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Unveiling the Ghost of the Mountain; Snow Leopard Ecology and Behaviour

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Abstract

The snow leopard (*Panthera uncia*) has remained an enigma – one of the most recognised yet least understood of the large carnivores. The lack of knowledge about the species' basic ecology causes conservation and management plans to be largely built on conjecture. The main aim of this thesis is to provide solid information on some of the key aspects of snow leopard ecology. The studies are primarily based on individual GPS-location data from collared snow leopards in the Tost Mountains of southern Mongolia. To increase our understanding of how large solitary carnivores adjust their home range utilisation to seasonal changes in key resources, data from GPS-collared pumas (*Puma concolor*) in the Cascade Mountains, USA were included in one chapter. In the last chapter photographic data from zoos across Europe were used to evaluate a critical assumption of one the most commonly employed survey methods for snow leopards

In this study, snow leopards were found to have killed more wild prey than livestock, despite livestock number being at least an order of magnitude higher. Choice of wild prey followed the spatial and seasonal distribution of the prey. Male snow leopards had larger home ranges than females. Both males and females displayed intrasexual territoriality. Only between three and 22% of the protected areas in the snow leopard distribution range were large enough to have a 90% probability of harbouring 15 adult females. Puma and snow leopard males did not monopolise females by encompassing their home ranges. Contrarily, males of both species decreased monthly home range size in the mating season or peak mating time period, showing that they employed a mate guarding strategy.

Snow leopards were crepuscular and facultative nocturnal, their activity peaks changed seasonally, occurring during dusk in the cold season and dawn during the warm season. Activity patterns of snow leopards appear to be driven by a combination of needs facilitating hunting (cover and visibility) and thermoregulation whereas no support was found for the common explanation that large carnivores mirror the activity of their prey. The critical assumption in abundance estimates based on capture – recapture calculations, that individuals are correctly identified, was severely violated in a test using known individuals. In our test the classifiers overestimated the number of individuals in the sample, which could have serious consequences for a threatened species.

Keywords: activity pattern, camera trap, conservation, home range, Mongolia, *Panthera uncia*, predation, social organisation

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Sammanfattning

I många av de länder där snöleoparden (*Panthera uncia*) lever kallas de för bergens vålnader av lokalbefolkningen. De karga och otillgängliga berg som utgör snöleopardens livsmiljö, tillsammans med artens skygghet och utmärkta kamouflage, innebär att få människor har fått se mer än en skymt av dem. Trots decennier av forskning visste vi fortfarande inte särskilt mycket om artens ekologi när den här studien startade 2008. För att naturvård, oavsett om den är riktad mot bevarande eller annan förvaltning, ska vara framgångsrik måste den baseras på solid kunskap om den aktuella arten.

Den här avhandlingen bygger främst på data från GPS-märkta snöleoparder i Tostbergen i södra Mongoliet. För att bättre förstå hur stora rovdjur utnyttjar sina revir, och hur säsongvariationer i fördelningen av de viktigaste resurserna påverkar, har jag även jämfört med data från GPS-märkta pumor (*Puma concolor*) i delstaten Washington, USA. Avhandlingen presenterar ny information om stora delar av snöleopardens ekologi.

Jag fann att snöleoparderna dödade fler vilda bytesdjur än tamboskap, trots att det fanns minst tio gånger fler tamdjur i området. Snöleopardhannar hade större hemområden än honor och båda könen hävdade revir. Endast mellan tre och 22% av de skyddade områden som finns inom snöleopardens utbredningsområde var tillräckligt stora att ha 90% sannolikhet att kunna hålla 15 vuxna honor. Varken puma eller snöleopardhannar monopoliserade honor genom att omsluta deras hemområden. Istället minskade hannarna sina rörelser under parningssäsongen, eller den tid då flest parningar skedde, vilket visar att deras strategi var att bevaka honorna snarare än att maximera sin area. Snöleoparderna var aktiva främst i gryning och skymning och delvis även nattetid. Aktivitetstoppen ändrades över året, under den varma årstiden inföll den i gryningen och under den kalla årstiden inföll den under skymningen. Aktivitetsmönstret verkar styras främst av behovet av skydd, sikt och termoreglering. Kamerafällor har under senare år blivit en populär metod för att inventera stora däggdjur såsom snöleopard. För att räkna ut hur många individer ett område hyser krävs att man kan identifiera individerna korrekt. Jag testade detta antagande och fann att kravet på korrekt identifiering av individer är svårt att uppfylla vilket leder till en överskattning av antalet individer. I små populationer av en hotad art kan det få allvarliga konsekvenser.

Keywords: aktivitetsmönster, bevarande, Gobiöknen, hemområde, kamerafälla, naturvård, Mongoliet, *Panthera uncia*, predation, revir,

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Dedication

To Marie and Eldar for all the times I've been away

For epochs to come the peaks will still pierce the lonely vistas, but when the last snow leopard has stalked among the crags and the last markhor has stood on a promontory, his ruff waving in the breeze, a spark of life will have gone, turning the mountains into stones of silence.

G. Schaller, Mountain monarchs (1977)

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Johansson, Ö*., McCarthy, T., Samelius, G., Andrén, H., Tumursukh, L. & Mishra, C. (2015). Snow leopard predation in a livestock dominated landscape in Mongolia. Biological Conservation, 184, pp. 251-258.

II Johansson, Ö*., Rauset, G. R., Samelius, G., McCarthy, T., Andrén, H., Tumursukh, L. & Mishra, C. (2016). Land sharing is essential for Snow leopard conservation. Biological Conservation, 203, pp. 1-7.

III Johansson, Ö*., Low, M., Koehler, G., Rauset, G. R., Samelius, G., Andrén, H., Lkhagvasuren, P., McCarthy, T. & Mishra, C. Sex-specific seasonal home range utilisation of pumas and snow leopards. (manuscript)

IV Johansson, Ö*., Chapron, G., Samelius, G., Lkhagvajav, P., McCarthy, T. & Mishra, C. Do large carnivores mirror the activity pattern of their prey? (manuscript)

V Johansson, Ö*., Low, M., Wikberg, E. & Samelius, G. Evaluating the critical assumption of correct individual identification in camera-trap studies. (manuscript)

Papers I and II are reproduced with the permission of the publishers.

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The contribution of Örjan Johansson to the papers included in this thesis was as follows:

I Main author. Collected the data together with L. Tumursukh and field assistants. Designed the study. Analysed the data together with HA and GS. Wrote the manuscript with contribution from co-authors

II Main author. Collected all data. Designed the study together with co-authors. Analysed the data together with GRR and GS. Wrote the manuscript with contribution from co-authors

III Main author. Collected all snow leopard data. Designed the study together with co-authors. Analysed the data together with ML and GRR. Wrote the manuscript together with ML and with contribution from co-authors

IV Main author. Collected all data. Designed the study. Analysed the data with support from GC and HA. Wrote the manuscript with contribution from HA and co-authors.

V Main author. Designed the study. Analysed the data together with ML and HA. Wrote the manuscript together with ML and with contribution from co-authors

1 Introduction

The snow leopard (*Panthera uncia*) has remained an enigma - one of the most recognised, yet least understood of the large carnivores. Given how much time and effort that research has devoted to the large felids, surprisingly little is known about snow leopard ecology and behaviour. The snow leopards' elusive nature combined with the inhospitable habitat and the vast ranges in which the species occur have made it inherently difficult to study. Even among the local people inhabiting the same areas as the snow leopards, much knowledge revolves around myths about these ghost-like creatures. The snow leopards' sandy coloured coat, speckled with rosettes and spots, provides them with a superb camouflage that blends perfectly with their rocky habitat. The short and rare glimpses of snow leopards almost exclusively occur in relation to livestock attacks, after which they slip back into the mountains and disappear. Consequently, throughout the species range the local people refer to them as 'the ghost of the mountain' or 'grey ghosts'. As a testament of the species' elusive nature, it was not until 1971 that a snow leopard was photographed in the wild. The photographer later described the meeting in a way that embodies the very essence of the snow leopard, and the challenges facing the people studying them:

> "…As we watched each other the clouds descended once more, entombing us and bringing more snow. Perhaps sensing that I meant her [the snow leopard] no harm, she sat up. Though more snow capped her head and shoulders, she remained silent and still, seemingly impervious to the elements. Wisps of clouds swirled around, transforming her into a ghost creature, part myth and part reality. Balanced precariously on a ledge and bitterly cold, I too stayed, unwilling to disrupt the moment. One often has empathy with animals, but rarely and unexpectedly one attains a state beyond the subjective and fleetingly almost seems to become what one beholds; here, in this snowbound valley of the Hindu Kush, I briefly achieved such intimacy. Then the snow fell more thickly, and, dreamlike, the cat slipped away as if she had never been…"(Schaller 1980)

Early snow leopard research yielded information on the very basic aspects of the species' ecology such as distribution and indications of feeding ecology (e.g. Hemmer 1972; Fox & Chundawat 1988; Fox 1989). However, the precipitous habitat hampered more detailed investigations, as snow tracking was not feasible and many areas could not be accessed. The advent of radio-telemetry (Craighead & Craighead 1965) allowed far more detailed information to be collected, and the first snow leopard was equipped with a Very High Frequency (VHF)-radio-collar in 1982 (Jackson 1996). Subsequently, four more studies utilizing VHF-collars were conducted (see Johansson, Simms & McCarthy 2016 for a summary). Combined, these studies substantially advanced the understanding of snow leopards. However, it once again became clear that the extreme habitat prevented systematic data collection; following the collared snow leopards on foot proved almost impossible, and the snow leopards could not be located for extended periods (Jackson 1996; Oli 1997; McCarthy et al. 2005).

