Nepal, the Soviet Union, and China have expanded knowledge of snow leopard distribution, habitat use, food habits, and characteristics of marking (Fox et al. in press, Koshkarev 1984, Mallon 1984, Schaller et al. 1987).

Since previously studied animals were not marked, the investigators were unable to learn much about snow leopard movements, activity patterns, or home-range characteristics. Noting their tendency to move along the base of cliffs and human footpaths, Schaller (1977:155) surmised that snow leopards 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."

Between January 1982 and July 1985, the authors radio-collared and



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tracked five snow leopards in an effort to learn more about the behavior and ecology of this endangered species. The study area provided an opportunity to investigate movement and home-range use patterns of snow leopards in habitat of high quality. No villages or grazing livestock occur within the core area, which supports dense numbers of blue sheep or bharal (*Pseudois nayaur*), the primary prey for snow leopards through much of its range. Snow leopards and musk deer (*Moschus chrysogaster*) have been subject to heavy hunting pressure in the study area (Jackson 1979), but this was curtailed during the period of research.

This article explores the following questions:

- Does the snow leopard's home range and land-tenure system resemble those of other large solitary cats such as the mountain lion (*Felis concolor*) or common leopard (*Panthera pardus*)?
- How do individuals use the home-range space with regard to conspecifics and food resources?
- How does snow leopard density in the study area compare with that in other areas?

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## *Study Area and Methods*

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The study area is located in the Langu Gorge, part of the newly established Shey–Phoksundo National Park of west Nepal (long 82°33' to 41' E; lat 29°30' to 35' N). Bisected by deeply incised gorges and ravines, the area is extremely rugged with elevations ranging from ~2700 to 6800 m, and an average slope >30° (Figure 1). Cliffs cover nearly 40% of the





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**Figure 1.** Researcher radio tracking at 4570 m on Tallisha Mountain. Locational abilities were improved by tracking from major ridge lines, which also served as travel lanes for snow leopards.

study area; smooth-surfaced but steeply inclined terrain covers another 40%; the remainder is moderately to strongly broken by rocky outcrops, ridges, and gullies. Aspects are primarily southerly or westerly.

Sequestered behind the Himalaya, the study area has a semiarid climate. Annual precipitation is <1000 mm, about equally distributed as winter snow and summer (monsoon) rain. An alpine steppe scrub community dominates dry, south-facing slopes, with small stands of birch (*Betula utilis*) and Himalayan blue pine (*Pinus wallichiana*) on some cooler, moister northerly slopes. Dominant shrubs are juniper (*Juniperus indicus* and *J. squamata*), *Caragana* spp., and *Artemisia* spp. Vegetation covers <10% of the ground on >49% of the area. (For a more detailed description, see Jackson & Ahlborn in press.)

Snow leopards were captured using leg-snare traps (Novak 1980) placed along frequented trails. Trapped animals were immobilized with ketamine hydrochloride (7 to 17 mg/kg), sexed, measured, weighed, tattooed on the inside of one ear with an identifying number, and fitted with a motion-sensitive radio-collar. Cats were classified according to three age-classes: cubs, 0 to <12 months of age; subadults,  $\geq 12$  to <36 months; and adults,  $\geq 36$  months. Criteria used included size, weight, reproductive condition, canine size and wear, general dentition, and subsequent behavior as determined by radio-tracking. Females were examined for evidence of previous lactation, as indicated by large, pigmented nipples.

Daily attempts were made to relocate radio-tagged snow leopards from the ground using triangulation by two or more observers and homing techniques (Cochran 1980). Bearings were taken using a hand-held

compass and plotted on a 1:24000 topographic map. Each location was classified according to the reliability of the fix. Good, fair, and poor locations were areas of < 25 ha, 25 to 50 ha, and > 50 ha, respectively. Except for locations with visual confirmation, the minimum error polygon was estimated to be ~3.2 ha.

Home-range size and configuration were determined using the minimum area polygon (Mohr 1947), defined by connecting the outermost locations. Activity centers within the home range were identified using the harmonic mean measure method (Dixon & Chapman 1980, as modified by Spencer & Barrett 1984). Dixon & Chapman's activity measure calculates centers related to the intensity of activity; lower-valued isopleths (contours) denote areas of increased activity or core areas (Samuel & Garton 1987). Core-area use was quantified according to Samuel et al. (1985). Day-after-capture locations, fixes with an error polygon > 50 ha, and duplicate same-day locations were excluded from the analysis. For those days with more than one location, the authors selected the first or that location having the smallest error polygon.

A cumulative area curve of home-range size was developed by computing the area within successive two-week, minimum-area polygons. Given the long time frame that most radio-tagged snow leopards were monitored ( $\geq 12$  months), and that most locations were separated by at least 24 hours, autocorrelation of locations is not likely to have biased the estimates (Swihart & Slade 1985).

