

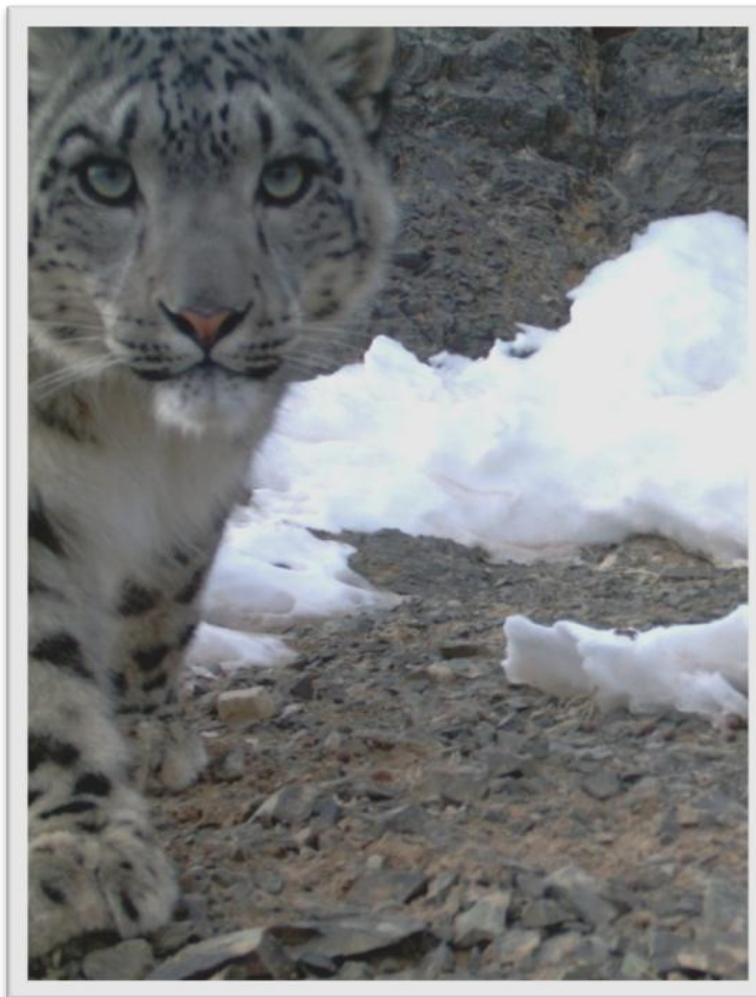


Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Grimsö Wildlife Research Station



Movement patterns of snow leopard (*Panthera uncia*) around kills based on GPS location clusters

Elin Grönberg



Movement patterns of snow leopard (*Panthera uncia*) around kills based on GPS location clusters

Elin Grönberg

Supervisor: Gustaf Samelius, Department of Ecology, SLU,
Grimsö Wildlife Research Station, 730 91 Riddarhyttan,
Email: Gustaf.Samelius@slu.se

Assistant Supervisor: Örjan Johansson, Department of Ecology, SLU,
Grimsö Wildlife Research Station, 730 91 Riddarhyttan,
Email: Orjan.Johansson@slu.se

Examiners: Henrik Andrén & Gunnar Jansson, Department of Ecology, SLU,
Grimsö Wildlife Research Station, 730 91 Riddarhyttan,
Email: Henrik.Andren@slu.se / Gunnar.Jansson@slu.se

Credits: 15 ECTS (hp)

Level: Ground Level C

Course title: Independent project/ Degree project in Biology C

Course code: EX0689

Place of publication: Uppsala

Year of publication: 2011

Cover: Trap camera, Snow Leopard Trust

Serial no: 2011:3

Electronic publication: <http://stud.epsilon.slu.se>

Key words: Cluster, GIS, GPS, Mongolia, movement behavior, *Panthera uncia*, Snow leopard



Grimsö Wildlife Research Station
Department of Ecology, SLU
730 91 Riddarhyttan
Sweden

Abstract

Research concerning movement patterns of wild animals has been advancing since GPS technology arrived. But studying the snow leopard (*Panthera uncia*) is still difficult because of the harsh territory it inhabits in Central Asia. This study took place in south Gobi, Mongolia, and aimed to estimate the time spent at kills and the maximum distance away from kills between visits. Snow leopards were monitored with GPS collars that took a location every five or seven hours. Potential kill sites were established by identifying clusters of GPS-locations in ArcGIS and visited in the field for confirmation. ArcGIS was used to calculate the distance between cluster and GPS-locations. I used two buffer zones (100 m and 500 m radius) to define the time snow leopards spent at kills. It was found that snow leopard age and prey category affected time spent at kills and also that snow leopard sex together with prey category affected the maximum distance moved away from kills between visits. Season had no significant effect on either time at kills or distance moved away from kills between visits. Snow leopards spent on average 3.2 days at their kills in the 100 m buffer zone and 3.5 days at their kills in the 500 m buffer zone. Subadults stayed longer at kills than adults and animals of both age categories spent longer time on larger prey. The mean maximum distance moved away from kills between visits was 179 m in the 100 m buffer zone and 252 m in the 500 m buffer zone. Female snow leopards moved further away from kills between visits than male snow leopards. Both the number of days spent on kills and maximum distance moved away from kills between visits increased when kills consisted of more than one animal. This study has provided some basic information on snow leopard behaviors around their kills but also highlights the need to monitor more snow leopards before more solid conclusions can be drawn as this study was based on based on a relatively small sample.

