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Snow leopard predation in a livestock dominated landscape in Mongolia

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ARTICLE INFO

ABSTRACT

Livestock predation is an important cause of endangerment of the snow leopard (*Panthera uncia*) across its range. Yet, detailed information on individual and spatio-temporal variation in predation patterns of snow leopards and their kill rates of livestock and wild ungulates are lacking.

We collared 19 snow leopards in the Tost Mountains, Mongolia, and searched clusters of GPS positions to identify prey remains and estimate kill rate and prey choice.

Snow leopards killed, on average, one ungulate every 8 days, which included more wild prey (73%) than livestock (27%), despite livestock abundance being at least one order of magnitude higher. Predation on herded livestock occurred mainly on stragglers and in rugged areas where animals are out of sight of herders. The two wild ungulates, ibex (*Capra ibex*) and argali (*Ovis ammon*), were killed in proportion to their relative abundance. Predation patterns changed with spatial (wild ungulates) and seasonal (livestock) changes in prey abundance. Adult male snow leopards killed larger prey and 2–6 times more livestock compared to females and young males. Kill rates were considerably higher than previous scat-based estimates, and kill rates of females were higher than kill rates of males. We suggest that (i) snow leopards prey largely on wild ungulates and kill livestock opportunistically, (ii) retaliatory killing by livestock herders is likely to cause greater mortality of adult male snow leopards compared to females and young males, and (iii) total off-take of prey by a snow leopard population is likely to be much higher than previous estimates suggest.

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1. Introduction

Carnivore-caused damage to human interests and welfare is a major obstacle to conservation (Woodroffe et al., 2005). Negative attitudes of local people towards large carnivores are associated with actual or perceived losses such as livestock predation, competition for game animals, or attacks on humans, and can lead to retaliatory killing (Linnell et al., 2001). Thus, one of the key components of carnivore management and conservation is to mitigate losses to local communities through efforts such as better livestock protection (Jackson and Wangchuk, 2004), damage compensation (Maclennan et al., 2009), and creating greater awareness and tolerance (Marker et al., 2003).

Effective management and conservation planning for large carnivores in habitats used for livestock grazing is dependent on reliable estimates of predation pressure on livestock and wild prey. The two key factors to estimate a predators' impact on its prey are kill rate and prey choice. These parameters need to be interpreted in relation to the underlying drivers of predation events (Suryawanshi et al., 2013). These drivers may include: (1) prey profitability and vulnerability: a given prey may be avoided depending on its size or density because the cost of searching or killing outweighs the benefits (Sunquist and Sunquist, 1989), or it may be unavailable for killing (e.g. fenced or housed during particular periods; (Jackson and Wangchuk, 2004); (2) availability of alternative prey: predators may shift the extent of predation if 'easier' or more profitable prey becomes available and some predators may kill

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livestock because their natural prey are depleted (Woodroffe et al., 2005); (3) demography: male and female predators may target different prey species or age/sex categories due to sexual size dimorphism, differences in life history strategies (Knopff et al., 2010; Mattisson et al., 2013), or different energetic needs (especially females rearing offspring; Anderson and Lindzey, 2003); (4) seasonality: prey choice and kill rate may show seasonal patterns, for example, when prey exhibits birth pulses the predator could intensify predation on neonates (Sand et al., 2008) or when migration alters prey availability (Sunquist and Sunquist, 1989). Knowledge of how these factors influence predation on natural prey or livestock can allow for more efficient mitigation efforts by directing them to the time periods and areas where predation is most likely to occur.

GPS locations of radio-collared animals can be used to identify possible kill sites, usually represented by spatially aggregated clusters of locations (Anderson and Lindzey, 2003). The snow leopard (Panthera uncia) is an endangered apex predator of the high mountains of central Asia that are extensively used for livestock production (Mishra et al., 2003). As with many other threatened large carnivores, livestock predation is a major conservation issue throughout the snow leopard's range (Kyrgyzstan, Jumabay-Uulu et al., 2013; China, Li et al., 2013; India, Mishra, 1997; Mongolia, Shehzad et al., 2012; Nepal, Wegge et al., 2012), often resulting in retaliatory killings (Li and Lu, 2014), and in some areas, possibly exacerbated by wild prey depletion (Bagchi and Mishra, 2006; Jackson et al., 2010). Correlative evidence suggests that livestock predation is primarily determined by the local abundance of snow leopards and their wild prey (Suryawanshi et al., 2013). Previously, attempts to search for kills from VHF-radio-collared snow leopards were deemed too difficult (Jackson, 1996), and consequently, predation patterns were inferred from faecal analyses (e.g. Jumabay-Uulu et al., 2013; Shehzad et al., 2012; Wegge et al., 2012) which does not allow for an understanding of the temporal, spatial or individual variation in prey choice. Thus, reliable individual based estimates of snow leopard kill rates or the understanding of individual variation in prey choice have been lacking.