Conflicts arise in most areas where large carnivores and humans co-occur, commonly related to predation on livestock or competition over game species (Treves & Karanth 2003; Inskip et al. 2009). Many large carnivores have extensive spatial needs (Goodrich et al. 2010; Mattisson et al. 2011), which complicates mitigations as the conflicts occur over vast areas (Linnell et al. 2001). To be successful, conservation and management actions must be based on sound knowledge of the target species ecology. This knowledge is especially important for species that experience conflict with human lives, livelihoods and financial interests. Poorly designed conservation or management plans may negatively affect human perceptions of the species as well as the organisations responsible for carrying out the plan. Hence, successful conservation must incorporate both the needs of the species as well as the local people, and must be based on robust science (Mishra et al. 2017).

Key parameters for designing evidence-based conservation actions of large carnivores include:

- Diet, which is a combination of species utilised (prey choice) and number of prey killed per unit time (kill rate)
- Individual space use (home range size) and social organisation (e.g. exclusive or overlapping home ranges)
- Temporal patterns in livestock depredation such as seasonal variation and daily patterns.
- Means to monitor population size and trends over time, for example to assess efficiency of conservation actions.

By intensively studying a population in a limited area, and collaring a large proportion of the population, it is possible to understand additional aspects of the species ecology such as social organisation or how demographic parameters are affected by resources (e.g. Bailey 1993; Logan & Sweanor 2001). Such a comprehensive study on any large carnivore species will require a substantial investment of funding and manpower. The benefit of the study, besides providing detailed information from one study area, is that subsequent studies can yield robust inferences with a lesser investment of funding and manpower because inferences can be compared and validated, or rejected.

A decade ago, the technology needed to collect robust data on snow leopards, such as remotely triggered trap-cameras and light-weight Global Positioning System (GPS)-collars with satellite communication, had become readily available. Therefore, in summer 2008, Snow Leopard Trust launched a study with the aim to thoroughly describe the snow leopard's ecology. At the outset of this study, much of this knowledge was lacking, consequently, conservation was largely built on conjecture.

2 Objectives

The aim of this thesis is to improve our understanding of snow leopard ecology and behaviour. Despite being a large and charismatic felid, receiving substantial public interest, much basic snow leopard ecology was not well understood at the outset of this study. To provide means for a science-based conservation and management of snow leopards, this thesis describes their diet, space use, home range utilization, daily activity, and evaluates the accuracy of a common survey method for the species.

The main questions were:

1 What is the prey choice and kill rate of snow leopards (*Paper I*)?

2 What is the home range size of snow leopards and to what extent does home ranges overlap, how effective will the existing protected areas in snow leopard range be to conserve the species (*Paper II*), and how does home range utilisation in snow leopard and puma change with seasonal changes in food distribution and mating opportunities (*Paper III*)?

3 What are the daily activity patterns of snow leopards and what are the main drivers of these activity patterns (*Paper IV*)?

4 How well can we identify individual snow leopards in trap-camera photos and what effects will potential identification errors have on population estimates (*Paper V*)?

3 Methods

3.1 Study areas

3.1.1 Tost Mountains (*Paper I – IV*)

The snow leopard data for this thesis was collected in the Tost Mountains (43^{o}N, 100^{o}E) in the Gobi Desert of southern Mongolia between 2008 and 2014. Tost, approximately 1700 km^2, consists of several mountain massifs separated by wide valleys. The mountains rise from the surrounding steppe at 1600 m above sea level to the highest peaks at around 2500 m. Although not very high, the mountains are rugged, with precipitous slopes traversed by steep ravines and narrow gorges. Average temperatures vary greatly over the year; mean daily temperatures in the nearby village Gurvantes, in the eastern corner of the study area (1650 m above sea level) was -14°C in January and 22°C in July. Average minimum and maximum daily temperatures were -27°C and 1°C respectively for January, and 11°C and 33°C respectively for July. Temperatures in Tost are generally lower than in Gurvantes but no weather data exists for the mountains. Winds are normally high (annual average wind speed was 16 km/h) and temperatures corrected for wind-chill would be substantially lower. Annual precipitation is less than 130 mm, most of which falls as rain from June through August. Vegetation is sparse and consists mainly of short grasses, dwarf shrubs and patches of shrubs dominated by *Amygdalus mongolica, Stipa* spp., *Caragana leucophlaea* and *Eurotia ceratoides*.

Approximately 90 herder families live in the study area. The herders are semi-nomadic and traditionally move four times during the year, living in the steppe from spring to autumn and in more mountainous areas in winter to seek shelter from the cold winds (Traditional knowledge, B. Agvantseeren Pers. Communication). In recent years, an increasing number of families have surrendered the nomadic lifestyle and settled in permanent campsites, often at the edges of the mountains. Livestock in Tost consist of ~32 000 goats (*Capra aegagrus*) and sheep (*Ovis aries*), ~1,100 camels (*Camelus bactrianus*), and ~120 horses (*Equus ferus caballus*). Horses and camels are largely free-ranging in small herds, whereas goats and sheep are actively herded and penned close to campsites at night. The herders' main source of income is cashmere wool that they comb from their goats in spring.

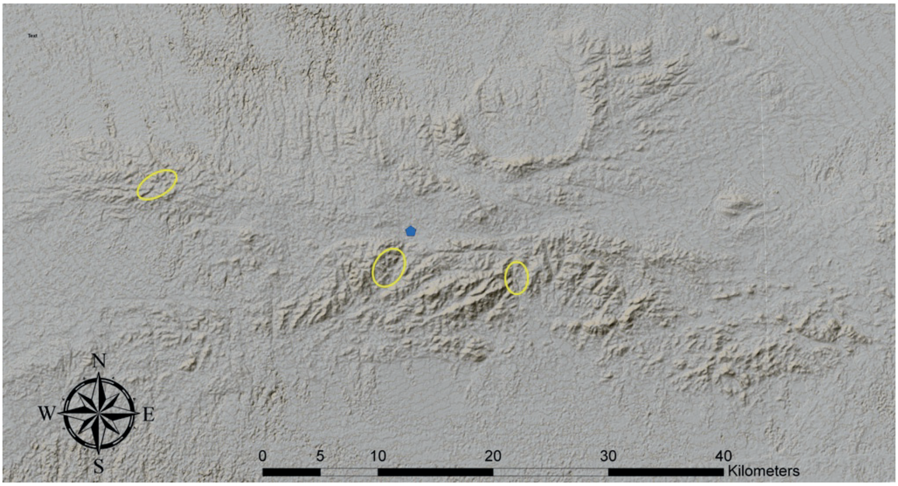

Figure 1. Satellite image (Aster DEM) of the study area, Tost Mountains in Southern Mongolia. The blue dot marks the base camp (Latitude 43.205 N, Longitude 100.622 E) and the yellow circles show the three main trapping areas.