An index of movement was obtained by measuring the straight-line distance between the first location of radio-tagged individuals on successive days. The authors excluded records with no movement; a cat was considered to have moved if, when relocated, its triangulated position had changed by  $\geq 200$  m. Same-day movements were derived by computing the linear distance between repeated locations made during a single day. The degree to which snow leopards socialize was examined by computing straight-line distances between cats located on the same day, and by interpretation of sign (Ahlborn & Jackson in press).

Distance moved and distance between individuals were tested for homogeneity of variance with Bartlett's test (Sokal & 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 leopards were similar. Distance between individuals of the same and different sexes, and 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.

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## Results

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Five animals—three males and two females—were radio-tagged (Table 1) and relocated a total of 711 times using radio-telemetry (Table 2); 82% of the relocations were assigned to good and fair location classes (i.e., < 50 ha). Tagged snow leopards were relocated on average every two to four days, animals 02 and 04 most frequently. Contact with 05 declined during the second season of monitoring when she started to range more widely.

Except for adult male 01, each was monitored over two successive winter and spring seasons. Contact with 01 was lost before the other cats were tagged. Judging by his age, he was reproductively active. At cap-



ture, males 02 and 03 were classified as subadults, aged ~30 and 35 months, respectively; they could have been littermates, as they were of similar size and appeared to be relatively tolerant of each other's presence, at least during the initial months of monitoring. When 02 was recaptured a year later, he had facial scars suggestive of intraspecific fighting. Long-distance vocalizations and movements by 02 during the time female 04 copulated suggest that he may have at least tried to breed with her. About this time, contact was lost with 03; he could have left the area. The authors continued to find tracks of his size class in areas where telemetry confirmed 02 had not recently visited, but these could have belonged to 03 or another individual.

Cat 04 was judged to be at least 4 years of age, and nipple coloration and size indicated that she had previously given birth. Female 05 is the presumed daughter of 04 as they associated for three days, a month before 04 gave birth to at least two cubs. The daughter's age at capture was estimated at 18 to 22 months. Thus she was tracked over a time when she was presumed to be establishing her range.

Based on concurrent observations from radio-telemetry and sign (tracks and scrapes), the authors estimate that the study area (~100 km<sup>2</sup> in extent) supported at least five and possibly as many as 10 cats, excluding cubs. In early 1984, the population consisted of two young adult males (02 and 03), a subadult female (05), and at least one adult female (04); tracks indicated three or four uncollared animals about the size of tagged individuals, as well as at least one larger, apparently widely roaming individual.

**Table 1. Snow Leopards Radio-tagged in the Langu Valley**

Cat No.	Age Class, Sex	Weight (kg)	Body Length (cm)	Capture Date
01	Adult ♂	~50-55	—	3 Apr 1982
02	Subadult ♂	28	114	15 Dec 1982
03	Subadult ♂	34	102	1 May 1983
04	Adult ♀	39	113	23 Mar 1984
05	Subadult ♀	21	96	30 Apr 1984

### Movements

Snow leopards were found in a different place on 72% of all consecutive days located ( $N=232$ , pooled data from five snow leopards). An animal was located in a specific grid square (6.25 ha) only once ~64 to 74% of the time, indicating that they tended to choose a different resting site each day unless on a kill or, in the case of 04, at a maternal den site.

The mean minimum distance (straight line) between consecutive daily locations ranged from 0.85 to 1.61 km (Table 3), excluding stationary locations (i.e., individual at a known or presumed kill-site, or locations < 200 m apart). Males moved slightly, but not significantly, farther than females (Mann-Whitney  $U = 7547$ ;  $p > 0.057$ ). The mean linear distance for all cats was 1.12 km ( $N=232$ ), with considerable variation (range=0.21 to 6.72 km) among individuals. Nearly 90% of the consecutive-day movements involved distances of  $\leq 2$  km; 58% were < 1 km apart. Movements of 04 decreased after she gave birth; by the time her cubs were 8 months old, she was again traveling typical distances.

On average, males moved linear distances of 1.16 km during the same day ( $n=13$ ;  $SE = \pm 0.40$  km; range=0.20 to 5.65 km), and females an average of 0.64 km ( $n=27$ ;  $SE = \pm 0.10$  km; range=0.22 to 2.25 km). No differences in same-day movements between the sexes was found (Mann-Whitney  $U = 803$ ;  $p > 0.300$ ). The average daytime distance moved by a snow leopard of either sex was  $0.81 \pm 0.15$  km ( $n=40$ ).