We present robust information on kill rates and prey choice of individual snow leopards of various age–sex categories (adult males, young males, single females and females with cubs). We radio-collared 19 snow leopards and by examining their prey-choice, we try to understand if livestock predation is opportunistic or whether snow leopards actively seek out livestock. We compare predation patterns of various age–sex categories, given that in large carnivores, males and sub-adults are considered to be more predisposed to killing livestock due to their wide-ranging movement or tendency to take greater risks (Linnell et al., 1999). We specifically seek to answer the following questions:

(1) How often do snow leopards kill wild ungulates and livestock?
(2) Are there seasonal variations in livestock predation?
(3) Are there differences in predation patterns on livestock and wild ungulates among snow leopard sexes and age/physiological classes?
(4) Do individual snow leopards maintain their diet composition or do they change their diet in response to spatial variation in prey abundance?

2. Materials and methods

2.1. Study area

This study was conducted over an area of c. 1700 km^2 in the Tost Mountains in South Gobi, Mongolia (43°N, 100°E), from September 2008 to November 2013. Tost consists of several rugged mountain massifs traversed by valleys and steep canyons (elevation ranges 1800–2500 m). Annual precipitation is <130 mm/year and temperatures range from −35 °C to 38 °C with strong winds year around.

Approximately 90 herder families live in the study area. The herders are semi-nomadic and move several times during the year; living in flatter areas in summer and in mountainous areas in winter to shelter from the cold winds (Traditional knowledge, B. Agvantseeren Pers. Communication). Their livestock are comprised of ~32,000 goats (Capra aegagrus) and sheep (Ovis aries), ~1100 camels (Camelus bactrianus), and ~120 horses (Equus ferus caballus). Horses and camels were largely free-ranging in small herds, predominantly in the plains or the lower, less rugged parts, whereas goats and sheep were actively herded and penned close to campsites at night.

Among wild ungulates, Siberian ibex (Capra sibirica) were common throughout the rugged parts of the mountains and argali (Ovis ammon) occurred mainly in the rolling hills in the northern and western parts of the study area (Tumursukh, 2013). A preliminary survey found 429 ibex and 11 argali or ~59 ibex/argali in the Southern range and 221 ibex and 74 argali or ~3 ibex/argali in the Northern range (K. Suryawanshi, unpublished data). Horses and camels mainly occurred in the Northern range whereas goat and sheep were evenly distributed. Smaller potential prey species included Tolai hare (Lepus tolai), chukar partridge (Alectoris chukar) and various rodents. Sympatric predators and scavengers included wolf (Canis lupus), 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).

We used Vector Ruggedness Measures to capture and describe the spatial variation in topography within the study area. This estimates terrain ruggedness based on variation in three-dimensional orientation between neighbouring cells in a grid, where values can range from 0 (no variation) to 1 (complete variation). We used eight neighbouring grid cells to estimate ruggedness, each with the size of 250 m^2.

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. The Southern range (mean ruggedness 0.089 (±0.0001 SE)) was more rugged and mountainous than the Northern (mean ruggedness 0.058 (±0.0001 SE), Fig. 1).

2.2. Snow leopard captures and cluster visits

Snow leopards were captured in foot-snares, chemically immobilized and equipped with GPS collars (North Star, King George, USA) in 2008–2009 and GPS-Plus collars (Vectronic Aerospace, Berlin, Germany) in 2010–2013 (Johansson et al., 2013). Collars were programmed to take one GPS fix every seven and five hours for the North Star and the Vectronic collars, respectively, and immediately uplinked data via satellite communication (Globalstar). GPS position clusters were investigated for 16 snow leopards (eight males, and eight females, of which two males transitioned from young to adult and three females transitioned between single to females with cubs during the study). Age was estimated by body size, coloration and wear of teeth and presence of facial scars where all adult males were severely scarred (Johansson et al., 2013). Snow leopards younger than 3.5 years were categorized as young.

