Does carnivore predation on livestock decline as wild-prey abundance increases?

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Abstract

1. Livestock depredation by large carnivores is an important conservation and economic concern. Facilitating an increase in wild-prey populations has often been recommended as a measure to reduce predator impacts. However, theory predicts that an increase in wild prey could either increase (apparent competition) or decrease (apparent facilitation) livestock damage by large carnivores, depending on their numerical and functional responses.

2. We developed theoretical predictions about patterns of livestock depredation and tested them by examining the density and diet of the endangered snow leopard *Panthera uncia*. Our data came from seven sites in Central Asia representing a gradient of wild-prey to livestock ratio.

3. Snow leopard density (range 0.4 to 3.3 individuals/100 km²) did not show any discernible response to livestock density but increased linearly by 1.01 individuals/100 km² for a wild-prey increase of 1 ungulate/km². Snow leopard diet suggested a type II functional response to wild-prey but a type III response to livestock. Together, the numerical & functional responses of the snow leopard predicted that with an increase in wild-prey density, the total number of livestock killed per unit time by snow leopards would increase initially, and then decline when wild prey outnumber livestock beyond a certain threshold.

4. Livestock depredation by snow leopards measured at five sites over a period of three years showed a hump-shaped pattern with ratio of wild-prey to livestock. The proportion of large-bodied free-ranging stock and small-bodied herded stock killed by the snow leopard peaked at ratios of 1:1 and 1:7 wild-prey to livestock, respectively.

5. Conservation and wild prey recovery in impoverished habitats therefore must be accompanied by better stock protection measures.
Keywords apparent competition, facilitation, snow leopard, *Panthera uncia*, human-wildlife conflict, functional response, numerical response, prey-predator relationship

Introduction

Increasing human population, related increase in resource use, widespread habitat destruction, and in some cases, recovery of wildlife populations, is increasing the interactions between wildlife and people (Inskip & Zimmerman 2009). Increased interactions between humans and large carnivores have led to escalated livestock damage by large carnivores and their retaliatory killing by people (Woodroffe et al. 2005). Carnivore conservation is thus a major challenge. Research has mainly focused on describing the socio-economic context of such negative aspects of human-carnivore interactions (Woodroffe et al. 2005). Mitigation measures have largely focused on reducing the interaction between carnivores and humans, and improved protection or compensation for damage of livestock (Ogada et al. 2003; Breitenmoser 1998; Treves & Karanth 2003; Mishra et al. 2003). The ecology of such negative interactions remains poorly understood. Building an understanding of the ecological aspects of livestock depredation by carnivores is important for framing policies of global relevance.

Wild-prey density is known to be a critical determinant of large-carnivore density (Carbone & Gittleman 2002; Karanth et al. 2004). Increasing the availability of wild-prey has been recommended as an important measure to reduce the dependence of large carnivores on livestock (e.g. Nowell & Jackson, 1996; Pedersen et al. 1999; Polisar et al. 2003; Bagchi & Mishra, 2006; Mishra et al. 2003). Indeed, facilitating an increase in wild-prey populations is often a desirable goal in itself, considering their functional roles and in many cases their endangered status. However, the impact of wild-prey availability on the foraging behaviour of the carnivore is debatable (Meriggi et al. 1996, Stahl et al. 2001, Odden et al. 2008). Few studies have actually assessed how an increase in wild-prey availability affects the rate of livestock depredation by large carnivores (Hemson 2004).

Theory suggests that increased availability of one prey could potentially, increase or decrease the predation level on the second prey species (Holt 1977). When increase in the density of one prey species increases the density of the predator (a numerical response)
that results in escalated predation on the second prey species, it is called apparent competition (Abrams and Matsuda 1996). Alternatively, when increase in density of one prey leads to a decrease in predation on the second species, it is called apparent mutualism. Apparent mutualism can arise because of predator satiation or prey switching (Long et al. 2012).

Increasing wild prey abundance can be an effective strategy in reducing livestock depredation by large carnivores only if the wild-prey species indirectly facilitates livestock via the shared predator. Such apparent mutualism is possible under two conditions; 1) predator populations are density dependent, and beyond a threshold do not respond numerically to a further increase in density of wild prey. This can potentially allow wild prey species to satiate the predator under conditions of food processing constraints, leading to reduced predation pressure on livestock. Large carnivore populations could show density dependence due to territorial behaviour, limited denning sites, limited water availability, disease etc. Food processing constraints for large carnivores could include search time, gut passage time, probability of successful hunt, disturbance by humans, harassment by scavengers etc. 2) Large carnivores exhibit prey-switching and they devote more attention to the prey species which is relatively more common, easier to catch or more preferred. Murdoch (1969; pp335) defined occurrence of prey switching as “the number of attacks on a species is disproportionately large when the species is abundant relative to the other prey, and disproportionately small when the species is relatively rare”. Such responses can arise when hunting efficiency is maintained by focusing on only one prey species. However, both these ideas do not have much empirical support from field studies of large carnivores.