**Table 2. Radio-location Data for Five Snow Leopards**

Cat	Number of Locations	Number of Days Located	Mean Number of Days Between Locations	Percentage of Days Contacted	Period Tracked
01, ♂	36	28	3.61	27.7	4/82–8/82
02, ♂	222	199	1.77	56.3	12/82–6/84
03, ♂	75	69	2.70	37.1	5/83–3/84
04, ♀	245	206	1.47	68.0	3/84–6/85
05, ♀	133	109	2.43	41.1	4/84–6/85
Total	711	611			

**Table 3. Linear Distance Between Locations of Radio-tagged Snow Leopards on Consecutive Days**

Cat	Consecutive Day Locations	Mean Distance + SE (km)*	Maximum Distance (km)	Frequency Distribution (%)		
				<1.0 km	1.0–<2.0 km	≥2.0 km
01, ♂	12	1.61 ± 0.31	3.37	33.3	33.3	33.3
02, ♂	68	1.31 ± 0.13	4.74	52.9	30.9	16.2
03, ♂	19	0.95 ± 0.13	2.15	63.2	26.3	10.5
04, ♀	88	1.09 ± 0.11	6.72	55.7	35.2	9.1
05, ♀	45	0.85 ± 0.09	2.35	73.3	17.9	8.9
All males	99	1.27 ± 0.10	4.74	52.5	30.3	17.2
All 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

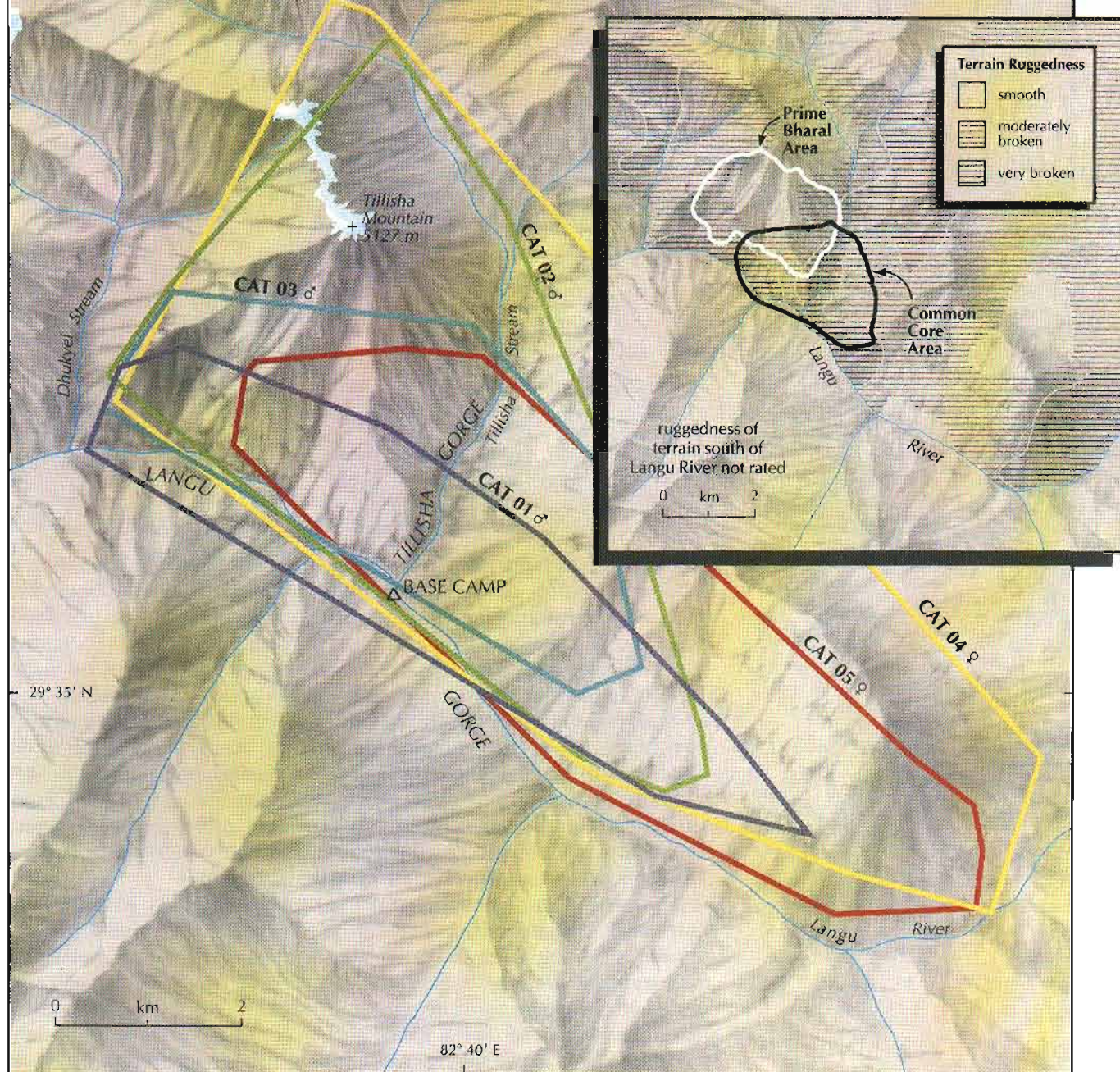
\*Stationary locations (<200 m) are excluded