We assumed that a kill site of a large prey will result in a cluster of GPS locations close to each other given the propensity of large carnivores to stay for extended periods at their kills (Anderson and Lindzey, 2003; Sand et al., 2008). However, all clusters of GPS locations are not necessarily kill sites, e.g. they can be
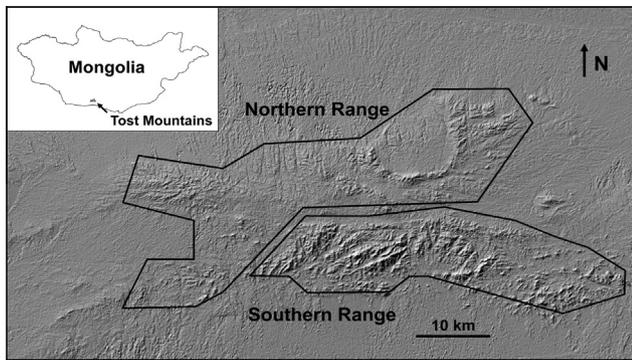
Fig. 1. The study area in Tost Mountains, Mongolia, divided into the more mountainous Southern range and the gentler Northern range. The two polygons delimit the area in which kills made by GPS collared snow leopards were located (11 and 8 snow leopards for the Southern and Northern ranges, respectively).

day-rests. Clusters were defined as $\geqslant 2$ locations within 100 m of each other and separated by less than 24 h. Twenty-seven initial visits to clusters with only daytime locations yielded only a single kill of an ibex kid, following which daytime only clusters were considered as day-rests and were not visited. Cluster visits were conducted over 26 periods during the duration of our study, ranging from 31 to 189 days (yielding a total of 2339 snow leopard-days). We searched 370 potential kill site clusters intensively for prey remains and snow leopard signs (faeces, tracks and scrapes). Age of prey killed was estimated by counting horn annular rings for ibex and argali males >2 years, from horn length for females and young (<2 years), and tooth wear and eruption for all species (Severinghaus, 1949). Live weights for prey species were set to 40 kg for goats and sheep, 150 kg for young (<1 year) camels and horses (http://www.mofa.gov.mn), 44 kg and 90 kg for female and male ibex, respectively (Fedosenko and Blank, 2001), and 71 kg and 149 kg for argali females and males, respectively (Kenny et al., 2008).

Cluster sites were visited only after a minimum of two days following the snow leopard's last location at the site. The mean time from the first GPS location in the cluster to the field visit was 20 days (range 2–79 days). While this could potentially lead to the removal of small carcasses by scavengers, we found in several revisits to clusters that in the dry landscape, parts like rumens, hair, horns, bone pieces, etc. remained in the cluster for several months. These parts are presumably not attractive to scavengers and we do not expect the time lag to have caused any significant biases in our data. We considered all carcasses as killed by radio-collared snow leopards if they were encountered within the cluster area and decomposition matched the dates of the cluster. When two snow leopards had been at the same cluster ($n = 14$) the kill was assigned to the individual that appeared at the cluster first. The second snow leopard appeared at the cluster between 10 and 145 h after the first and hence could not have made the kill. We also documented scavenger signs such as tracks, faeces and feathers at the kill sites. Prey remains were found on 258 of the clusters, of which nine could not be confidently identified to species. On four additional clusters, we found signs such as hair and blood that suggested but could not confirm a kill. These, and the nine undetermined kills, were not included in our analyses. The remaining 108 clusters were likely resting sites or sites where the snow leopards had killed small prey that we could not detect.

2.3. Kill rates

While analysing the stored GPS data from 10 retrieved collars, we found that all clusters had not been uplinked. The 370 clusters we visited constituted 81% of the total number of clusters

($n = 461$). Therefore, to calculate kill rate we first derived kill intervals, which were defined as the number of days between two consecutive kills from the time of the first GPS fix in the first cluster to the first GPS fix in the second cluster. All intervals containing unvisited clusters ($n = 51$) were removed prior to analysis (Cavalcanti and Gese, 2010). Kill rate was considered the inverse of the kill interval, and expressed as the number of prey killed per month (Knopff et al., 2010).