Focusing on the snow leopard Panthera uncia, we asked whether an increase in the abundance of wild ungulate prey would reduce or escalate the number of livestock killed by this endangered cat. The species occurs across the mountain ranges of Central Asia. Its survival is threatened due to persecution over its livestock killing behaviour (McCarthy and Chapron 2003; Mishra et al. 2003). Livestock use of the landscape encompassing the snow leopard range is pervasive even inside protected areas. However, little effort has been made to understand the ecological determinants of livestock killing by this large
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felid. Local pastoral communities are reported to lose between 3-12% of their livestock annually to the snow leopard (Mishra 1997; Namgail et al. 2007; Ikeda 2004; Oli et al. 1993). Livestock contribution to snow leopard diet is variable, and has been reported to be as high as 70% (Bagchi & Mishra 2006; Anwar et al. 2011; Shehzad et al. 2012). Facilitating the recovery of the wild ungulate prey of the snow leopard is therefore considered an important measure to reduce the extent of livestock depredation (Mishra et al. 2003).

We assessed the numerical and functional responses of the snow leopard to examine the impact of wild-prey availability on its livestock depredation behaviour. Numerical response is defined as the change in predator density as a function of prey density (Solomon 1949) while functional response is the intake rate as a function of prey density (Holling 1959). Numerical and functional response were assessed by examining the density and diet of snow leopards at seven sites in Central Asia along a gradient of wild-prey to livestock density. Based on the results, we built a predictive model of livestock depredation by snow leopard along increasing wild prey and livestock scenarios. We tested the predictions of this model against a three-year dataset of livestock depredation by snow leopards from across five sites in the Indian Trans-Himalayan region.

Methods

STUDY SITES

We sampled at seven sites across South and Central Asia. These sites were Kibber (32.36° N; 78.01° E), Lingti (32.32° N; 78.33° E), Lossar (32.41° N; 77.63° E), Pin (31.89° N; 77.94° E) and Tabo (32°06 N; 78°32 E) in Himachal Pradesh India, Rumtse (33°72 N; 77°76 E) in Jammu and Kashmir, India and Tost (43.17° N; 100.46° E), South Gobi, Mongolia. The area and effort are summarized in table 4.1. The ungulate (wild and domestic) assemblage varied across sites. The primary wild prey species were: blue sheep Pseudois nayaur, ibex Capra sibirica (four sites), Argali Ovis ammon (one site). The primary domestic ungulates were horse Equus caballus, cattle Bos primigenius, sheep Ovis aries, goat Capra hircus (seven sites), yak Bos grunniens, donkey E. asinus (six sites), Bactrian camel Camelus bactrianus (one site). Based on herding practices, livestock could be classified as (i) Large-
bodied free ranging, henceforth referred to as large stock (yaks, horses and camel), and, (ii) Medium and small-bodied herded, henceforth referred to as herded stock (cow, donkey, cow–yak hybrid, goat and sheep). Herded stock is shepherded to the pastures every morning and brought back to the stocking pens inside the villages in the evening. At the six sites in India small-bodied stock of the entire village was herded together whereas in Tost, Mongolia each family herded its own livestock. Unlike the sites in India, herders in Tost were often accompanied by dogs.

ESTIMATING WILD PREY ABUNDANCE
Wild-prey abundance was estimated using the double observer survey technique. Details of the survey at the five sites of Kibber, Pin, Lingti, Tabo and Lossar have been described in chapter (3) and Suryawanshi et al. (2012). For the two other sites, the study area was divided into three and eight survey blocks for Rumtse and Gobi, respectively. Rumtse and Gobi were surveyed over three and eight consecutive days, respectively. Results summarized in Appendix S4.1.