### Home Ranges

Initial asymptotes in home-range size were reached after individuals had been located on 40 to 65 days. However, home-range size continued to periodically increase for all animals, which was attributed to the difficulties of ground-based tracking and changes in individual movement patterns. Locating cats within little-used peripheral areas of the mountainous terrain was time consuming. Three cats (02, 03, and 05) were classified as subadults at first capture, and thus could have been in the process of establishing their respective home areas. Sharp increases in cat 04's home range may reflect pressures of finding sufficient prey for her increasingly mobile cubs. Her range increased by 44%, 22%, and 68% when her two cubs were 8, 10, and 12 months old, respectively. A large portion of the 68% increase in the minimum area polygon encompassed terrain within which 04 was never located. Increases in female 05's home area after 80 days of monitoring may reflect apparent avoidance of her presumed mother, then accompanied by relatively young cubs. Although both females' home areas overlapped, 05 tended to use areas toward the eastern section of 04's range.

Table 4 shows the home-range size and dimensions for the five radio-tagged snow leopards, based on the minimum-area polygon method. Home-range size varied widely among individuals, from ~12 to 39 km<sup>2</sup> but without significant difference (Kruskal–Wallis = 4.0; *df* = 4; *p* > 0.406) or between sexes (Mann–Whitney U = 1.0; *df* = 1; *p* > 0.248). Snow leopard 01 occupied a larger home area than the data indicate: poor access restricted the authors' ability to locate this cat. The strongly linear home-range shapes (~2.5 times as long as wide) reflect the deep gorge topography and the cats' underuse of elevations higher than 4200 m. Home-range estimates are not adjusted to account for the considerable relief, which could increase actual surface area by > 25%. None of the radio-tagged leopards was ever located south of the Langu River, although they could have easily crossed it in winter. Sign confirmed that several other snow leopards occupied the slopes south of the





**Table 4. Home-range Sizes of Five Snow Leopards**

Cat	Minimum Area (km)	Width (km)	Length (km)	Width-to-length Ratio	Number of Locations
01, ♂	11.7	1.5	8.8	5.9	26
02, ♂	22.7	3.9	8.1	2.1	143
03, ♂	11.7	2.6	6.4	2.7	51
04, ♀	38.9	5.7	10.8	1.9	167
05, ♀	19.7	2.6	9.7	3.7	99
Mean ± SE	20.9 ± 4.9	3.7 ± 1.5	8.8 ± 1.3	3.2 ± 1.4	

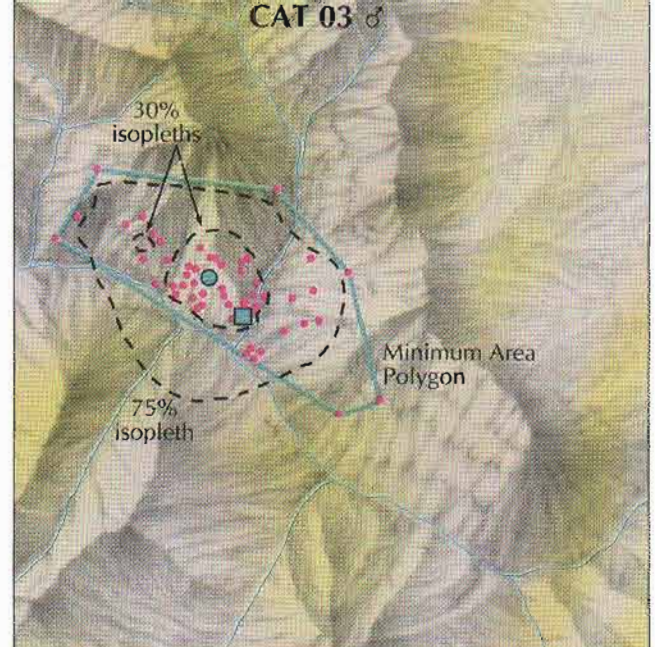
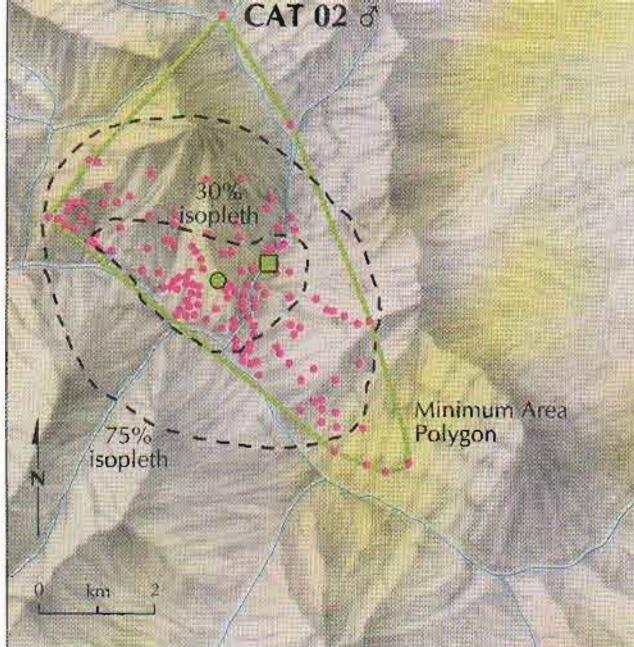
\*Based on the minimum area method of Mohr (1947); day-after-capture locations, duplicate same-day locations, and fixes with an error polygon > 50 ha excluded from analysis