2.4. Statistical analyses

We examined differences in prey choice among snow leopard categories (young male, adult male, single female and female with cubs) using χ^2-contingency tables and Fishers exact test, when the expected number of observation in a cell was less than 5 (Proc Freq, SAS Institute Inc., Cary, North Carolina) using count data. We first used a 5-by-4 table to test for differences at the species level and then partitioned the data by (1) livestock versus wild prey and (2) small versus large prey (camel, horse and argali were pooled as large prey and sheep, goat and ibex as small prey), to test for differences in choice among prey types. Further, we partitioned data by (1) spatial range (Northern versus Southern) to test for spatial differences in prey choice and (2) sex of wild prey, which was used as a proxy for differences in prey choice based on size. We also compared prey choice for snow leopards utilizing both spatial ranges to those that were restricted to a single spatial range to test if predation differences between the two spatial ranges were due to individual specialization or related to local prey abundance. In all the tables we have shown the proportions with the sample size for each column, instead of the count data.

To assess time of day when herded livestock (sheep and goats) were killed, we considered the time when the first GPS location was acquired at the cluster. We did not include clusters if the last GPS location before the cluster was missing since the five-hour positioning interval would make the estimate uncertain. We considered all hours between sunrise and sunset to be daytime.

We used linear mixed models to analyse (1) kill interval in relation to snow leopard category and different prey species and (2) seasonal changes in proportion of livestock and wild prey using R 2.12.1 with package lme4 (R-Development Core Team, 2014). Because we had multiple samples from the same individual, we included individual as a random effect in both these comparisons as an approximate control for repeated measures sampling. We derived four a priori candidate models for the analysis on kill interval (Table 1). We included a null model of variation around the

Table 1
Models evaluating the variation in snow leopard kill intervals on different prey type in the Tost Mountains in Mongolia, using Akaike information criterion (corrected for sample size, AIC_c).

Model	AIC_c	ΔAIC_c	Model weight
Snow leopard category + Prey type[a]	845.1		0.80
Prey type	847.9	2.8	0.20
Snow leopard category	862.1	17.0	0.00
Null model	865.7	20.6	0.00

[a] Model coefficients:
Kill interval for Females with cubs on Goat & sheep was set as Intercept (reference value): 4.75 ± 1.18 (SE).
Corresponding kill intervals for snow leopard categories and prey type compared to the reference:
Single females: 0.38 ± 1.10 (SE).
Adult males: 1.87 ± 1.87 (SE).
Young males: 1.40 ± 1.35 (SE).
Ibex: 2.66 ± 1.00 (SE).
Argali: 2.90 ± 1.71 (SE).
Camel: 0.56 ± 3.34 (SE).
Horse: 6.79 ± 2.13 (SE).

grand mean to control for no effect of either of the variables included. In this analysis snow leopard category and prey species were included to examine if kill rate was influenced by size of prey killed at the beginning of the interval.

To test the effect of season on the type of prey killed (livestock coded as 1 and wild prey coded as 0) by snow leopards, we used two methods. First we used circular analysis in the R package CircStats. However, CircStats cannot handle binomial errors and random factors, therefore, we also used logistic regression (logit model with binomial errors) with snow leopard individual as a random factor. In the logistic regression we included month and month^2 (non-linear). Raw data ($n = 249$) was used in both tests but to present the data we pooled it into months.

We used Akaike's information criterion with small-sample adjustment (AIC_C) to rank the models. The model with the lowest AIC_C value was selected as the best model and models within two AIC_C units were considered to be of similar support (Burnham and Anderson, 2002).

3. Results

Snow leopards killed a higher proportion of wild prey (73%) than livestock (27%), with ibex being the most common prey taken

(Table 2). We found signs of scavengers on 176 kill sites (71%), including birds (157 kill sites), foxes (114), martens (6) and wolves (4).

3.1. Prey choice

Prey choice differed between snow leopard categories (Fisher exact test, $P < 0.001$; Table 2) with adult males killing more goats and horses than the other categories (Fisher exact test, $P < 0.001$). Both categories of males killed a higher proportion of large prey than the two female categories ($\chi^2_{(1)} = 9.38$, $P = 0.0022$). Adult males and females with cubs killed more male ibex and argali compared to young males and single females ($\chi^2_{(1)} = 14.3$, $P < 0.001$; Table 3). Livestock predation was higher for adult males than for the other categories ($\chi^2_{(1)} = 30.6$, $P < 0.001$).