Sammanfattning

Djurs rörelsemönster styrs till stor del av deras behov av att finna föda och en partner. Forskning om djurens rörelsemönster har underlättats av GPS teknologin, vilket gjort att organisationerna "Panthera" och "Snow Leopard Trust" startat en långsiktig ekologisk studie för snöleoparder i Mongoliet. Snöleoparden lever i central Asiens otillgängliga bergsmassiv, vilket gör den ytterst svåra att studera. Idag finns bara 4,500 till 7,350 individer kvar i det vilda varav mellan 500-1000 individer lever i Mongoliet. Studieområdet var beläget i södra Gobiöknen och studien har pågått sedan 2008. Snöleoparder fångades i fotsnorer och försågs med ett GPS-halsband som registrerade en position var femte eller sjunde timma.

Denna studie syftade till att undersöka rumsliga och tidsmässiga aspekter på snöleopardens rörelsemönster runt sina kadaver. Jag undersökte om variablerna; ålder, kön, bytesdjur och säsong påverkade hur länge snöleoparden stannade vid sitt byte och hur långt ifrån sina kadaver de rörde sig under tiden de stannade vid bytet. För att försöka finna svar på dessa frågor har snöleopardernas positioner bearbetades i kartprogrammet ArcGIS. Om ≥ 2 efterföljande GPS-positioner befann sig inom 100 m från varandra, kallades detta ett kluster. Dessa platser besöktes sedan för att bekräfta om ett byte hade slagits, genom att leta efter bytesrester så som blod, ull och skelettdelar. Totalt besöktes 141 kluster varav 89 visade sig vara bytesplatser. Sedan räknade jag ut avståndet mellan snöleopardens positioner och klustret i ArcGIS, genom att använda två zoner runt bytesdjuret med 100 m eller 500 m radie.

Jag fann samband som tyder på att snöleopardernas ålder och bytesdjurets storlek påverkade hur många dagar de stannade vid kadavret. Hur långt de rörde sig från sina bytesdjur påverkades av snöleopardens kön och bytets storlek. Säsong hade ingen signifikant påverkan på varken tid vid kadavren eller avstånd från kadavren. Snöleoparderna spenderade i medel 3,2 dagar vid bytet i 100 m zonen och 3,5 dagar i 500 m zonen, värdena varierade mellan 1-11 dagar. Ungdjur stannade längre vid bytesplatsen än vuxna snöleoparder. Både vuxna och subadulta djur stannade längre vid sina kadaver desto större bytesdjuren var. Medelvärde på maxavståndet från bytesdjuret var 179 m för 100 m zonen och 252 m för 500 m zonen, värdena varierade mellan 7- 2264 m för båda zonerna. Honor rörde sig längre bort från bytesdjuren än hanarna. Både antalet dagar vid kadavren och avståndet till bytesdjuren ökade om det var flera djur dödade på samma plats.

Arbetet med att märka flera snöleoparder fortsätter och mer data samlas hela tiden in. Än så länge finns inte tillräckligt med data för att några säkra slutsatser ska kunna dras, bara trender kan anas.

Table of Contents

Introduction	1
Objectives and goals.....	1
Materials and methods	1
Study area.....	1
Telemetry and cluster visits.....	2
GIS analysis.....	2
Statistical analysis	3
Result.....	3
Discussion	7
Number of days at kills	7
Maximum distance away from kills between visits	8
References	11

Introduction

Movement patterns of animals are affected by their surroundings and the distribution of the resources they need to grow, reproduce and survive (Begon et al. 1986). The spatial ecology and movement patterns of predators are influenced by key habitat features that determine the distribution of their prey (Valeix et al. 2010). The movement patterns of predators are also affected by competition that for some species results in territoriality (Gordon 1997). The advantage of defending a territory must exceed the cost of doing so regardless whether it is a solitary or group-living animal (Gordon 1997).

The snow leopard (*Panthera uncia*) is a medium size carnivore that lives in the remote and rugged mountains throughout Central Asia. Because of the harsh terrain it is one of the least studied cat species (McCarthy et al. 2005). Basically no information exists on seasonal movements, home-range size, or basic population parameters such as birth and mortality rates, dispersal or cub survival (McCarthy et al. 2010). The number of snow leopards has declined considerably during the second half of the last century and it is estimated that only between 4.500 and 7.350 individuals remain in the wild today whereof 500-1000 individuals live in Mongolia (see McCarthy and Chapron 2003 for review). Threats towards the snow leopard are mainly loss of habitat and prey, poaching due to trade of bones and pelts and retaliatory killing by herders for killing their livestock (McCarthy et al. 2010). The snow leopard diet varies across Central Asia. In Mongolia their main prey is ibex (*Capra siberica*), argali sheep (*Ovis ammon*) and livestock. To learn more about this secretive cat, a long-term ecological study was started by Panthera, Snow Leopard Trust and Snow Leopard Conservation Fund in South Gobi, Mongolia, in 2008 (McCarthy et al. 2010).