Langu. No evidence for seasonal home ranges was found.

Home ranges of the five snow leopards overlapped almost entirely, both between and within sexes (Figure 2). For cats 02 to 05, 75% and 30% harmonic mean isopleths were computed, based on the entire period they were monitored (Figures 3). Since the amount of time an animal

**Figure 2.** Minimum area polygons for five radio-tagged snow leopards in the Langu Valley, Nepal. Inset (same area as large map), location of overlapping snow leopard core area, prime bhara habitat, and an indication of terrain ruggedness.





spends in a particular place is an important factor in estimating its home range and activity pattern (Samuel & Garton 1987), the authors also computed harmonic mean usage distributions using time-weighted data sets. The resultant isopleths were very comparable to unweighted data sets, suggesting that peripheral areas were not undersampled at the expense of more accessible parts of the study area. Also, as monitoring was not undertaken over fully comparable intervals, the authors recomputed each cat's activity center using loci from overlap periods between it and each of the other snow leopards. To assess whether spatial use differed, the activity centers were compared to the core area derived from full data sets for the same animal. No important differences were found; the authors therefore accepted core-area boundaries derived from data sets using all loci as representative for that individual.

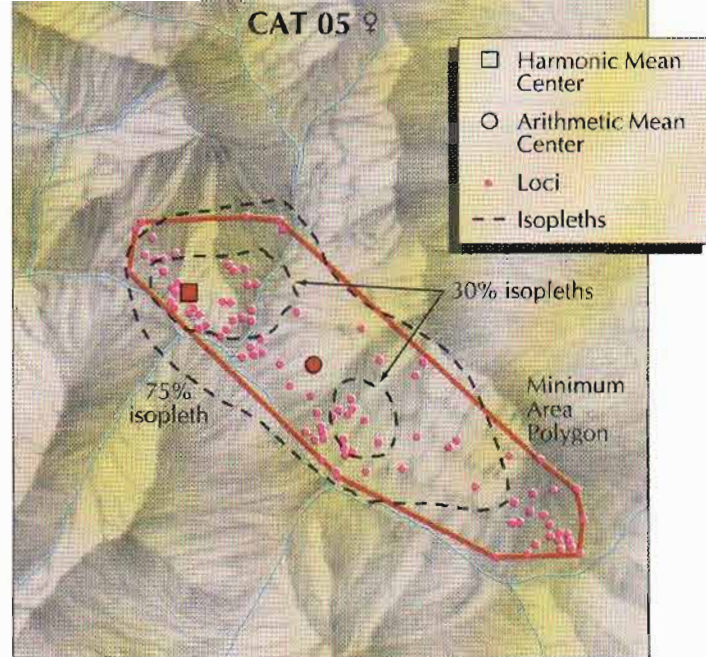
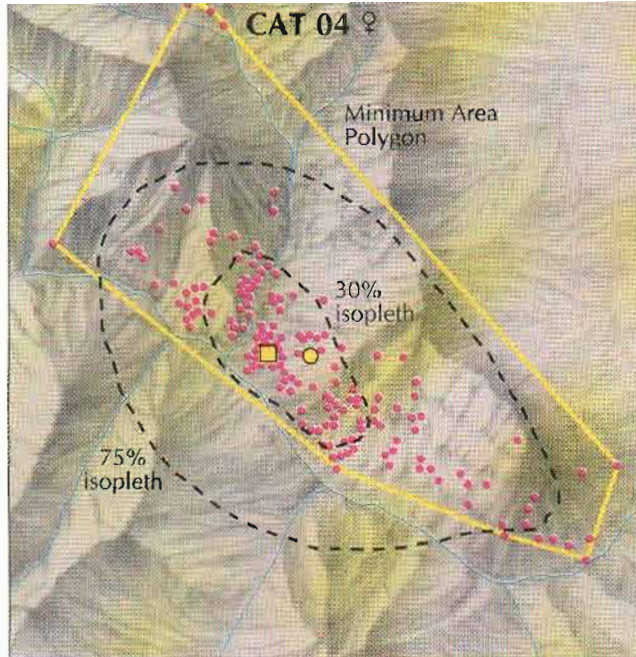
All individuals demonstrated areas of concentrated use within the home area. These disproportionately used core areas are defined as areas that probably contain "home sites, refuges and most dependable food sources" (Samuel et al. 1985:712). The 75% activity isopleth approached circularity and encompassed large areas of infrequently used habitat, as well as unused terrain south of the Langu River. By contrast, the 30% isopleth delineated areas within which leopard sign were most often found or the tagged animals most often located. The authors accepted the 30% isopleth as best representing core-use areas. The data suggest that a relatively high percentage of home-range use (42 to 60%) occurred in the 30% isopleth, which encompassed only ~14 to 23% of the total home area (Table 5). Cat 05 used her core area least intensively; cat 04, most intensively, presumably reflecting her temporary use of a small area surrounding a natal den-site.