The snow leopard population in Tost has been surveyed with cameras-traps annually since 2008 and was estimated to contain 10-14 adult individuals during this study (Sharma et al. 2014). To understand how snow leopards responded in their prey choice with changes in local prey abundance, we divided our study area into Southern (556 km^2) and Northern (807 km^2) ranges (*Paper I*). The Southern range is more rugged and mountainous than the Northern range. Siberian ibex (*Capra sibirica*) were common throughout the rugged parts of the mountains whereas argali sheep (*Ovis ammon*) occurred mainly in the rolling hills in the northern and western parts of the study area (Tumursukh 2013). Camels and horses were mainly found in the steppe or the lower, less rugged parts of the mountains in the Northern range. In addition to ibex and argali, we had occasional sightings of black-tailed gazelles in the mountains. Smaller potential prey species included Tolai hare (*Lepus tolai*), chukar partridge (*Alectoris chukar*) and various rodents. Sympatric predators and scavengers included wolf (*Canis lupus*), Eurasian lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), marten (*Martes spp*.), bearded vulture (*Gypaetus barbatus*), golden eagle (*Aquila chrysaetos*), black vulture (*Aegypius monachus*) and raven (*Corvus corax*).

3.1.2 The Cascades (*Paper III*)

The puma data were collected within a 1652 km^2 area along the eastern slope of the Cascade Mountains of Washington State U.S.A. (47° N 121° W). Elevation ranged from 460 to 2300 m with sagebrush (*Artemisia tridentata*) steppe below 550 m; at higher elevations the slopes were covered by trees, dominated by ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*). Mean temperatures ranged from –7° C in January to 27° C in July. Precipitation increased with elevation, averaging 5630 mm/year, which fell mostly as snow during the winter (Western Region Climate Center, 2013). Ownership and management of the area included U.S. Forest Service, commercial forests, agricultural lands, and private residential properties. Residential developments primarily occur along the wide valley bottoms and interspersed on the lower slopes surrounding the valleys with a density of 6.6 humans/km^2 (United States Census Bureau, 2010). The main prey species were mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) (White et al. 2011), which aggregate at lower elevations in winter (Smith 2007), resulting in clumped food resources for pumas beginning in November and lasting until May (Washington Department of Fish and Wildlife. The Colockum Elk Study II, 2013, unpublished data). Although mating and births can occur at any time of the year, there are distinct seasonal patterns of reproduction in pumas, with peak mating in February to April and little to no mating in August to November based on Yellowstone data in Quigley and Hornocker (2010).

3.2 Captures and monitoring (*Paper I – IV*)

Snow leopards were captured with modified Aldrich-style foot-snares placed at sites with fresh markings, scrapes and scent marks, in steep-walled, narrow ravines. The snares were anchored to the ground using four metal stakes with a nut welded to one end, hammered in perpendicular to one another at about 45° angle. A spring was attached between the anchor and the snare-loop to cushion the impact of the struggling snow leopard. Each snare was equipped with a VHF trap-site transmitter (Telonics TBT-500, Telonics inc., Mesa, Arizona, USA) emitting a continuous signal at a unique frequency. If an animal got caught in the snare, a plunger was pulled out from the transmitter and the signal pulse rate changed. Trap transmitter signals were checked with a handheld receiver every third hour from early evening to late morning by climbing a nearby mountain from 2008 to 2010. A custom-built trap surveillance system that constantly monitored the snares (Johansson et al. 2011) was used from 2011 and onwards. The system scans the trap-transmitters one at a time and sounds an alarm within a few minutes after an animal has been caught. This system minimized the time the snow leopards had to spend in the snare and hence the risk of injuries. Captured snow leopards were immobilized with a combination of medetomidine and tiletamine-zolazepam delivered by a CO_2 powered dart rifle (Daninject J.M. Special, Daninject, Borköp, Denmark) from a single person at 10-15 m distance (see Johansson et al. 2013 for details about the immobilization).

Between 10 and 17 snares were placed at a distance of up to three km from the mobile trapping camp, a traditional Mongolian ger. Once the resident snow leopards in the area had been captured, or if the same snow leopard had been caught three times, the camp was moved to a new location. Three different trap areas were mainly used with an additional two areas used one time each, camp was moved in total 15 times. The average number of trap nights per area was 43 (range 21 to 90). The total number of trap nights was 598, resulting in 45 captures of 19 snow leopards, 10 males and nine females.

Captured snow leopards were equipped with North Star GPS-collars (North Star, King George, USA) in 2008-2009 and Vectronic GPS-Plus collars (Vectronic Aerospace, Berlin, Germany) from 2010 and onwards. Collars were programmed to acquire one GPS location every seven and five hours, for the North Star and Vectronic collars respectively, and immediately uplink the data via Globalstar satellites. The collars were programmed to release from the snow leopards after a pre-defined length of time had elapsed, ranging from 12 to 22 months. The Vectronic collars were also equipped with an activity sensor consisting of two single axis accelerometers that measured movements four times per second and stored mean values for five minute intervals (*Paper IV*).

Pumas were captured using trained dogs or large steel cage traps with methodologies described by Cooley et al. (2009). Pumas were immobilized with either a mix of ketamine and xylazine or tiletamine-zolazepam and fitted with either of the following collars: Vectronic GPS Plus-2 (Vectronic Aerospace, Berlin, Germany), Followit Tellus or Simplex, (Followit, Lindesberg, Sweden), or Lotek 4400 (Lotek Wireless, New Market, Ontario, Canada). The collars were programmed to take a GPS location every four hours and GPS data were retrieved via UHF or VHF remote communication during telemetry sessions, from recovered collars, or via satellite transmission. All puma captures and handling were performed in accordance with Sikes and Gannon (2011) (*Paper III*).

3.3 Predation patterns (*Paper I*)

To determine kill rates and prey choice, we visited sites where collared snow leopards had potentially killed prey. We assumed that similar to other large carnivores (e.g. Anderson & Lindzey 2003; Sand et al. 2008), snow leopards would remain close to the kill site when they had killed a large prey animal (i.e. an ungulate). This should result in a cluster of GPS locations close to each other. Clusters were defined as ≥2 locations within 100 m of each other and separated by less than 24 hours. Cluster visits were conducted over 26 periods from 2008 to 2013, ranging from 31 to 189 days (yielding a total of 2339 snow leopard-days). All carcasses encountered within the cluster area were considered to have been killed by the collared snow leopard if decomposition matched the dates of the cluster. We searched 370 potential kill site clusters intensively for prey remains and snow leopard signs (faeces, tracks and scrapes). Prey remains were found on 258 of the clusters, and of these, the species could be identified in 249 cases.

Kill intervals were defined as the number of days between two consecutive kills, starting at the time of the first GPS location in the first cluster and ending at the first GPS location in the second cluster. Kill rate was considered the inverse of the kill interval.

3.4 Spatial analyses (*Paper II and III*)

3.4.1 Home range estimators

I calculated both long-term and monthly home ranges to examine how home range utilisation and overlap changed temporally. To define long term home ranges, I employed net squared displacement (Bunnefeld et al. 2010) in the R package adehabitatLT (Calenge 2011). Long-term home ranges were calculated by identifying data driven temporal break-points in space use and home range shifts instead of pre-defined break-points such as annual home ranges (*Paper II and III*). Three different home range estimators were used to calculate long term (*Paper II and III*) and monthly (*Paper III*) home ranges for snow leopard (*Paper II and III*) and puma (*Paper III*) using minimum convex polygons (MCP), fixed kernels (Kernel) and adaptive local convex hulls (aLoCoH). I estimated 95% MCPs and 95% Kernels (bivariate normal smoothing curve and h_{REF}*0.6) in the R package adehabitatHR (Calenge 2006). Adaptive local convex hulls (aLoCoH) were estimated using the R package TLoCoH (Lyons et al. 2013). All three estimators were included to test for the most accurate estimates and for comparison with earlier studies.

3.4.2 Home range overlap

Overlap was calculated as the proportion of each individual's home range that overlapped with neighbouring individuals. As home range size is not constant between individuals and the proportion of overlap varies depending on the size of the home range, two overlaps were calculated for each neighbouring pair; Y/X and X/Y. The LoCoH home range estimates were used because LoCoH is considered as one of the most accurate methods to identify sharp borders of home ranges (Getz & Wilmers 2004; Getz et al. 2007) and all three home range estimators produced qualitatively similar results of home range size.

3.4.3 Home range size compared with the size of protected areas

By combining a map of the global snow leopard range (McCarthy et al. 2016), using the areas defined as definite and probable occurrence, with a digital database of protected areas (Deguignet et al. 2014), the proportion of each protected area that overlapped with snow leopard distribution was calculated with the intersect function in ArcGIS 10.1 (ESRI, Redlands, CA). The size of the protected areas was compared with the average size of a male snow leopard home range (aLoCoH), and with 15 randomly drawn home range sizes of adult females (aLoCoH and MCP with no overlap and with overlap of two neighbours). The comparison was repeated with a 50% reduction of home range size (aLoCoH) to account for the possibility that home ranges may be smaller in parts of the distribution range. These simulations yielded the number of protected areas that had ≥90% probability to contain at least 15 adult females.