Prey choice differed between the two spatial ranges with a greater proportion ibex and goats killed in the more rugged Southern range and more argali, horses and camels killed in the Northern range (Fisher exact test, $P < 0.001$; Table 4). Similarly, prey choice of individual snow leopards that utilized both the Northern and Southern ranges differed between the two areas (Fisher exact test, $P < 0.001$; Table 4). However, the proportions of wild prey and livestock killed by snow leopards were similar in the two ranges ($\chi^2_{(1)} = 0.078$, $P = 0.78$; Table 4).

Table 2
The proportion of prey species found at kill sites (represented by GPS clusters of radio-collard snow leopards) for different snow leopard categories in the Tost Mountains. Also shown is prey choice based on snow leopard faeces collected in the same area (Shehzad et al. (2012).

Prey type	Current study					Shehzad et al. (2012)
	Single females ($n = 69$ kills) (%)	Females with cubs ($n = 52$ kills) (%)	Young males ($n = 36$ kills) (%)	Adult males ($n = 92$ kills) (%)	All combined ($n = 249$ kills) (%)	($n = 81$ faeces) (%)
Wild prey						
Ibex	77	79	78	45	65	70
Argali	3	8	17	9	8	9
Total Wild	80	87	94	53	73	79
Livestock						
Horse	0	0	0	12	4	0
Camel	4	0	6	2	2	0
Goat & sheep	16	13	0	33	20	20
Total Livestock	20	13	6	47	27	20
Small prey						
Birds	0	0	0	0	0	1

Table 3
The number and ratio of adult (⩾2 years) male and female ibex and argali killed by different social status of snow leopards in Tost Mountains, Mongolia. Weights represent average live body mass of the prey.

	Male ibex (90 kg) & argali (149 kg)	Female ibex (44 kg) & argali (71 kg)	Ratio male prey/female prey
Single female	11	15	0.7
Female with cubs	24	5	4.8
Young male	7	9	0.8
Adult male	25	7	3.6

Table 4
The proportion of prey killed by snow leopards in the Southern and Northern ranges in Tost Mountains, Mongolia. The prey killed by one young male that roamed over the entire study area was removed prior to analysis since he could not be assigned to either of the two areas ($n = 5$ prey).

Prey type	All individuals ($n = 15$)		Individuals utilizing both areas ($n = 7$)	
	Southern range ($n = 165$) (%)	Northern range ($n = 79$) (%)	Southern range ($n = 109$) (%)	Northern range ($n = 41$) (%)
Ibex	72	52	70	54
Argali	1	23	1	20
Horse	4	6	6	12
Camel	1	5	1	5
Goat & sheep	24	14	23	10