Objectives and goals

The objective of this study was to examine movement patterns of snow leopards around their kills, located from GPS-locations. The main questions were:

- How long do snow leopards stay at their kills?
- How far do snow leopards move from their kills between visits?
- How do the variables snow leopard age and sex, prey category and season affect the movement patterns around kills?

Such knowledge is of vital importance for the conservation of snow leopards as the ecology of this rare and elusive species is virtually unknown.

Materials and methods

Study area

The study was conducted in Tost Uul and Tost Tosonbumba, two mountain ranges in the South Gobi province, Mongolia (100°36'E, 43°11'N), in August 2008 – December 2010. South Gobi is the largest but least populated aimag (state) in Mongolia, with a population density of only 0.3 people per km². The study area is occupied by approximately 230 semi-nomadic herder families and their livestock consisting of around 40 000 goats, sheep, camels

and horses (McCarthy et al. 2010). Most herders in the area travel by motorbike with most of the roads being dirt tracks. The study area has an average annual precipitation of 130 mm per year. During summer, temperatures reach 38°C whereas in the winter, temperatures dip to -40°C. The area has a relatively high density of snow leopards, compared to other areas in their distribution range (McCarthy 2000). Other large animals in the area include wolf (*Canis lupus*), lynx (*Lynx lynx*), red fox (*Vulpes vulpes*), corsac fox (*Vulpes corsac*), ibex, argali sheep (McCarthy et al. 2010), plus various raptors such as the endangered lammergeyer (*Gypaetus barbatus*).

Telemetry and cluster visits

Snow leopards were trapped in foot-snares located at scrapes or sent marks made by the snow leopards. Animals that were captured were anaesthetized and fitted with a GPS-collar (North Star Science and Technology or Vectronic Aerospace). The collar communicated via satellites (Globalstar) and was programmed to take a location every five or seven hours.

Kills were established through field visits to sites where collared animals stayed for extended periods, resulting in clusters of GPS-locations (Sand et al. 2005). I defined a cluster as minimum two sequential locations within 100 m radius, by using a Geographical Information System (ArcView GIS 3.3; Environmental Systems Research Institute, Redlands, California). On site it was concluded if it was a kill or not, by looking for blood, wool, bones, rumen etc. If remains of a kill was found, then species, age (size of horns), sex, amount eaten and scavenger species that had been present, was recorded, if possible. A location was taken on top of the rumen to define the exact location of the carcass. I divided the kills in to five categories: small (yearlings 0-1year), medium (adult goat, sheep and female ibex or argali), multi-medium (>1 animal killed at same location), large (ibex or argali > 3 years), x-large (Horse). Similar categories were used by Knopff (2010).

GIS analysis

To determine how long snow leopards stayed at kills, I defined two buffer-zones around the kills and defined snow leopards to “stay at kills” from the first GPS-location inside the buffer zone and then as long as one GPS-location was located within the buffer zone every 48 hours. I used one buffer zone of 100 m radius and one buffer zone of 500 m radius, to avoid that my definitions of buffer zone affected the results (Sand et al. 2005). I defined the “maximum distance away from kills” as the GPS-location furthest away from the kill between visits to kill, i.e. on the condition that the animal had to return to the kill at least every 48 hours.

I determined the relationship between GPS-locations and kills by using the spatial join function in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, California). The spatial join function was also used to calculate maximum distance from kill between visits. Then I manually selected the GPS-locations that met the definition for “staying at kills” and “maximum distance from kill” and calculated average and maximum distance moved from kills and number of days spent on kills, for both buffer zones, using Microsoft Excel (2010).

Statistical analysis

I examined how time spent at kills and maximum distance away from kills varied among sex and age of snow leopards, season and type of prey by a General linear model (Proc GML, SAS Institute Inc., Cary, North Carolina). I analyzed the time spent at kills and maximum distance from kills separately. I also tested whether the distribution of large and small prey killed by male and female snow leopards was the same with a Fisher's exact test (Proc freq, SAS Institute Inc.), here both the small and medium prey categories were included as small prey and the large and x-large prey categories were included as large prey. I did not include the multiple-kill category in this analysis.

Result

One hundred and forty-one clusters from seven different animals (5M, 2F) were visited in this study and prey remains were found at 89 of these clusters. It was not possible to determine prey species, sex or age for all clusters, which resulted in that 65 kills were used in the analysis. The distribution of prey species was 38 ibex (58.5%), 5 argali sheep (7.7%), 19 domestic goats (29.2%), 2 horses (3.1%) and 1 domestic sheep (1.5%; Table 1). The distribution of prey size categories used in the statistical analysis, are shown in the lower part of Table 1.