3.5 Individual identification in photographs (*Paper V*)

3.5.1 Individual identification

To assess the accuracy in individual identification of snow leopards from camera-trap photographs, we placed camera-traps in enclosures in seven zoos throughout Europe. Only one snow leopard at a time was present in the enclosure with the camera to ensure knowledge of identity. Photographs were organised in a photographic library of 40 folders, where each folder contained three to 11 photos taken consecutively of the same snow leopard (a capture event). Sixteen snow leopards were included in the study, each individual was found in one to five folders. Eight observers, four experts who work with identifying snow leopards from trap-camera photographs, and four non-experts who had experience of animals in captivity but had never identified trap-camera photographs, were asked to identify the individuals in the folders.

Classification errors were defined as (1) 'exclude', where the folder was excluded by the observer as being unidentifiable, (2) 'split', where the folder was incorrectly split from other folders containing the same individual and placed by itself, thereby creating a new individual, (3) 'shift', where the folder was incorrectly split from other folders containing the same individual and added to another individual's set of folders, or (4) 'combine', where the folder(s) from an individual was combined with another individual, resulting in the loss of that individual.

3.6 Statistical analyses

Most analyses were performed in R (R Development Core Team 2014). To examine differences in prey choice among snow leopard categories (*Paper I*), χ^2-contingency tables and Fishers exact tests were used in SAS (Proc Freq, SAS Institute Inc., Cary, North Carolina). ArcGIS 10.1 was used to calculate topographic ruggedness using the Vector Ruggedness Measure (Sappington et al. 2007) (*Paper I and II*).

3.6.1 Mixed linear models (*Paper I and II*)

I used generalised linear mixed models (R package lme4: Bates et al. 2015) to analyse (i) if the kill interval was affected by age and sex of the snow leopard or by prey species; (ii) if the proportion of livestock and wild prey in the diet changed seasonally; and (iii) if home range size or overlap changed with age and sex of the snow leopard. Snow leopard ID was included as a random effect in all models to account for repeated measures of the same individuals.

3.6.2 Seasonal changes in livestock predation (*Paper I*)

Two models were used to test the effect of season on the type of prey killed (livestock versus wild prey) to account for the cyclical nature of the year, i.e. that December and January are connected, to include binomial errors (livestock and wild prey) and random factors (repeated measures of the same snow leopards). The first model, circular regression (R package Circstats: Jammalamadaka & Sengupta 2001), accounted for the cyclical nature of the year, and the second model, logistic regression, included binomial errors and random factors.

3.6.3 Seasonal home range utilisation (*Paper III*)

Analyses of how home range utilization and overlap changed seasonally were modelled in a Bayesian framework in JAGS (Plummer 2003). Bayesian modelling was used because: (i) the appropriate observational uncertainty could be incorporated into estimates, and (ii) all estimated and derived parameters are posterior distributions where the probability of an effect being different from zero can be directly calculated. For the sex and species-specific home range estimates the raw observations were used to generate (Gamma) probability distributions from where the expected means and standard deviations for each group could be calculated. To examine how monthly home range size and overlap between neighbours changed throughout the year a sine wave function was used to incorporate its annual cyclical nature, with this modelled for sex and species-species groups.

3.6.4 Daily activity (*Paper IV*)

Seasonal changes in activity pattern were examined using generalised additive models in the (R package mgcv: Wood 2011) where I included month as a smoothed fixed effect, and time of day (dawn, day, dusk, night), sex (male, female) and age (adult, subadult) as fixed effects in the first model. In the second model I included fraction of moon illuminated and month as smoothed fixed effects for data collected at night. Due to the very large dataset (906 824 activity readings) all coefficients were highly influential, despite some very small effect sizes. Therefore, the deviance explained by each effect was used to compare the relative importance of coefficients.

3.6.5 Effect of individual identification error on population estimates (*Paper V*)

Identification errors from camera-trap photographs were analysed with a binomial likelihood model in a Bayesian framework. Each observer's answers were compared to the correct identities and the probabilities of the different errors were calculated, and these were compared between experts and non-experts.

4 Results and Discussion

4.1 Predation patterns (*Paper I*)

The snow leopards killed more wild prey (73%) than livestock (27%), despite livestock abundance being at least an order of magnitude higher than wild prey abundance. The relative proportion of species killed mirrored the spatial distribution in the two subdivisions with more argali, camels and horses killed in the Northern range and more ibex killed in the more rugged Southern range. More herded livestock (goats and sheep) were killed in the Southern range, probably because the higher ruggedness prevented the herders from monitoring their entire herd, providing the snow leopards with opportunities to kill a goat unnoticed, or some goats were left behind overnight and subsequently killed. Proportion of livestock in the diet changed seasonally, following the temporal changes in abundance with more livestock in the mountains in winter (Figure 2).

Prey choice differed among snow leopard categories (young males, adult males, single females and females with cubs), with the highest utilisation of wild prey found in young males (94%) and the lowest in adult males (53%). Single females utilised more livestock than females with cubs, but the differences were small (20% and 13% respectively). Similarly, adult males and females with cubs killed more large wild prey (ibex and argali males) than young males and single females. With increasing age, the snow leopards probably became experienced enough to handle the commotion and risks associated with killing livestock and developed the skills needed to kill the larger wild prey. Adult females are associated with cubs for most of their lives and perhaps unwilling to subject the cubs to the risks involved in livestock predation, which would explain why females kill less livestock.

Kill intervals were similar for single females and females with cubs, whereas they were larger for young and adult males. Kill intervals increased with the size of the prey killed, which could explain the increased interval in adult males compared to the other groups as they utilized the highest proportion of large prey (ibex and argali males, horses and camels). The kill rates estimated from our results were 50 - 120% higher than what has previously been reported, based on energetic requirements (Jackson & Ahlborn 1984).

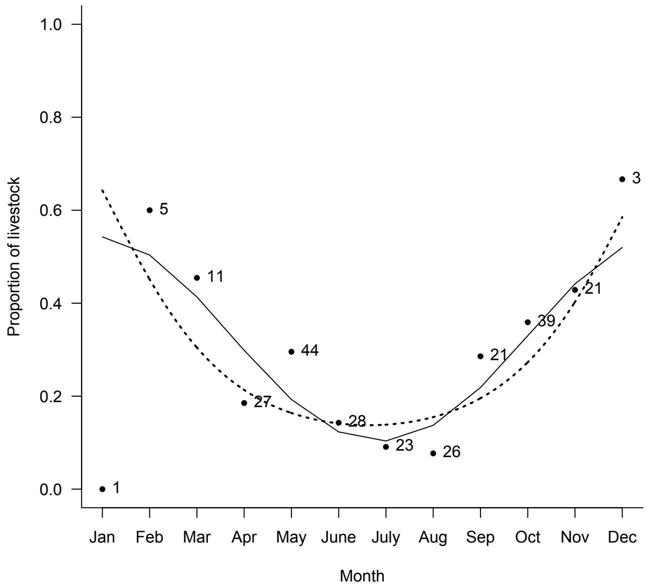

Figure 2. Proportion of livestock killed by snow leopards in relation to month of year. Dots represent the pooled data for each month with sample size represented by the number. The dotted line was derived from a mixed logistic regression model with individual as random factor. The black line indicates the fitted circular regression line.

4.2 Home range size, overlap and space use in relation to size of protected areas (*Paper II*)

Home range sizes were qualitatively similar between demographic groups for all three estimators, however MCP and Kernels were almost three times larger than the aLoCoHs (Table 1). The home ranges calculated with aLoCoH had similar proportions of mountains and steppe as the GPS-locations. For the GPS locations and the aLoCoH home ranges, the areas classified as steppe were mainly valleys and smaller flat areas inside the mountains. In contrast, the MCP and Kernels contained substantially more steppe with a substantial proportion outside of the mountains where no GPS-locations were obtained. This suggested that the

LoCoH home ranges were biologically more meaningful and were therefore used in all comparisons.