ESTIMATING LIVESTOCK ABUNDANCE AND DEPREDATION
The professional livestock herders of each village in the five sites of Kibber, Pin, Lingti, Tabo and Lossar were first contacted in September 2009. We requested the professional herders of each village to maintain a record of all livestock mortality on a monthly basis. The herders maintained records of the species and age of livestock, month, cause of mortality and the total number of livestock in each village throughout January 2009 to December 2011. Identity of the predator was confirmed through direct sighting or signs around the kill. By cross-checking their knowledge, the team ensured that the herders keeping records were experienced at identifying signs of snow leopards and wolves. A local representative maintained contact with each herder every 4–6 months and recorded all the livestock mortalities. We expect the herder’s records to be accurate, as they also had to report any mortality to the livestock owner. For the Rumtse site, data on population of livestock was collected from the headman of the Gya village who maintains a record of livestock holding in all the four villages (Namgail et al. 2007). In Gobi we
conducted a door to door survey to assess the total population of livestock at the study site.

All livestock mortalities were recorded from herder observations for the five sites of Kibber, Pin, Lingti, Tabo and Lossar for the years 2009, 10 and 11. Livestock mortalities could not be recorded at Rumtse and Gobi due to the migratory behaviour of the herd.

**ESTIMATING SNOW LEOPARD DIET AND ABUNDANCE**

*Snow leopard scat collection protocol*

Scats were collected from predetermined trails laid along prominent snow leopard habitats such as ridge-lines and cliff bases. The trails were distributed across the study area to avoid any large 'holes' where a snow leopard had a zero probability of detection achieving full spatial coverage (table 4.1). On encountering a relatively fresh scat, we recorded data on the size of the scat (length and diameter), GPS location, presence of snow leopard pugmark, scrapemarks or spray, the strata on which the scat has been deposited, the general microhabitat and any other general remark were recorded. Only scats that were likely to belong to snow leopards were collected. The scat samples were carefully collected to avoid contamination and stored in absolute alcohol.

*DNA extraction and species identification*

DNA was extracted from the scat samples in a separate, UV irradiated pre-PCR laboratory space using the commercially available QIAamp DNA Stool mini kit (QIAGEN Inc.) following the manufacturer’s instructions with slight modifications by Mondol et al. (2009). All extractions (in sets of eleven samples) included a negative control to monitor contamination. The DNA samples were then amplified using the snow leopard specific primer (UNC-1) developed by Mondol et al (unpublished). This primer amplifies 111 base pairs of the NADH2 gene and was found to be specific to the snow leopard when tried with other sympatric carnivores and prey species. This ensured that only genuine snow leopard samples were used for further analysis.
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Microsatellite primer selection

We adopted seven microsatellite loci characterised for snow leopard from Janecka et al. (2008) and Mondol et al. (2012) based on their polymorphic information content, amplification success with field collected fecal samples and low error rate.

PCR and Genotyping

Amplification was carried out in 10 μl reaction volumes containing 4 μl Qiagen multiplex PCR buffer mix (QIAGEN Inc.), 0.2 μm labelled forward primer (Applied Biosystems, Carlsbad, CA, USA), 0.2 μm reverse primer, 4 μm BSA and 3 μl of the template DNA and 1μl of ultrapure distilled water. The temperature regime included an initial denaturation (94°C for 15 min); 45 cycles of denaturation (94°C for 45 secs), annealing (Ta for 45 secs) and extension (72°C for 45 sec); followed by a final extension (72°C for 30 min) in an Eppendorf thermocycler. We incorporated PCR negatives in all reaction to check any cross contamination. One microlitre of the amplified product was added into 12 μl of formamide (Applied Biosystems) and 0.5 μl GeneScan –500 LIZ ® size standard (Applied Biosystems) then run into an automated sequencer ABI3100XL (Applied Biosystems). Microsatellite alleles were scored with GENEMAPPER version 4.0 (Applied Biosystems). To get reliable genotypes, we followed the multiple tube approach by Taberlet et al. (1996) and repeated the PCR, genotyping and scoring process four times. Samples with consistent results for at least three repeats were considered for further analysis. This implies that quality index of 0.75 was used following Miquel et al. (2006).

Individual identification and abundance

We then compared these genotype profiles using the identity analysis module in program CERVUS (Marshall et al. 1998), which identifies samples with identical genotypes for the specified number of loci. Identical genotype profiles at all the seven loci were used to identify multiples instances of the same individual. This analysis allowed us to discern both number of unique individual and number of recaptures. We used Capwire (Miller et al. 2005) to estimates the abundance of snow leopard at each site. We used the even capture probability model (ECM). The ECM assumes equal capture probability for each
individual. We expect this to be true in our case as all transects were equally spaced from each other.