3.2. Seasonal changes in livestock predation

The extent of livestock predation changed seasonally. The proportion of livestock killed by snow leopards was higher in winter than in summer according to both the circular regression and the logistic regression. The best logistic regression model included month and a quadratic effect of month (ΔAIC = 7.1 better than the null model; Fig 2.). The mean (±SE) proportion of livestock in the winter (Dec–Feb) diet was 42 ± 21% (n = 9), spring (Mar–May) 32 ± 8% (n = 82), summer (June–Aug) 10 ± 2% (n = 77) and autumn (Sep–Nov) 35 ± 3% (n = 81). The sample size was too small to test
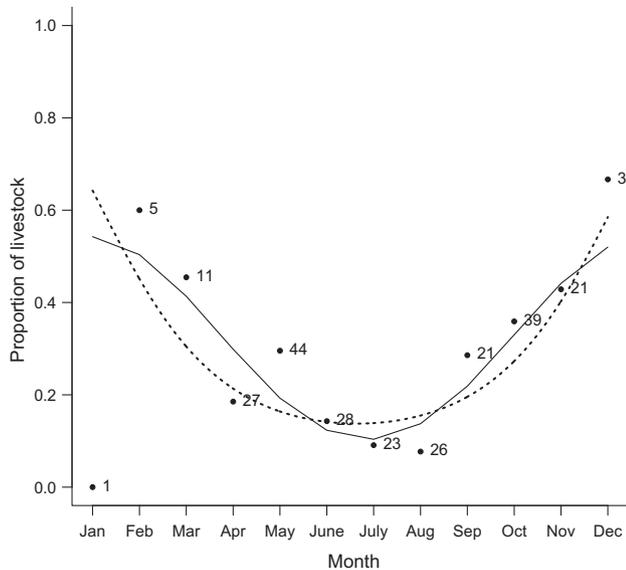
Fig. 2. Proportion of livestock killed by snow leopards in relation to month of year. Dots represent the pooled data for each month with sample size represented by the number. The dotted line was derived from a mixed logistic regression model with individual as random factor, logit(proportion livestock) = 1.52 (±1.18 SE) − 1.01 (±0.36 SE) ∗ month + 0.076 (±0.02 SE) ∗ month^2). The black line indicates the fitted circular regression line.
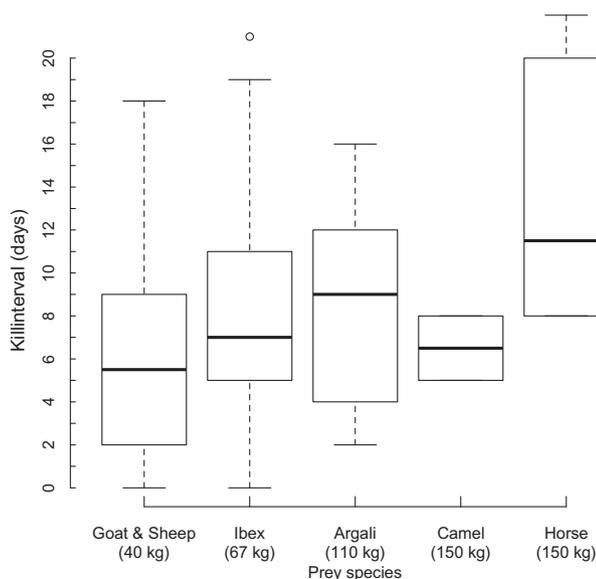

Fig. 3. Kill interval of snow leopards in relation to the prey species killed at the start of the interval. Prey species are ordered by body mass. All camels found were less than 6 months old.

for seasonal differences among snow leopard categories. Sixty-two percent of the sheep and goats for which we could estimate the time of predation were killed at night (n = 29).

3.3. Kill rate

Kill interval was influenced by snow leopard category and prey species (Table 1). On average (±SE), snow leopards killed one ungulate every 8.0 (±0.53) days. Kill intervals were similar for single females (7.2 ± 0.9, n = 42 intervals from 5 individuals) and females with cubs (7.2 ± 1.2, n = 34 intervals from 5 individuals), whereas they were longer for young males (9.0 ± 1.5, n = 20 from 4 individuals) and adult males (8.9 ± 1.3, n = 49 intervals from 5 individuals). Kill intervals corresponded to average kill rates of 4.2 kills/month for single females and females with cubs, and 3.4 kills/month for young and adult males. Kill intervals increased with the size of the prey killed at the beginning of the interval (Fig 3).

4. Discussion

We present information on kill rate and prey choice of individual snow leopards, and predation patterns for different age and sex categories of snow leopards. We have also been able to assess the potential influence of spatial and temporal changes in local prey abundance on predation patterns of snow leopards. We found that 73% of the snow leopards kills were wild ungulates despite livestock abundance being at least one order of magnitude higher than wild prey abundance (Tumursukh, 2013).

4.1. General prey choice and diet

Our data were restricted to larger prey that generated clusters of snow leopard GPS locations, and we could not assess the extent of predation on small bodied prey (rodents, lagomorphs and birds) that are unlikely to generate GPS clusters (Knopff et al., 2010). However, the diet of snow leopards in our study was very similar to the results of Shehzad et al. (2012) who analysed snow leopard faeces collected in the same area (Table 2). The minor contribution (1.2%) of small prey that Shehzad et al. (2012) found suggests that this is not an important prey type for snow leopards in the Tost Mountains. The limited use of small prey in our study area may be related to the absence of marmots (*Marmota* spp.), which seem to be consumed more frequently in areas of high abundance (e.g. recorded in 8% of snow leopard scats in summer; Jumabay-Uulu et al., 2013).