Home ranges of adult males were about twice as large as those of adult females, which is the common pattern in large solitary carnivores (e.g. Sandell 1989; Sunquist & Sunquist 2002), but see cheetah [*Acinonyx jubatus* (Broomhall et al. 2003)]. Subadult females had the second largest home ranges, while adult females and subadult males had similarly sized home ranges (Table 1). Home range overlap differed between demographic groups; the lowest overlaps occurred between adults of the same sex and the largest overlaps occurred between adult females and adult males. Home range overlaps between adult males were the same as between adult females (0.17), suggesting that adult snow leopards displayed intersexual territoriality.

Table 1. *Mean home range size (km^2 ± SD) for GPS-collared snow leopards in Tost Mountains, Mongolia in 2008-2014.*

Demographic group	MCP[a]	Kernel[b]	aLoCoH[c]	n
Female Adult	327± 200	336± 136	124± 41	7
Female Subadult	589± 83	554± 114	223± 277	4
Male Adult	615± 319	617± 317	207± 63	9
Male Subadult	474± 386	451± 265	138± 65	4
Average snow leopard	503± 286	497± 255	174± 71	24

[a] MCP = 95 % Minimum convex polygon
[b] Kernel = 95 % Fixed Kernel utility distributions
[c] aLoCoH= adaptive local convex hull

The estimated home range sizes found were 6-44 times larger than previous VHF-based studies when comparing the same home range estimators, i.e. MCP (Jackson 1996; Oli 1997; McCarthy et al. 2005). The home range overlaps also differed greatly from previous studies but, contrary to what could be expected given that the home ranges were so much larger, the overlap was considerably lower than previously reported (Jackson 1996; Oli 1997; McCarthy et al. 2005). The great differences to earlier studies are likely attributed to the different technologies used; earlier studies employed VHF (radio) collars that require the researcher to locate the animal with radio-signals. It has proven extremely difficult to locate snow leopards on foot in the precipitous terrain that they inhabit. All earlier studies reported significant time periods when the collared snow leopards could not be found, indicating that they were using a larger area than what the researchers could survey with the VHF-equipment.

A total of 170 protected areas overlapped with the areas classified as definitely and probably inhabited by snow leopards. Of these, 40% were smaller than an adult male's home range, which shows that it is not likely that they will harbour a breeding pair of snow leopards. The proportion of protected areas that had a 90% probability of harbouring 15 adult females ranged from three to 13% depending on the estimator used and number of overlapping neighbours. When reducing the home range size by 50%, the proportion of protected areas large enough to have a 90% probability to harbour 15 adult females increased to 22%. The estimates based on MCP are probably the most appropriate to use because protected areas were not separated into habitat types; all areas were assumed to be saturated with snow leopards and edge effects were not included. This study shows that conservation efforts of snow leopards cannot rely on land sparing alone, but must rely on a combination of land sharing and land sparing, implemented at a landscape level.

4.3 Home range utilisation in relation to seasonal changes in key resources (*Paper III*)

Males in both pumas and snow leopards had larger long-term and monthly home ranges than females. No evidence that males 'monopolised' or attempted to maintain exclusive access to females was found in either species, as the proportion of long-term home range overlap between a focal female and the male most strongly associated with her home range was only 0.28 for pumas and 0.64 for snow leopards. Each month, snow leopards occupied almost half of their long-term home range, while pumas occupied less than a quarter. Males of both species displayed much larger seasonal variation in home range size than females. In both snow leopards and pumas, male home range size was at its minimum during winter, which corresponds to clumped food resources and peak mating for pumas, and to the mating season for snow leopards (Figure 3). This suggests that males in both species used a mate proximity strategy, i.e. they reduced their movements to the area around fertile females during the mating season or mating peak, contrary to the hypothesis that the males would adopt an area maximisation strategy. Furthermore, as males increased their home ranges, the female - male monthly overlap decreased, to a higher degree in pumas than in snow leopards. This result indicates that the females were located so that the males could not encompass them, i.e. that the female home ranges were centred at the border between two or more males. Female felids have been shown to mate with several males in the same mating season, probably to confuse paternity as a counterstrategy against infanticide (Balme & Hunter 2013; Allen et al. 2015). By mating with the neighbouring males, the female increase the chance that future encounters will be amicable and, should one of the males be replaced, the female can also adjust space use to avoid the new male.

Females showed less seasonal variation in home range size than males for both species (especially snow leopard females). Seasonal home range variation in puma females was linked to changing resource distribution, whereas seasonal home ranges in snow leopard females were more stable and the food resources varied much less.

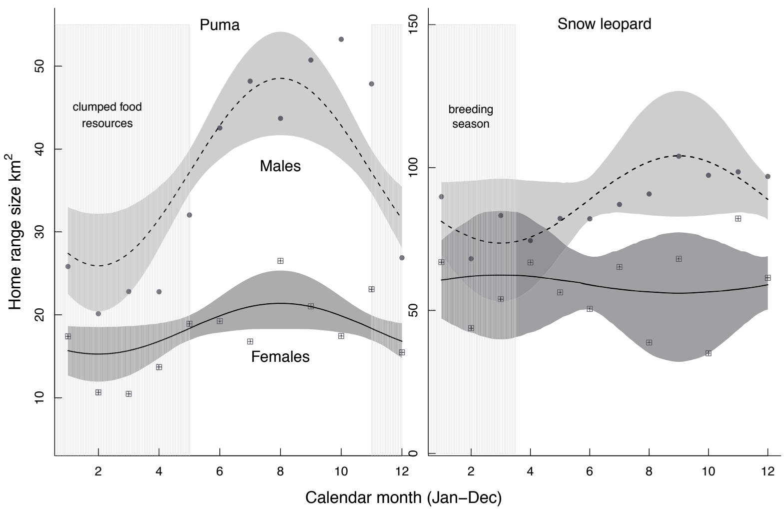

Figure 3. Species-specific seasonal variation in home range size (LoCoH, km^2) for males (dashed lines) and females (solid lines). Lines show medians of the posterior distribution and shaded areas 95% CIs. Also highlighted is the period for pumas when food resources are clumped during winter (November – May) and for the breeding season for snow leopards (January – March).

Large carnivores primarily define their territorial boundary with olfactory cues (Wolf & Ale 2009; Powell 2012; Allen et al. 2015). These marks allow neighbours to determine identity of the individual and the time since they last visited the area. Thus, neighbours can use this information to decide when to intrude into a territory, and boundaries therefore should become somewhat dynamic over time. The male snow leopards showed higher rates of male-male long-term home range overlap compared to pumas (0.21 versus 0.11); however, on a monthly basis, male snow leopard home ranges showed almost no overlap (0.02). This result shows that snow leopard males are territorial and that the time frame is important when evaluating territoriality and estimating overlap of home ranges. Consequently, annual estimates, which are commonly used, may not be appropriate to determine if individuals are territorial or not.

4.4 Daily activity patterns

Activity patterns were not affected by age or sex of snow leopards; the model that included time of year (month) and period of day (dawn, day, dusk, night) explained 5.82% of the deviance compared to the model that also included sex (male, female), 5.85%, age (adult, subadult) 5.82% and the model including sex and age, 5.86%. Snow leopards were most active in dusk and dawn followed by night and day (Figure 4), and could be classified as crepuscular and facultatively nocturnal. However, activity patterns changed with season, where activity in dawn and night increased in summer contrary to activity in dusk and day, which increased in winter (Figure 4). Therefore, describing the snow leopards as crepuscular is accurate, but simplistic, and does not adequately describe their activity peaks. The fraction of the moon illuminated had a negative influence on activity but the effect was very small (0.08% of the deviance explained). The patterns in daily movements of adult males and females followed the same trends as the activity data whereas females with young (<5 months old) cubs had less pronounced patterns.

Several drivers appear to affect the daily activity patterns where the most important are cover, visibility and thermoregulation. Activity in the two coldest periods, dawn and night, followed the same seasonal pattern, whereas the activity of the two warmest periods, dusk and day, were opposite. This indicates that snow leopards adjust their activity patterns seasonally to avoid the periods of most extreme temperature. However, activity level was highest during the darker parts of the day (twilight and night) in all seasons, showing that thermoregulation is not the only driver. Rather, snow leopards appear to benefit from the cover of darkness, though improved visibility in the semi-darkness of twilight appears optimal for a snow leopard stalking its prey.