Core-use areas overlapped extensively between individuals, although the use was usually temporally separated. Harmonic mean activity centers were located within 2 km of each other, further evidence of shared space. The area of most overlap was estimated at ~6.0 km<sup>2</sup>; it is centered at the confluence of the Langu River and Tillisha Stream, in an area where topography, habitat, and prey abundance appeared to be very favorable for snow leopards (Figure 2, inset).

### Sociality and Land-tenure Pattern

Although snow leopards used a common space, they were separated temporally, confirming the species' solitary social structure.





On the same day, males were separated by an average distance of 1.93 km ( $n = 45$ ;  $SE = \pm 0.18$ ; range = 0.31 to 5.51 km); females, by an average of 2.18 km ( $n = 109$ ;  $SE = \pm 0.17$ ; range = 0.02 to 7.88 km); while the mean distance between cats of different sexes was 3.16 km ( $n = 55$ ;  $SE = \pm 0.29$ ; range = 0.31 to 7.03 km). A significant difference was detected in distances between cats of the same and different sex during the same day (Kruskal-Wallis = 8.91;  $df = 2$ ;  $p > 0.012$ ), which may reflect changing social patterns during the study. Thus, female-to-male distances largely represented information gathered between male 02 and female 04 after the mating season, when she was pregnant or raising cubs; and between male 02 and female 05 from her independence, but before she reached breeding age. Cat 04 may have been avoiding close contact with males. The female-to-female records represent approximately the first 14 months of 05's independence and the period when 04 was raising cubs (until 1 month of age, and then 5.5 to 12 months of age).

**Figure 3.** Home areas for leopards 02, 03, 04, and 05 showing all loci, minimum area polygons, activity centers, and isopleths.

## Discussion

Snow leopards in the Langu exhibit many traits shown by other solitary felids. For example, they were mobile, changing location from one day to the next unless on a kill. Given the precipitous terrain, it is hardly surprising that snow leopards tended to move an average of ~1 km (straight line) between consecutive days. Tiger (*Panthera tigris*), jaguar (*P. onca*), and mountain lion traveled linear distances about twice as large (Schaller & Crawshaw 1980, Seidensticker et al. 1973, Sunquist 1981). Pugmarks showed that all cats typically traveled circuitous, zigzag routes; therefore, actual distances moved are greater than this study's telemetry data indicate. Snow leopards occasionally moved from one end of the range to the other within a 12- to 24-hour period, thereby covering linear distances of ~7 km.

Preferred bedding sites were located on or near ridges, cliffs, and other steep sites with good vistas. Freeman (1975) reported that captive snow leopards prefer to rest in elevated sites. Many bedding sites were situated along repeatedly traveled routes: both telemetry and tracking indicated that snow leopards strongly prefer moving along major ridgelines, bluff edges, gullies, and the base or crest of broken cliffs. This pattern of traveling along prominent terrain features or edges apparently



**Table 5. Patterns of Core-area Use for Four Snow Leopards**

Cat	Total Number of Loci*	Number of Loci in Core Area	Core Area Size (km) <sup>2</sup>	Percentage of Home Range Within Core Area	Percentage of Home-range Use Within Core Area	INTEN <sup>†</sup>
02, ♂	143	86	5.25	23.1	60.1	2.60
03, ♂	51	30	2.39	20.4	58.8	2.88
04, ♀	167	99	5.39	13.9	59.2	4.25
05, ♀	99	42	4.31	21.9	42.4	1.94

\*Number of loci used to compute core area

<sup>†</sup>Core area = area enclosed by 30% harmonic mean measure isopleth

INTEN = percentage of home-range use within core area ÷ percentage of home range within core area, a measure of intensity of use within the core area (adapted from Samuel et al. 1985)

occurs in other populations (Koshkarev 1984, Mallon 1984; G. B. Schaller, personal communication).