Previous studies on snow leopard diet, based on faecal analyses (e.g. Jumabay-Uulu et al., 2013; Shehzad et al., 2012; Wegge et al., 2012), report high variation in the proportion of prey types, with wild ungulates constituting 25–90%, livestock 0–67% and smaller prey such as rodents and birds 1–40%. Variation in prey availability between study areas may explain some of the differences; there is for example no livestock in Sarychat Reserve (Jumabay-Uulu et al., 2013) whereas there are very few wild ungulates in Gilgit Baltistan where 67% of the diet was reported to be livestock (Anwar et al., 2011). However, with a few recent exceptions, earlier studies were not able to use genetic tools to confirm which species had deposited the faeces. Recent studies that used faecal DNA to ascertain the identity of the predator found that 31–57% of the assumed snow leopards scats belonged to other species such as wolves, foxes, dogs (*Canis familiaris*) and martens (Anwar et al., 2011; Jumabay-Uulu et al., 2013; Shehzad et al., 2012; Wegge et al., 2012). It is thus probable that some faeces assigned to snow leopards in earlier studies were deposited by carnivores that rely more heavily on small prey (e.g. foxes and marten), thereby overestimating the contribution by small prey to snow leopard diet.

4.2. Livestock predation

Livestock herds in our study area ranged in size from 100 to 800 goats and sheep, they scattered over the mountainsides while grazing, often attended to by a single herder, and corralled near the camps at night (Mijiddorj, 2011). The majority of sheep and goats (62%) were killed at night (20.00–6.00). Although during the course of our five years fieldwork we did observe seven cases where a snow leopard had entered a corral, our data recorded no clusters within 100 m of any corral. Instead the killed livestock were most likely stragglers that were inadvertently left behind in the pastures. The daytime kills of goats and sheep probably take place in more rugged habitats where it is difficult for the herders to keep the livestock in sight, which could also lead to more livestock being left behind. The Southern range of our study area was more rugged, and that perhaps explains the higher proportion of herded livestock being killed there compared with the Northern range. In an interview-based study, the herders in our study area estimated that 41% of the livestock predation by snow leopards involved stragglers. Another 23% of the predation instances were estimated to occur in the corrals at night (the occurrence of the remaining 36% losses was not reported; (Mijiddorj, 2011). Therefore, it appears that livestock losses to snow leopards could be reduced by avoiding livestock grazing in very rugged areas.

4.3. Predation by different age–sex classes

Our study demonstrates notable differences in prey choice between snow leopard age–sex categories, with adult males killing two to six times more livestock than the other categories. In a review of solitary carnivores, Linnell et al. (1999) suggested that wider ranging behaviour of males and their tendency to take more risks could explain their greater livestock killing compared to females. Furthermore, adults perhaps gain more experience to know how to access protected livestock, since attacking livestock is often associated with deterrents such as corrals, dogs barking, humans shouting and general commotion. With age, individuals gain experience, become more efficient and perhaps more assured at hunting (Holekamp et al., 1997; Sand et al., 2006). This may explain why adult male snow leopards killed more livestock. Older females, on the other hand, are associated with cubs for most of the time and may avoid subjecting the cubs to the risks associated with livestock predation.

Similarly, prey size choice by snow leopards that we documented also seems to be explained by the age of the individual. In dimorphic carnivores such as the lynx and the cougar (Felis concolor), where males are 35–50% heavier than females, males kill relatively larger prey (Knopff et al., 2010; Mattisson et al., 2013). However, the sexual size dimorphism in adult snow leopards in our study area was lower (<20%), with mean weights of 43.5 ± 0.55 kg (n = 7) and 36.7 ± 1.12 kg (n = 7) adult males and adult females, respectively. We found that adult males and females with cubs killed larger (male) wild prey. Like in the case of livestock predation, with increased experience, males are perhaps better able to handle larger sized ungulates. Females with cubs tend to be older and represent the category that needs most energy. It is likely that the other categories cannot utilize a male ibex or argali kill efficiently, whereas females with cubs can and hence they benefit form selecting the larger classes.

4.4. Spatial and temporal variation in prey choice

Seasonal movements by herders and the corresponding increase in sheep and goat abundance in snow leopard habitats (i.e.

mountains) in winter likely explains the increased levels of winter livestock predation recorded in our study. Snow leopards preyed on ibex and argali in proportion to their relative abundance, with more argali killed in the Northern range and more ibex in the Southern range. This pattern was also consistent in the prey choice of individual snow leopards that hunted in both the mountain ranges, and appeared to change prey choice according to the relative abundance of ungulates in the respective range. Predation patterns on large livestock also appeared to reflect their relative abundance, with more camels and horses killed in the Northern range, though sample sizes were small and results should be interpreted with caution.