Table 1. Number of kills divided into species (upper part) and into prey size categories (lower part) by different snow leopards. * Value in the multi-medium category shown as number of killing events

	Aztai Adult	Tsagaan Adult	Khavar Subadult	Saikhan Subadult	Shonkhor Subadult	Tenger Adult	Khasha Adult
Prey type	M	M	M	M	M	F	F
Ibex	16	4	5	4	3	1	5
Argali	2	-	-	1	2	-	-
Goat	11	6	2	-	3	1	1
Sheep	1	-	-	-	-	-	-
Horse	2	-	-	-	-	-	-
Condensed categories							
Small	3	2	2	5	1	-	-
Medium	10	6	-	-	2	1	2
Multi-medium	2 *	-	1 *	-	1 *	-	-
Large	13	2	3	-	2	1	4
X-Large	2	-	-	-	-	-	-

Time spent at kills was affected by snow leopard age and by prey size (Table 2), while sex of snow leopard and type of prey influenced maximum distance from kills. Season had no detectable effect on either of these parameters (Table 2). The proportion of variation explained (R^2) by the full models (i.e. including all main effects) were 0.36 and 0.34 for “the time spent at kill” when using the 100 m and 500 m buffer zone, respectively and 0.25 and

0.24 for “maximum distance from kill” when using the 100 m and 500 m buffer zone, respectively.

Table 2. P-Values for variables affecting days at kills and maximum distance away from kills. Significant values ($P < 0.05$) are highlighted in bold

	Day's at kill (100m)	Day's at kill (500m)	Max distance (100m)	Max distance (500m)
Sex	0.88	0.83	0.072	0.031
Age	0.073	0.047	0.21	0.20
Season	0.52	0.20	0.64	0.52
Prey Category	< 0.001	< 0.001	0.0069	0.016

The mean time spent at kills was 3.2 days (range = 1 to 11 days) in the 100 m buffer zone and 3.5 days (range = 1 to 11 days) in the 500 m buffer zone. Days at kills increased significantly for larger prey and when the kills consisted of more than one animal ($P < 0.001$; Figure 1). There was no significant difference in the time male and female snow leopards spent at kills ($P > 0.05$; Figure 2). Subadult snow leopards stayed significantly longer at kills than adult snow leopards in the 500 m buffer zone ($P = 0.047$; Table 2, Figure 3) and this trend could also be seen in the 100 m buffer zone ($P = 0.073$; Table 2, Figure 3). However, the trend for subadult animals to spend more time at kills was driven by one subadult male, spending 11 days on one kill where he killed multiple goats. About two of these 11 days were spent on a resting place >2000 m from the kill. So, the generality of the observation that subadult animals stayed longer at kills than adult animals is therefore unclear.

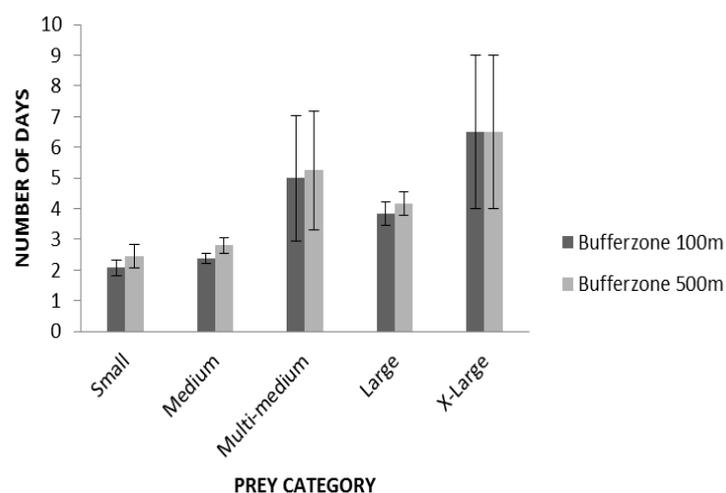


Figure 1. Mean number of days spent at kills in relation to prey size category and size of buffer zone. Error bars show SE

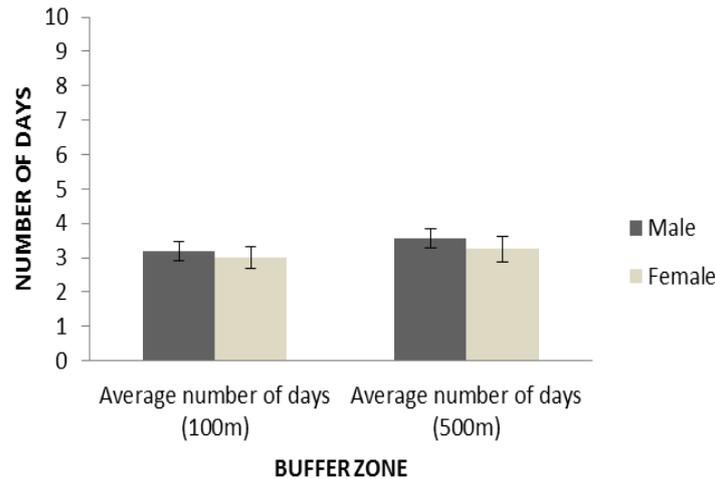


Figure 2 Mean numbers of days spent at kills by female or male snow leopards at the different buffer zones. Error bars show SE