Contrary to the general hypothesis that large carnivores adjust their activity pattern to mirror their prey's activity (Curio 1976; Schmidt 1999; Linkie & Ridout 2011; Heurich et al. 2014; Soria-Díaz, Monroy-Vilchis & Zarco-González 2016), no evidence that prey activity influenced snow leopard activity was found. The main prey in the study area, ibex were primarily active during daytime, in contrast to the snow leopards that were mainly active when it was dark or semi-dark. Previous studies that have found resembling activity patterns have not explored causation, and similarity in activity patterns of prey and predators could be caused by a common proximate driver, such as thermoregulation or avoidance of human disturbance. Activity patterns of large carnivores in general need not mirror that of their prey, and a closer examination of their drivers is warranted.

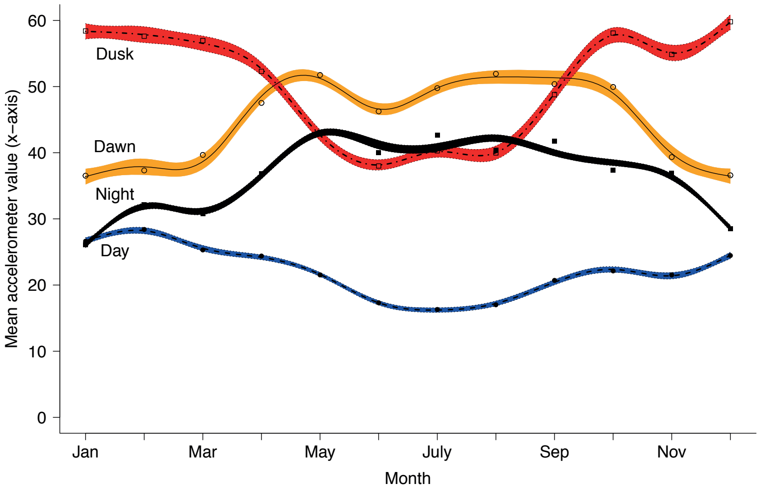

Figure 4. Seasonal changes in daily activity patterns in snow leopards derived from predictions of the response variable in a generalized additive model; dawn (orange), day (blue), dusk (red) and night (grey). Dots show mean values and shaded areas 95% confidence intervals.

4.5 Individual identification in camera-trap studies

There was a 12.5% probability that a folder (capture event) would be incorrectly classified, with the majority of mistakes coming from splitting errors (probability of error = 0.111) rather than combination errors (probability of error = 0.041). When encountering photographs that are difficult to identify, it is probably more likely to classify them as a new individual (splitting) than it is to match them to an existing individual (combination) if the match feels uncertain. Experts were generally less likely to make errors than non-experts, but still had a 9.9% probability of misclassifying a folder compared to 14.6% for non-experts. This shows that the fundamental assumption in abundance and survival estimates, that individuals can be correctly identified from photographs, was violated.

There was an 8.7% probability that a folder would be excluded from classification and removed from further consideration. Because splitting errors were more common than combination errors, observers generally created more animals than the true number, and these had smaller numbers of recaptures. The mean (±SD) difference in the number of individuals identified compared to the true number (i.e. the true number 16 individuals minus any individuals excluded by non-classified folders) was 2.3 (±1.7) snow leopards for experts and 3.0 (±0.8) for non-experts (Figure 5).

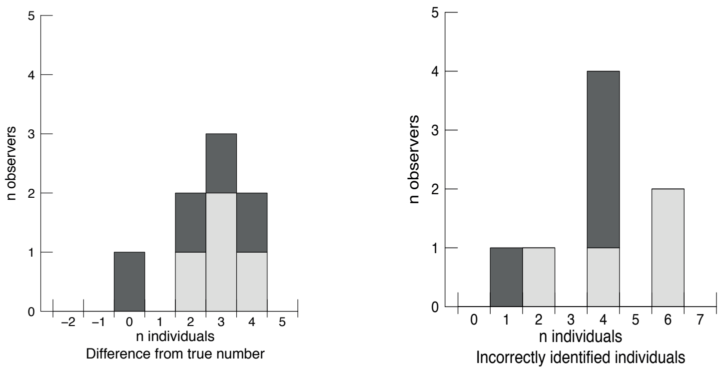

Figure 5. The left panel shows the difference in number of individuals identified from the true number after correcting for excluded individuals, positive numbers indicates an overestimation. The right panel shows the total error on identified individuals (lost when folders were deemed impossible to use, lost in combination errors and created ghosts) for each observer. Experience of observers is illustrated by colour (dark grey = experts, light grey = non-experts).

Abundance estimates of camera-trap data are most often derived in a capture – recapture framework where the basic principle to estimate the population (N) is: the number of individuals encountered (n), divided by the capture probability (p). When observers make more splitting errors than combination errors and exclude capture events of known individuals as impossible to identify, this will inevitably result in: (i) the number of individuals identified as encountered (n) will be higher than the true number in the sample, (ii) the number of capture events will be divided among more individuals, and (iii) the number of capture events in the sample will be reduced. Hence, when analysed in a capture – recapture framework, the population estimate (N) must be inflated since the numerator (n) increases and the denominator (p) decreases. For a threatened species this could have serious consequences.

4.6 Concluding remarks and future perspective

The results presented in this thesis will change some of our views of the snow leopard. By searching for prey remains I could show that snow leopard prey choice followed both spatial and temporal changes in prey abundance and that a snow leopard kill substantially more prey than previous estimates suggested. What previously was considered a species utilising small [10 to 142 km^2 (Jackson 1996; Oli 1997; McCarthy et al. 2005)] and overlapping home ranges have now been shown to be wide ranging and territorial. Conservation plans consequently need to determine that there is a sufficient prey base for such predation pressure without snow leopards resorting to livestock predation, and must be viewed from a landscape perspective rather than targeting smaller areas. The main reason why I found diverging patterns from previous studies is that I was able to utilise GPS-collars and capture a large number of individuals. While VHF-collars have yielded good-quality data for other large felids (e.g. Bailey 1993; Logan & Sweanor 2001) it is clearly not suitable for a felid in such inaccessible terrain as the snow leopards utilise.

Since the review on social organisation of solitary carnivores by Sandell (1989), there has been few attempts to explain the strategies employed by males and females in large solitary carnivore to utilise their home ranges in relation to key resources. By GPS-collaring a large proportion of the individuals within a limited area and comparing how seasonal changes in key resources affected space use, we were able to provide additional insights into felid social behaviour. While snow leopards are most often associated with snow capped ridges of the highest mountains ranges in Asia, they inhabit a vast area and exist in several types of habitat, though always in mountains (Jackson et al. 2010). That snow leopards adjust their activity patterns and avoid being active at the coldest times to facilitate thermoregulation sounds reasonable. But that they do it in the Gobi Desert probably comes as a surprise to many. Besides thermoregulation, the activity patterns were driven by the need for cover and visibility. Contrary to the common claim that large carnivores mirror the activity of their prey we found no relationship between snow leopard and ibex activity.

Until recently, snow leopards were seen as notoriously difficult to census due to their remote and inaccessible habitat and cryptic nature (Snow Leopard Network 2014). Using the best methods available, researchers originally relied on sign (scrapes, faeces, pugmarks) surveys and interviews to obtain measures of abundance (e.g. McCarthy et al. 2016). With the development of camera-traps, new avenues to survey snow leopards became available (Jackson et al. 2005; Janečka et al. 2008; Sharma et al. 2014). This technique has been embraced by the snow leopard community, and for the first time what has been regarded as scientifically robust population estimates have been reported (e.g. camera trap studies). However, the fundamental assumption in camera-trap studies, that individuals are correctly identified, has been largely ignored. When I tested it using a sample of individuals with known identity, I found that the assumption was violated and that the number of individuals was overestimated. This raise questions about the population densities reported from camera-trap studies. Even more so when considering that many of the areas surveyed have been smaller than one snow leopard's home range and few have been as large as two or three home ranges (Snow Leopard Network 2014; Johansson, Simms & McCarthy 2016).

There is one obvious key aspect of snow leopard ecology missing in this thesis – how the species use and select their habitat. It is intriguing to plot the GPS locations from the collared snow leopards and see that virtually all locations fall within the mountains. Why are they so bound to the mountains, could it be hunting opportunities or protection? To thoroughly answer this question data on prey distributions, both wild and domestic would be needed, preferably by GPS-collaring. It would also be beneficial to compare the collar data from Tost with studies in other countries to gain understanding of how habitat selection may vary among different areas.

There is currently very little data on demographic parameters such as inter-birth interval, litter size, cub survival and natal dispersal, which all are desperately needed for population modelling. Our data indicates that snow leopard cubs follow their mother for 18 to 22 months (Johansson, unpublished data), this means that a female will at most give birth every second year, provided that the litter survives. Therefore, acquiring data on these parameters will require a substantial investment and much work remains before we have a thorough understanding of the snow leopard's ecology.