The Langu leopards were primarily crepuscular, being most active around dawn until ~1000 hours, and then again in the late afternoon and evening. Not infrequently, they shifted the bedding site several times during the daytime, but it was difficult to quantify such localized movement because of the time required to relocate animals in precipitous terrain. This diurnal activity pattern apparently contrasts with the more nocturnal activity of snow leopards in Ladakh (Mallon 1984), an area where cats must subsist partially or largely upon domestic livestock and are therefore subject to human retribution.

Home ranges of the tagged snow leopards overlapped almost completely. They were similar in size to those of common leopards in Africa (Hamilton 1976, Smith 1978), but larger than common leopards in Chitwan or Sri Lanka (Eisenberg & Lockhart 1972, Seidensticker et al. in press). By contrast, mountain lions range over areas >60 km<sup>2</sup> for females and >450 km<sup>2</sup> for males (Anderson 1983, Hemker et al. 1984, Hopkins et al. 1986, Seidensticker et al. 1973). The males' ranges are typically two to three times larger than the females', and mountain lions migrate between summer and winter ranges in areas of deep winter snow, as in Idaho (Seidensticker et al. 1973) or Wyoming (Logan et al. 1986). The Langu snow leopards did not occupy separate summer or winter ranges, obviously reflecting the largely sedentary bharal prey population and a relatively mild climatic regime with little winter accumulation of snow on the mostly south- or west-facing slopes. Furthermore, elevational extremes were well represented within distances of a few kilometers. Novikov (1956) and Roberts (1977) reported seasonal movements in snow leopards in the Tien Shan and Karakorum areas where ungulates migrate elevationally and winters are severe. Seasonal movement would also be expected in arid areas where the availability of such prey as wild ungulates, livestock, and marmots fluctuate markedly.

The authors have no evidence that snow leopards patrol home-range boundaries. Each resident cat visited most portions of its range at intervals of several days to two or more weeks; on rare occasions, one would cross the entire home area in a single 24-hour period, while at other times a cat remained in a tract ≤0.5 km<sup>2</sup> for a week or more. Typically, they remained in a general area several kilometers in extent for several weeks before shifting to another part of the home area. Rabinowitz & Nottingham (1986) reported a similar pattern for jaguars.

Packer's (1986) review of sociality in solitary felids notes that females are intolerant of any conspecifics except their dependent offspring, or males during the female's periods of sexual receptivity. While telemetry and tracking data (adult female spoor cannot be distinguished from that of subadult males) neither confirm nor deny exclusive adult-female



home ranges, they suggest little overlap between adult females accompanied by young. The authors observed one set of tracks made by another female with a single cub within the common core area when 04's litter was 10 months old.

Because of limited success at locating adult male 01, the authors could not determine whether his range was larger than that of a female or whether it overlapped more than one adult female's range. Noticeably large male tracks were irregularly and infrequently seen during this study, suggesting either the absence of this size-class, or perhaps a situation where fully grown males range over very large areas and rarely remain long in any particular place.

Interpretation of home-range and land-tenure data is obviously complicated by the small sample, the uncertain breeding or social status of tagged males, and the relatively long time that they used a defined area. All tagged leopards met residency criteria given by Hemker et al. (1984) for mountain lions. Typically, among solitary felids, subadults use areas within parental ranges until they disperse, become transients, and then find or establish ranges of their own. Dispersal usually occurs soon after offspring become independent of the mother. Male 02 used a well-defined range until he was ~4 years old, when he shed his radio-collar. Male 03 resided in the same area until > 3 years old, when contact with him was lost. One possible explanation for lengthy residence by young adults might be the abundance of food in the study area, which permitted offspring to remain within the mother's range for extended periods before dispersing. However, male 02 showed some evidence of becoming reproductively active during the study.

Recent studies of solitary felids seem to indicate that land-tenure systems may be much more flexible than previously suspected, presumably reflecting differences in prey availability, habitat components, or other factors. For example, Hopkins et al. (1986) observed varying degrees of range overlap between male mountain lions in their California study area, and Rabinowitz & Nottingham (1986) found overlapping male ranges in a Belize jaguar population with a high turnover of males. Extensively overlapping ranges with temporally separated but spatially shared favored-use areas were observed in both sexes in another part of California (Neal et al. 1987). Discussing this flexibility in felids, Sunquist (1981:52) states, "... 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." Sunquist suggests that the major factors that influence variability are the seasonal distribution and abundance of prey, and the cost of "defending" home-range boundaries from intrusions by conspecifics. Rabinowitz & Nottingham (1986:156) notes 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.