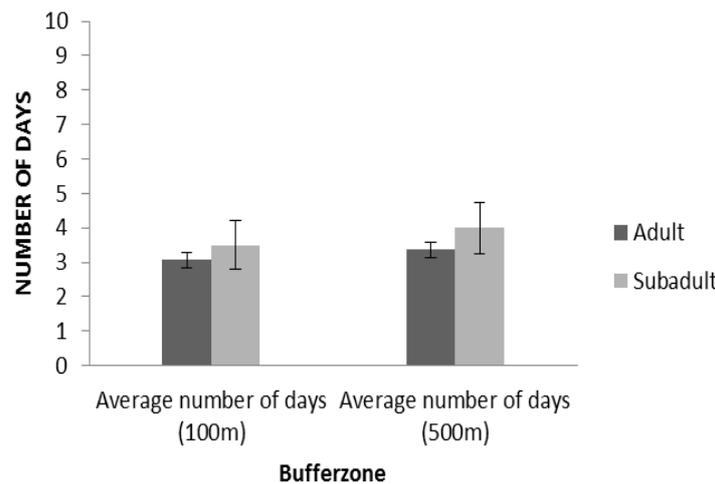


Figure 3. Mean number of days spent on kills by adult and subadult snow leopards at the different buffer zones. Error bars show SE

The mean distance away from kills was 43 m when using the 100 m buffer zone and 60 m when using the 500 m buffer zone. The mean of the maximum distance away from kills in the 100 m buffer zone was 179 m (range = 7 to 2264 m) and 252 m (range = 7 to 2264 m) in the 500 m buffer zone. The maximum distance from the kills significantly increased with the size of prey ($P < 0.05$), with the longest maximum distance from kills found when there were multiple kills (Table 2, Figure 4). The maximum distance away from kills at the 500 m buffer was significantly greater for female snow leopards than it was for male snow leopards ($P = 0.031$; Table 2, Figure 5b) and this trend could also be seen for the 100 m buffer zone ($P = 0.072$; Table 2, Figure 5a). However, this result should be used with caution as the majority of data from female snow leopards were from large prey (Figure 5) and it is therefore

unclear whether this result is true also for other prey categories. Maximum distance away from kills was not significantly different for subadult snow leopards and adult snow leopards at either the 100 m or 500 m buffer zone ($P > 0.05$; Table 2, Figure 6).

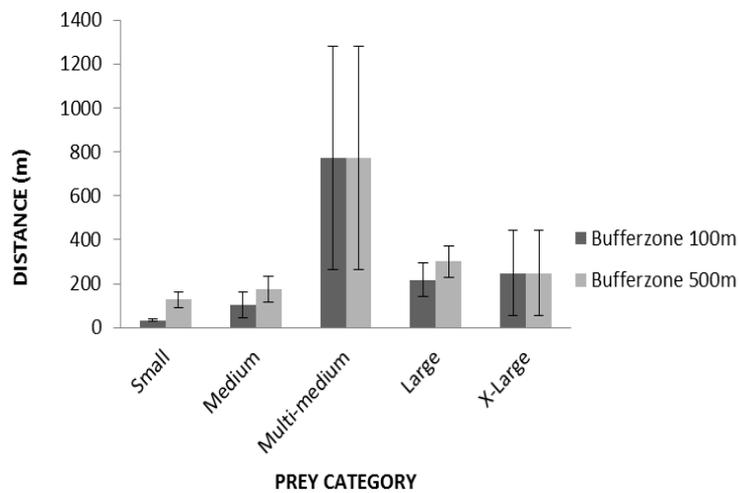


Figure 4. Mean of maximum distance to kills in relation to prey size category and size of buffer zone. Error bars show SE