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Popular science summary

Tost Uul, the Gobi Desert, 02:00 am

I wake reluctantly to the sound of my second alarm bell, ringing loudly two meters from my bed. The horrible sound of the first alarm is not enough to wake me anymore. I have, once again, turned it off in my sleep, so I keep a second alarm bell out of reach. I turn on the headlamp, open my warm sleeping bag and crawl out, shivering. While I have not taken off my thermal underwear for the last two months (except for the weekly wash), it still feels cold in the ger – the traditional Mongolian tent that I now call my second home. I put on several layers of warm clothes, concluding with a windproof layer. Equipped with my telemetry-receiver – a small device designed to pick up signals from radio-transmitters, I start the hike up the small, but steep, mountain. It is freezing cold and utterly quiet. The stars and moon are bright enough that I could easily see the trail, but I dare not turn off the headlamp because should I fall and injure myself, several days would pass before help arrives. It is exciting to think of all the desert-dwelling animals that are watching me as I ascend the mountain. At the same time it is a little frightening, perhaps I will once more come across a snow leopard. Sure, snow leopards are notoriously peaceful and there is only one confirmed instance of an attack on a human. But as I'm ascending the mountain alone in the dark I can't help wondering if anyone else ever hiked around alone, smack in the middle of the snow leopards' mountains and if this could somehow change the odds of being attacked.

There are 14 snares hidden in the narrow ravines surrounding my camp, each one equipped with a trap-transmitter that changes pulse once an animal gets caught. It is because of them that I make this hike; every third hour, from early evening to late morning, the trap-transmitter signals are checked to see if anything has been caught. This signal-check continues night after night, for up to three months in a row, whether or not I have help from anyone else.

During the more than one thousand days that I have spent here in the Tost Mountains since we launched the study in August 2008, I have caught 23 different snow leopards, several of them more than once: in total 50 captures. The capture techniques have evolved and been fine-tuned over the years. The greatest change happened when my brother, Torbjörn, developed an automatic trap-surveillance system that monitors the snares continuously for us. As long as the system works, I get to sleep and the snow leopards only have to spend a minimal time in the snares; our record so far is 27 minutes from capture to arrival at the snare. Once a snow leopard has been caught, it is equipped with a GPS-collar, programmed to acquire a location every five hours for about one and a half years, after which it drops off. Many of our snow leopards have worn several collars, and one has been followed for four and a half continuous years. Twenty-three snow leopard may not sound like many, but the amount of GPS-data that these animals have provided equals, or probably exceeds, the data collected by all other snow leopard studies combined.

Why do this to yourself, and to the snow leopards?

To answer that question, you first need some background information about the snow leopard. The species is found in the highest mountains of Asia, from the Himalayas in the south to the Altai in the north. Here, they lead secretive lives; thanks to their excellent camouflage and elusive nature, people almost never see them. The rare glimpses of snow leopards almost exclusively occur when a leopard attacks livestock, after which they disappear back into the mountains. As a testament of their elusive nature, in many areas where they occur, the local people call them mountain ghosts. Predation on livestock has been long regarded as the major threat to the species survival because local people often kill the cats in retaliation or to prevent future attacks. In recent years, the demand for fur and body parts used in traditional Asian medicine has increased, probably causing an increase in poaching. The remoteness and inaccessibility of snow leopard habitat was long seen as a safeguard against habitat destruction, but climate change and rapidly increasing developments such as mining, hydrology power dams and the infrastructure following such developments has changed this.

The remote and inaccessible habitat and elusive nature of the snow leopard made it almost impossible to study. Observation studies were originally not possible since one never saw them, and snow tracking was not feasible since one could not follow them in the precipitous slopes. The breakthrough happened in 1982 when the first snow leopard was equipped with a radio-collar. With the aid of technology, fundamental questions on the species ecology such as how large an area does one individual use, are they territorial, how often do they kill prey, and what are their daily activity patterns could finally be answered.

However, it soon became clear that even with this new technology, it was extremely difficult to collect solid knowledge; the radio-collars require that the signals from the marked animal is located with handheld receivers and the snow leopards covered much larger areas than what the researchers could do on foot in the mountainous terrain. In total, 14 snow leopards were equipped with radio-collars in five different studies conducted in Nepal, India and Mongolia. The researchers conducting these studies were heroic pioneers, and each data point they collected was hard earned. Nonetheless, by the mid 1990's the last study was concluded, probably because it was perceived that the data collected did not justify the suffering of either the researchers or the snow leopards.

A few years after the millennium, new technology that appeared promising for snow leopard studies were developed, such as trap-cameras and GPS-collars small enough to attach to a snow leopard. This study was launched in August 2008 to study all aspects of the snow leopard's ecology, evaluate new conservation measures, and train key staff for snow leopard conservation. Now, nine years later, we have learned that snow leopards have much higher kill rates than previously thought. We can also show that they are territorial, and that a snow leopard roams over a much larger area than previously thought. This finding shows that the protected areas in the snow leopard distribution range are too small to safeguard the population and to save the species, so we need to help local people co-exist with the snow leopards outside of the protected areas.

A small part of the knowledge we have gained has been summarised in this thesis. Hopefully it can aid in designing more efficient conservation measures, and increase politicians' awareness of the conservation issues at stake. The irony is that in striving to save the snow leopard, we reduce it from a ghostlike creature to something so square and dull as statistical tests and numbers in tables. However, while these simplistic descriptions can adequately describe key aspects needed for conservation, they can never provide a good enough description to understand what a snow leopard truly is. Much work remains, hopefully we will one day have all the knowledge needed to save the species, be it that some aspects of the snow leopard cannot be described in words and will be kept to themselves. Nonetheless, with better knowledge, our chances to safeguard the persistence of snow leopards will increase, and thereby diminish the risk that one day they will be remembered as nothing but ghosts from generations past.

Populärvetenskaplig sammanfattning

Tost Uul, Gobiöknen, kl 02:00

Motvilligt vaknar jag till ljudet av min andra väckarklocka som står och ringer för fullt, två meter från sängen. Den obarmhärtiga signalen från den första väckarklockan räcker inte längre till för att väcka mig, den har jag stängt av i sömnen. Därför använder jag en extra klocka, placerad utom räckhåll från sängen, för att vara säker på att vakna. Jag öppnar dunsovsäcken, kryper huttrande ut ur den och tänder pannlampan. Underställen har jag inte tagit av på drygt två månader, annat än då jag tvättar mig en gång i veckan. Utanpå det klär jag mig i flera lager varma kläder och längst ut vindtäta skalplagg. Med pejlutrustningen i handen lämnar jag min jurta, det traditionella mongoliska tält jag numer kallar mitt andra hem. Väl ute påbörjar jag klättringen uppför det lilla men branta berget. Natten är isande kall och helt tyst. Ljuset från månen och stjärnorna skulle egentligen räcka för att följa den vältrampade stigen men jag vågar inte stänga av pannlampan för om jag skulle ramla och skada mig skulle det dröja flera dagar innan någon hjälp kom. Samtidigt som tanken på ett par lysande ögon i skenet av pannlampan kan vara skrämmande, så är det också spännande att tänka på hur många ökendjur som följer min klättring på avstånd, och att jag kanske än en gång kommer få möta en snöleopard.

I ravinerna runt mitt läger ligger 14 väl kamouflerade fotsnaror utplacerade, var och en försedd med en radiosändare som ändrar puls när en snöleopard fastnar i snaran. Det är dessa radiosändare som pejlutrustningen jag burit med mig ska fånga upp. Var tredje timme från tidig kväll till sen morgon klättrar jag upp på berget för att lyssna på signalerna från fällorna. Detta sker varje natt under fångstperioden, även när jag är ensam i lägret, ibland i upp till tre månader i sträck.

Sedan studien startade i augusti 2008 har jag fångat 23 olika snöleoparder, vid 50 olika tillfällen under de drygt tusen dygn som jag spenderat i Tostbergen.