A review of available literature could lead to the conclusion that snow leopards tend to travel in pairs or in small groups. Dang (1967:74) writes, "One fact has been repeatedly noticed, and that is the incidence of pairs working valleys in co-ordination, the prey, generally bharal, being chased from one part of the valley into the area where the other animal of the pair lies in waiting . . ." Other reports of two or three leopards traveling together are numerous, but unfortunately very few observers are explicit about the animals' age or size. The authors suspect that such sightings most likely involve a female and her nearly indepen-



dent offspring, the only prolonged social contact in snow leopards. An adult male and female consort for a brief period during the mating season, which extends from late January through mid March (this study). Other than breeding pairs, female-offspring groups, or recently independent siblings, physical contact between individuals is the exception. On a typical day, for example, individual radio-tagged snow leopards were  $\geq 2$  km apart. Further evidence of the species' essentially solitary nature accrued from tracking: the authors recorded  $> 250$  sets of tracks during the four-year study, and  $< 20$  involved more than one cat. Of 20 sightings, 18 involved solitary individuals, one a female (04) with 12-month-old cubs, and one a female with a large juvenile. The authors' data do not confirm Dang's observations of pairs hunting together.

The study area supports a high density of snow leopards, estimated (excluding cubs) at 5 to 10/100 km<sup>2</sup>. Elsewhere densities have been crudely estimated at 0.66/100 km<sup>2</sup> in Ladakh (Mallon 1984), 1.2/100 km<sup>2</sup> in a remote area 25 km southeast of the Langu Gorge (Schaller 1977), but only 0.35 to 0.53/100 km<sup>2</sup> in the Taxkorgan Reserve of Xinjiang, China (Schaller et al. 1987). Densities comparable to those observed in this study are reported for the Nar-Phu area of Nepal (4.3/100 km<sup>2</sup>) (Sherpa & Oli 1987) and two valleys in Ladakh, with densities of 5.8 and 8.3/100 km<sup>2</sup> (Osborne, cited in Green 1982). All density estimates except the authors' are based entirely on spoor, scrapes, or other sign, without regard to age or reproductive status. None of the surveys used a standardized data-gathering procedure, nor was the basis for converting sign to numbers specified. Data for facilitating sign to cat density transformation are limited to this study (Ahlborn & Jackson in press). Like Mallon (1984), the authors found it impossible to reliably distinguish between track sets made by known individuals, even with the benefit of radio-telemetry.

Although the authors' data indicate that bharal density varied widely within different parts of the snow leopard home ranges, much of the area was judged to support 4 to 8 animals/km<sup>2</sup>. A notable exception was the rolling slopes and cliff bands of Tillisha Mountain, where post-rut densities may have exceeded 15 to 20/km<sup>2</sup>. These compare with densities of 2.6/km<sup>2</sup> in a population harvested by humans (Wilson 1981), and winter concentrations of 8.8 to 10.0/km<sup>2</sup> at Shey near the study area (Schaller 1977). The Shey bharal occupy much more barren habitat than do the Langu herds, and must also compete with livestock. Jackson & Ahlborn (1984) estimate that an adult snow leopard would require 20 to 30 bharal annually. Telemetry data suggest that tagged snow leopards killed large prey about once every 10 to 15 days (with the interval between kills varying from about two to perhaps  $> 30$  days), a figure that compares with kill rates in mountain lions (Ackerman et al. 1986, Horner 1970, Shaw 1977).

Snow leopards seem to use their kills efficiently. The Langu cats almost completely consumed their kills, leaving only skeleton and skin along with some viscera. They remained on known or suspected kills for as long as a week, but averaging three to four days. Judging by how well snow leopards guarded kills, loss to vultures or other scavengers appeared negligible; neither were many animals interrupted or chased away from their meals by humans, as happens in other areas.

The Langu Gorge is characterized by a heterogeneous habitat, an abundant and reliable food source in the form of bharal, the absence of other large predators, and a snow leopard population that shares a common core area. Tagged snow leopards exhibit a strong preference for broken terrain: the core areas contained more cliffs, edges, and im-

proved juxtapositions compared with non-core areas. The shared core area partially overlapped a shoulder of Tillisha Mountain, which supported the most extensive grassland and obviously productive bharal habitat in the study area (Figure 6).

Ahlborn & Jackson (in press) speculate that the well-developed social marking system of snow leopards 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 confers some home-area "ownership right" over periods of time. The incidence of marking within the core area was four times greater than in non-core sites. Significantly more marking was found along linear topographic features, such as major ridge-lines that form 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 were 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 >2 km apart. This implies that the Langu cats actively avoided 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 leopards. Different patterns of home range, land tenure, and social marking are likely to be found in less favorable habitats where snow leopards are fewer and where humans and wildlife coexist precariously. Future research should focus on snow leopard populations in marginal situations, to better understand important ecological relationships. Such knowledge is vital for effective protection of snow leopards and sustained utilization of their fragile habitat.

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