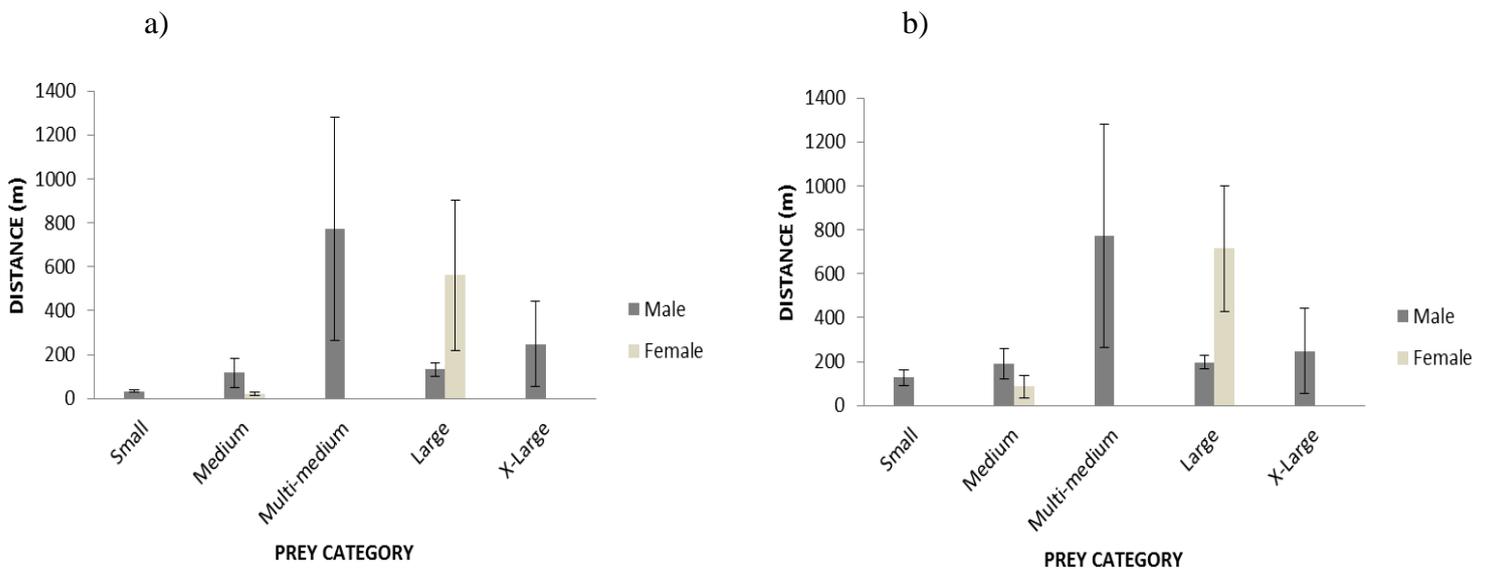


Figure 5. Mean of maximum distance to kills for male and female snow leopards in relation to prey size category. 5a show the distance for the 100 m buffer zone and 5b show the result for the 500 m buffer zone. Error bars show SE

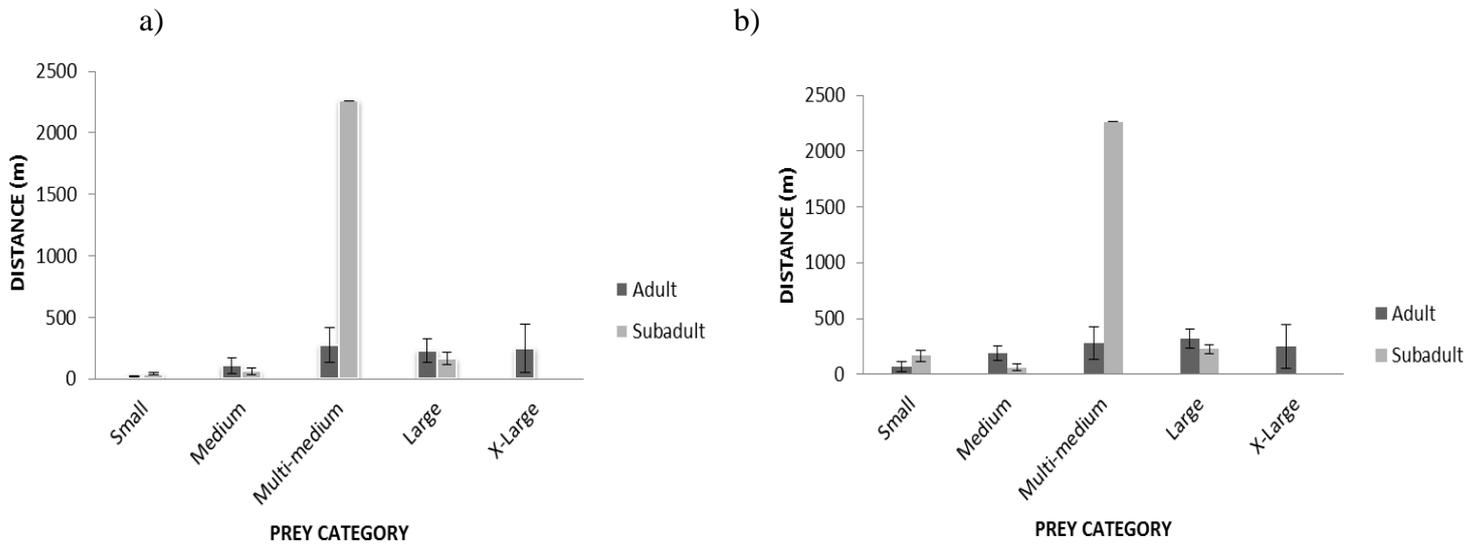


Figure 6. Mean of maximum distance to kills for adult and subadult snow leopards in relation to prey size category. 5a show the distance for the 100 m buffer zone and 5b show the result for the 500 m buffer zone. Error bars show SE

There was no difference in the frequency at which male and female killed large and small prey (Fisher's exact test, $p = 0.45$).

Discussion

This study showed that (1) snow leopards stay, on average, 3-4 days at their kills, (2) that they generally stay close to their kills if not disturbed, and (3) that it appeared as if age, sex and prey size category affected the time spent at kills and the maximum distance moved from kills between visits (although the skewed distribution of data results in the need to collect more data before more solid conclusions can be drawn on the effects of age, sex, and prey category). Moreover, this study also showed that identifying clusters of GPS-locations appeared to work well as a technique to determine predation of snow leopards main prey as the distribution of prey in this study corresponded well with prey remains found in snow leopard scat in a study by McCarthy et al. (2010).