Fångstmetoderna har utvecklats och förfinats allteftersom. Den största utvecklingen skedde när min bror, Torbjörn, byggde ett system som automatiskt övervakar fällsändarna. Så länge systemet fungerar som det ska får jag sova och snöleoparderna behöver bara sitta i snaran under en mycket begränsad tid innan de sövs. Rekordet är 27 minuter. När snöleoparderna fångats förses de med GPS-halsband vilka har programmerats att ta en position var femte timme i ungefär ett och ett halvt år, därefter faller de automatiskt av. Många av snöleoparderna har fått nya halsband när de fångats på nytt. Som längst har vi kunnat följa en individ kontinuerligt i fyra och ett halvt år. Det kanske inte låter så mycket med 23 individer, men ingen annan studie har kunnat följa levnadsvanorna för så många snöleoparder tidigare.

Varför utsätter vi oss och snöleoparderna för det här?

För att svara på det krävs lite bakgrundsinformation om snöleoparden. Arten lever i de högsta bergsmassiven i Centralasien, från Himalaya i söder till Altaibergen i norr. Här för de en undanskymd tillvaro, tack vare sitt utmärkta kamouflage och skygga beteende är det ytterst sällan någon ser dem. När människor upptäcker snöleoparder sker det nästan alltid i samband med att de attackerar tamboskap, varefter de försvinner in i bergen igen. Detta förklarar kanske varför snöleoparderna kallas för bergens vålnader. Just boskapsangreppen har länge utgjort den största risken för snöleoparden då herdarna ibland avlivar dem i samband med dessa attacker eller sätter ut fällor i bergen för att minska risken för framtida attacker. Under senare år har dock tjuvjakt troligtvis ökat, som en följd av ökande efterfrågan på päls och kroppsdelar, vilka används inom traditionell asiatisk medicin. Snöleopardens livsmiljöer har länge ansetts skyddade från yttre påverkan eftersom de är så otillgängliga, men klimatförändringar och landutvinningar såsom gruvdrift, vattenkraft och den infrastruktur som medföljer sådana satsningar innebär att det inte längre är en självklarhet.

Den branta och otillgängliga livsmiljön och snöleopardens skygga beteende innebar däremot att det länge var nästan omöjligt att studera dem. Observationsstudier var omöjliga för man såg dem aldrig och snöspårning var mer eller mindre omöjligt eftersom det inte gick att följa efter dem i branterna. Genombrottet skedde 1982 när den första snöleoparden försågs med ett radio-halsband. Med hjälp av denna teknik kunde man äntligen svara på grundläggande frågor som hur stora områden en individ rör sig över, om de hävdar revir, när på dygnet de är aktiva och hur ofta de dödar byten. Det visade sig dock snart att även med denna teknik var det svårt att samla in särskilt detaljerad information. Radio-halsbanden kräver att man hittar signalerna med en handhållen mottagare och snöleoparderna rörde sig snabbt över mycket större ytor än vad forskarna kunde göra till fots i bergen. Totalt märktes 14 snöleoparder i fem olika studier i Nepal, Indien och Mongoliet. Forskarna bakom de här studierna var pionjärer som slet otroligt hårt för varje enskild pejlposition. I mitten av 1990-talet avslutades dock den sista av de fem studierna, troligtvis på grund av att informationen som genererades inte längre var värd besväret för varken forskarna eller djuren.

Nästa genombrott för att studera snöleopard kom några år efter millennieskiftet då ny teknik lanserades, bland annat fällkameror och GPS-halsband som var tillräckligt små för att en snöleopard skulle kunna bära dem. Denna nya teknik utvärderades i några år, bland annat märktes en snöleopard med GPS-halsband i Pakistan, innan Snow Leopard Trust bestämde att det var dags att starta en heltäckande studie för att äntligen hitta svaren på vad en snöleopard egentligen är. Studien startades 2008 med syftet att studera alla aspekter av snöleopardens ekologi, utveckla nya bevarandeprogram, och utbilda personal som arbetar med artens bevarande. I augusti 2008 anslöt jag till studien för att sköta fältverksamheten, sedermera mynnade det ut i att jag anställdes som doktorand på Sveriges Lantbruksuniversitet (SLU). Nu, nio år senare, har vi kunnat visa att snöleoparden dödar många fler byten än man tidigare trodde. Vi har också kunnat visa att snöleoparderna hävdar revir och att varje snöleopard rör sig över mycket större områden än man tidigare trodde – så mycket som upp till 44 gånger större än tidigare skattningar. Det här innebär att de naturreservat som finns i snöleopardens utbredningsområde är alltför små för att arten ska kunna överleva i enbart dem och för att skydda arten måste vi därför hjälpa lokalbefolkningen så att de kan samexistera med snöleoparderna utanför naturreservaten.

En del av den nya kunskapen som vi nu har om arten har sammanfattats i denna avhandling. Denna kunskap kommer förhoppningsvis användas för att utforma mer effektiva bevarandeprogram samt för att uppmärksamma förvaltare och politiker på vilka åtgärder som måste vidtas. Men även om vi kommit en bit på vägen för att förstå arten återstår mycket. I avhandlingen reduceras snöleoparden ner till något fyrkantigt och odramatiskt i form av statistiska modeller och siffror i tabeller. För att kunna beskriva arten är detta nödvändigt, om än djupt orättvist. Men även om tabeller och modeller kan beskriva vissa delar av bergens vålnader, finns det aspekter som vi aldrig kommer kunna beskriva så, och kanske inte heller förstå. Snöleoparden är kapabel att jaga ikapp 200 kg tunga argalifår nerför bergbranter och döda dem. Hur kan det då komma sig att när de trängs in i boskapshagar kan ett par åldringar slå ihjäl dem med käppar utan att de ens försöker försvara sig? När jag kommit fram till de infångade snöleoparderna har de för det mesta försökt gömma sig. Visst har det hänt att några morrat och visat tänderna men så fort bedövningspilen träffat har de sjunkit ihop och mest sett förorättade ut. Trots alla dagar jag spenderat i bergen har jag aldrig sett en snöleopard dagtid utan hjälp av halsbanden. Men nattetid har våra vägar korsats flera gånger, förutom de gånger vi mötts på väldigt nära håll har snöleoparderna aldrig reagerat nämnvärt, ibland har de snarast varit nyfikna och till och med följt vid sidan av mig på säkert avstånd.

Kanske priset vi måste betala för att snöleoparden ska överleva är att en del av mystiken försvinner och ersätts med siffror på ett papper, men hellre det än att den i framtiden beskrivs som en vålnad från en svunnen tid.

Acknowledgements

Yamaan Uus, 20th April 2017

Fittingly, as I'm looking back at the years that have passed, I'm sitting in my ger placed at the same campsite as when I first came to Tost, almost nine years ago. The vast emptiness of the desert night, illuminated by thousands of stars, is deafly quiet with no sounds but the sparks from the small branches I just put in the stove to keep the heat. Next to the laptop sits the surveillance system, monitoring the snares. All lights are green now, but should any turn red and that heart-attack-causing siren starts, it will only be a few minutes before the night is interrupted by the sound and lights of two ATVs leaving camp.

This has been a very long and adventurous journey and it's hard to know where to begin. My entrance to the world of snow leopards took place in Beijing in March 2008. A few years earlier I attended a dissertation where the opponent started by saying that he always advised his students against doing PhDs on large mammals. If they had to work with large mammals, then by all means, don't work with large carnivores. And if they insisted on working with large carnivores, just don't chose wolverines, cause the species' remote habitat and elusive nature makes it almost impossible to collect enough good data. That sounded like good advice and I promised myself to remember it. Yet, somehow, when Tom McCarthy offered me to lead the capture work on the first ever long-term study of snow leopards, and do my PhD here I could hear myself replying "Wow, that sounds amazing".

There are so many people that have been involved in this study, from donors to office staff, researchers, volunteers, students and friends that it will be impossible to mention you all. Things that we take for granted back home can mean the world when you have spent more than 200 consecutive days in a desert, either freezing cold or sweating hot, with little more than canned food and salty water from which you have filtered away most of the goat poop, and not a shower in sight. At times, I've had tears in my eyes when someone has thought of me and sent a juice package, a bag of candy or just an encouraging e-mail to the sat phone. I am very grateful to all of you and wish to extend a huge thank you!

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Doctoral Thesis No. 2017:67

The snow leopard (*Panthera uncia*) has remained an enigma – one of the most recognised yet least understood of the large carnivores. This thesis is based on six years of field studies in the Tost Mountains of southern Mongolia. It describes key parts of snow leopard ecology; predation patterns, home range size and overlap, seasonal variation in home ranges, daily activity patterns, and finally, evaluates one of the most common survey methods of the species.

Örjan Johansson received his graduate education at Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences (SLU). He received his Master of Science in Forestry at SLU in Umeå.

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