4.5. Kill rate

Our estimated kill rate of 3.7 kills/month by snow leopards is similar to that of cougars (3.5 kills/month; Knopff et al., 2010) and Amur tigers (Panthera tigris altaica; 3.7 kills/month; Miller et al., 2013), respectively. Kill rate for others species such as jaguars (Panthera onca; 7.1 kills/month; Cavalcanti and Gese, 2010) and leopards (Panthera pardus) in Namibia (6.3 kills/month; Stander et al., 1997) has been reported to be much higher, while it was much lower for leopards in South Africa (2.2 kills/month; Martins et al., 2010). The differences in kill rates are likely explained by varying sizes of prey species, carcass loss to other predators or scavengers, and variation in environmental conditions (e.g. faster decomposition of meat in areas with higher temperatures and humidity).

Kill rate in our study was negatively correlated with the size of the prey at the beginning of the kill interval, suggesting that the snow leopards stayed longer at larger kills as they provided more biomass (see also Cavalcanti and Gese, 2010 and Knopff et al., 2010 for similar behaviour in jaguars and cougars). The higher use of larger prey by male snow leopards may explain their lower kill rate, as compared with females.

Only one of the female snow leopards we followed had cubs older than 1 year. Her estimated kill rate (5.7 kills/month) was substantially higher than the mean (4.2 kills/month) for females with cubs. It is likely that the energy requirements for older cubs leads to an increased kill rate, as has been found for cougars (Knopff et al., 2010) and leopards (Stander et al., 1997). In fact, we may have underestimated the kill rate of the female with old cubs as we found several of her kills on clusters with only two locations, indicating that she and her cubs finished the carcass quickly and moved on. There is also the possibility that they may have consumed some kills and moved on even before a cluster was generated. Our value for the kill rate for females with cubs may therefore be an underestimate, and largely represents females with young cubs.

Poor GPS coverage in steep terrain and 5–7 h GPS fix intervals likely resulted in us missing some small kills such as ibex kids that were consumed quickly. While the kill rates reported here may therefore be somewhat underestimated, they are considerably higher than the only previous estimate of snow leopard predation rate of 1.7–2.5 kills/month that was based assumptions of energy requirements for a snow leopard sized felid (Jackson and Ahlborn, 1984). Thus, a snow leopard population is likely to kill many more livestock and wild ungulates than previous estimates of kill rate suggest.

5. Conclusions

Our results show that even in a landscape with many more livestock than wild ungulates, snow leopards preyed upon wild ungu-

lates rather than livestock. Predation on livestock largely appeared to result from chance encounters with free-ranging livestock, stragglers that got left behind in pastures overnight, or herded animals grazing in broken terrain that were out of view of the herder. Our data suggest that livestock predation could be reduced considerably by reducing the number of stragglers and avoiding grazing in very rugged terrain that provides cover for snow leopards. Such adjustments in herding practices, in combination with the use of predator-proof corrals at night can substantially reduce livestock predation (see Jackson and Wangchuk, 2004 for predator-proof corrals). However, free-roaming large bodied livestock such as horse and camels may be difficult to protect and community-based insurance may provide a more suitable conservation strategy (Mishra et al., 2003). If conservation efforts lead to increased snow leopard densities as suggested by Suryawanshi et al. (2013), that could lead to increased livestock predation and should therefore be accompanied with efforts to better protect livestock and improve vigilance through better herding practices.

Retaliatory killing in response to livestock predation has been a major threat to snow leopards (Li and Lu, 2014). Our results suggest that if retaliatory killings occur in proximity to the kill sites of livestock, male snow leopards will likely be more susceptible, given their higher propensity for livestock predation than females. During our study period, one adult male snow leopard was confirmed to have been killed in retaliation against repeated attacks on livestock in the same corral, and two other males may have been killed given their last GPS locations were close to corrals that they had raided multiple times. While for population demographics, this is less threatening than retaliatory killing of reproductive females, the small and sparse populations of snow leopards may be vulnerable to rapid demographic skews.

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