Number of days at kills

I found that snow leopards stayed at their kills for a mean of 3.2- 3.5 days with the range spanning 1-11 days. A study found that cougars spent similar time at kills, varying between 3-6 days depending on the size of the carcass (Anderson and Lindzey 2003). That the time spent at kills correlated with prey size was also found by Knopff et al. (2010).

I did not find any difference between numbers of days spent at the kill by female and male snow leopards; one reason could be their similar size (females: 35- 40 kg and males ca. 45 kg; Johansson, unpublished data) and therefore similar energetic need, which resulted in similar time at kills. I found that subadult animals stayed longer at their kills than adult animals, which may result from them killing fewer animals and therefore spending a longer time at their kills. Subadult cougars were found to have a lower kill rate than adults (Knopff et al.

2010). However, this difference in time spent at kill by subadult and adult snow leopards was largely driven by one subadult male that had his resting place >2000 m from the kill. I found no significant difference between numbers of days spent at kills during different seasons, whereas cougars were found to increase their handling time during winter (Knopff et al. 2010).

The numbers of days spent at kills also increased when kills consisted of more than one animal. This may have resulted from either there being more food to eat at multiple kills or because the snow leopards got disturbed by herders (all multiple kills were domestic livestock), which caused them to move away from the kill in order to come back later. Multiple killings occurred at least four times during this study and only male snow leopards were responsible for the multiple killing where goats were killed in all of these situations. Similar results have been found in Norway where it was mostly male lynx responsible for multiple killings (Odden et al. 2002). One theory is that males have a bigger home range, so there is a bigger chance of encounter livestock while moving around the area (Odden et al. 2002). Moreover, when it comes to killing of domestic animals it is still debated whether they are regarded as prey that affect movement patterns of the predators or whether they are just encountered during movements related to territory defense or hunting of non-domestic prey (Odden et al. 2002).

Kruuk (1972) theorized that when predators encountered livestock, the killing was less likely to stop if prey still was available, resulting in multiple killings. So, that multiple killings by snow leopards in my study occurred only for domestic prey may have resulted from the abundance of prey encountered in domestic herds: multiple killings were found only for goats (two or three at the time) never for ibex or argali sheep. It also followed the predation pattern of Eurasian lynx in Scandinavia (Odden et al. 2002). Multiple killings of domestic animals also followed the patterns of surplus killing by large carnivore being more common for domestic prey than for wild prey (see Odden et al. 2002 for review). However, given that surplus killing is defined by killing of more prey than consumed at one occasion (Kruuk 1972) no obvious case of surplus killing was found by snow leopards since all carcasses from multiple kills were eaten in this study. The question of surplus killing was further complicated by the fact that it was difficult to establish how much of the carcasses that were consumed by the snow leopards contra scavengers. Most of the goats that were killed by the male snow leopards in this study were not actively herded at that time (pers. obs., 2010); therefore they could stay at the kill without being disturbed by herders moving around in the area. However, it may still be possible that the subadult male that spent 11 days feeding on two goats probably was disturbed by herders because these goats were killed on the steppe close to a settlement and a road. Potential disturbance may explain why the male rested > 2000 m away from the kill between visits. This one event of the subadult animal spending a long time at the kill probably influenced the result that subadult snow leopards spent longer time at kills than adult animals and the generality of this result therefore remains unclear.

Maximum distance away from kills between visits

Snow leopards went further away between visits to multiple kills than they did for other prey categories. This may have been related to herders disturbing the snow leopard thereby forcing

them to move further away between visits to the kills. Similarly, that snow leopards moved further away between visits to the kills for larger prey could be a result of them staying longer to consume the kill and therefore moving around more between visits to the kills.

Snow leopards generally stayed very close to their kills with the mean distance from the kill of 43-60 m. One reason why they stayed so close to their kills may have been to protect them against scavengers like vultures and foxes. This behavior contrasts sharply against Eurasian lynx in Scandinavia where the mean distance to kills were ranged 1254 – 1810 m (Falk, 2009). One reason for the difference in the distance that these felids moved from kills between visits may have resulted from differences in their ability to defend kills against competitors. Specifically, Eurasian lynx in Scandinavia may not be able to defend their kills against competitors such as wolverines, bears and wolves (wolves were not present in the study area of Falk 2009 at the time when the study was conducted but wolves have been part of the predator assemblage of that system in the past thereby potentially shaping the behavior of lynx behaviors around their kills). Snow leopards in my study, in contrast, were capable of defending their kill against competitors in the area. The importance of defending carcasses can be exemplified by the Ruppell's griffon vulture that is estimated to eat 2 kg meat per day (Ruxton and Houston 2002) and that more than one vulture often feeds on a carcass at the same time. For example, I once saw more than 20 vultures feeding on a dog carcass (pers. obs. 2010). So, kills may disappear quickly if they are not protected.

Other felids like cougars, tigers and leopards drag their kills over distances ranging from about 50-400 m to hide it from scavengers and other predators (Beir et al. 1995; Karanth and Sunquist 2000). In this study, I found only one occasion where a carcass was dragged for 300 m and there were rarely any signs of snow leopards trying to hide their kills. This could be due to the absence of lush vegetation to conceal the prey, resulting in that staying close to the kill until there is no food left, to be the optimal strategy.

On two occasions during the fall, a male snow leopard visited a female snow leopard, sharing her kill. This behavior has also been seen with puma, leopard, tiger and jaguar (Schaller and Gransden Crawshaw 1980); these large solitary cats in most respects have a similar social system (Schaller and Gransden Crawshaw 1980). Thus male and female snow leopards do not seem to fight or attempt to exclude each other. It is difficult to determine how adult snow leopards would react to subadult snow leopards approaching their kills – especially if it is a snow leopard of the same sex. However, based on the two occasions in this study, where snow leopards shared kills, it does not appear as if adult snow leopards are forced to abandon their kills by other snow leopards when the individual is in its own home range.

This study showed that female snow leopards appeared to move further away between visits to their kills than male snow leopards. However, this could in part be driven by the fact that females mostly killed larger preys like ibex, which takes a longer time to consume. This may result in females moving around more between visits to kills than males who killed smaller prey more commonly than female snow leopards. Although there was no significant result for this pattern; that females killed large prey more frequently than males. One of the females

also had a two year old daughter with her, which may have caused them to move around more between visits to the kills.

In summary, the results from this study should be used with caution as it is based on relatively few individuals and skewed distribution of the data (e.g. few observations from female and subadult snow leopards). Nevertheless, this study showed that (1) snow leopards stay on average 3-4 days on a kill and (2) that they generally stay close to their kills if not disturbed. This information, although somewhat rudimentary, is important for the understanding of movement patterns and space use of snow leopards.

Acknowledgment

- I would like to thank my supervisor Gustaf Samelius for his enthusiasm, assistance with statistic and proof reading. Örjan Johansson for his willingness to share his collected data and his patience and inspiring discussions during my field stay in South Gobi, making the experience a memory of a lifetime. Sida for supplying the Minor Field Study scholarship and SLU for granting me one, making this fieldtrip possible. Snow Leopard Trust for food and board during the field study.

References

- Anderson, Jr. C. R., and F. G. Lindzey. 2003: Estimating Cougar Predation Rates from GPS Location Clusters. *The Journal of Wildlife Management*, 67(2): 307-316.
- Falk, H. 2009: Lynx behaviour around reindeer carcasses. Master thesis, Uppsala: SLU.
- Gordon, D. M. 1997: The population consequences of territorial behavior. *Trends in Ecology and Evolution*, 12(2): 63-65.
- Beir, P., D. Choate, and R. H. Barrett. 1995: Movement patterns of mountain lions during different behaviours. *Journal of Mammalogy*, 76(4): 1056-1070.
- Begon, M., J. L. Harper, and C. R. Townsend. 1986: Ecology; Individuals, Populations and Communities. Oxford: Blackwell scientific publications, 876pp.
- Karanth, K. U., and M. E. Sunquist. 2000: Behavioural correlates of predation by tiger (*Panthera tigris*), leopard (*Panthera pardus*) and dhole (*Cuon alpinus*) in Nagarhole, India. *Journal of Zoology*, 250: 255-256.
- Knopff, K. H., A. Knopff, A. Kortell, and M. S. Boyce. 2010: Cougar Kill Rate and Prey Composition in a Multiprey System. *Journal of Wildlife Management*, 74(7): 1435-1447.
- Kruuk, H. 1972: Surplus killing by carnivores. *Journal of Zoology*, 166(2): 233-244.
- McCarthy, T. M., T. K. Fuller, and B. Munkhtsog. 2005: Movements and activities of snow leopards in Southwestern Mongolia. *Biological Conservation*, 124: 527-537.
- McCarthy, T. M., and G. Chapron. 2003: Snow leopard survival strategy. Seattle, Washington: ISLT and SLN, 108pp.
- McCarthy, T. 2000: Ecology and conservation of snow leopards, Gobi brown bears, and wild Bactrian camels in Mongolia. Ph.D. Dissertation, Amherst, MA: University of Massachusetts, 133pp.
- McCarthy, T., K. Murray, K. Sharma, and Ö. Johansson. 2010: Preliminary results of a longtermstudy of snow leopards in South Gobi, Mongolia. *Cat News*, Autumn No 53: 15-19.
- Odden, J., J. D.C. Linnell, P. Fosslund Moa, I. Herfindal, T. Kvam, and R. Andersen. 2002: Lynx depredation on domestic sheep in Norway. *Journal of Wildlife Management*, 66(1): 98-105.
- Ruxton, G. D., and D. C. Houston. 2002: Modelling the energy budget of a colonial bird of prey, the Ruppells's griffon vulture, and consequences for its breeding ecology. *African Journal of Ecology*, 40: 260-266.

- Sand , H., B. Zimmermann, P. Wabakken, H. Andrén, and H. C. Pedersen. 2005: Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*, 33(3): 914-925.
- Schaller , G. B., and P. Gransden Crawshaw, Jr. 1980: Movement Patterns of Jaguar. *Biotropica*, 12(3): 161-168.
- Valeix, M., A. J. Loveridge, Z. Davidson , H. Madzikanda, H. Fritz , and D. W. Macdonald. 2010: How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, 25: 337-351.