*Camera trapping (one site; Tost)*

The study area was divided into ten equal grids of approximately 25 km². One Reconyx RM45 or HC500 camera trap was deployed per grid at the most suitable location. This was part of a larger camera trapping study which covered the 2000km² around our study area. Although we used a single camera trap per grid, we could identify the individual snow leopard in 96% of the photo captures. Individuals were identified using unique markings (McCarthy et al. 2008). For consistency, data were analyzed using *Capwire* (Miller et al. 2005) such that each camera trap capture was considered as an independent sample.

**SNOW LEOPARD DIET**

Only samples confirmed to be from snow leopards using the molecular technique were used for diet analysis. We used the micro-histological method of assessing snow leopard diet following Oli (1993), and Bagchi and Mishra (2006). We collected reference hair samples of all the potential prey of the snow leopard from three sites representing all our field sites. A minimum of three reference slides were prepared per animal per site. Hair remains from snow leopard scat samples were used for prey species identification. Shape, size, colour and structure of the cuticle and medulla were used in identification. We examined 10 hairs from each scat sample at random. We recorded the relative occurrence of each prey species in snow leopard diet, i.e, the proportion of hair samples of a particular prey species to the entire hair sample positively identified. Asymmetric 95% confidence intervals were calculated through Monte Carlo simulations with a scat as a sampling unit with 1000 permutations using random draws from the observed distribution with replacement (Krebs 1989). The results have been summarized in table 4.2.
EXAMINING SNOW LEOPARD FUNCTIONAL RESPONSE

To predict the total number of livestock killed over a unit period of time, for a given abundance of livestock and wild prey we took the product of predator abundance (Numerical response $P$) and the rate of livestock depredation (Functional response $F$).

We examined the functional response ($F$) of the snow leopard as the ratio of the relative occurrence of different prey types in the diet.

$$\frac{F_1}{F_2} = c \left( \frac{N_1}{N_2} \right)^m$$  \hspace{1cm} (1)

Where $N$ is the population density of the prey type 1 and 2; and $m$ is the extent of switching (see Garrot et al. 2007); and $c$ is a measure of the “bias in the predator’s diet to one prey species” indicating preference towards a prey species (Murdoch 1969; pp 337). Values of $m$ significantly larger than 1 indicate prey switching or type III or sigmoidal functional response (Greenwood & Elton 1979; Elliott 2004). Larger values of $m$ indicate stronger switching. To assess the functional response of the snow leopard we examined the relationship between the proportion of wild-prey and livestock in the diet with their proportionate availability.

To predict the total number of livestock killed over a unit period of time, for a given abundance of livestock and wild prey we took the product of predator abundance (Numerical response $P$) and the rate of livestock depredation (Functional response $F$).

MODELING IMPACT OF WILD-PREY AVAILABILITY ON LIVESTOCK DEPREDATION BY THE PREDATOR

We took the product of snow leopard abundance ($Pr$) and their functional response towards livestock ($F$) to predict the trend in livestock depredation along increasing wild-prey and livestock abundance. Our results indicate that snow leopard density was a function of wild prey alone. Density of livestock did not influence snow leopard density. Thus, snow leopard abundance ($Pr$) was modeled as a function of wild-prey abundance:
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\[ Pr = a + W \cdot b \]  \hspace{1cm} (2)

Where \( W \) is wild-prey abundance.

Since snow leopards are known to be territorial carnivores (McCarthy et al 2010) we used ratio-dependant functional response (Arditi & Ginzburg 1989). We used ratio-dependant multi-species functional response adapted from Garrot et al. (2007) and Smout et al. (2010). Functional response of snow leopard towards livestock (\( F_l \)) was modeled as:

\[ F_l = \frac{a_l N_l^{m_l}}{Pr + a_l t_l N_l^{m_l} + a_w t_w N_w^{m_w}} \]  \hspace{1cm} (3)

where \( a \) is the attack rate, \( t \) is the handling time and \( m \) determines the extent of switching. Values significantly greater than one indicate switching. In the above function the shape of the function depends on the value of \( m \) and the absolute values depend on ‘\( a \)’ and ‘\( t \). Since we were mainly interested in the shape of the function, we assumed \( a \), \( t \) and \( m_w \) to be constant at 1. The parameters \( m_l \) & \( m_w \) were assigned the values of 1 for type II functional response and 2 for a switching functional response. Values of \( N_l \) and \( N_w \) were simulated to range from 30 to 960 consistent with the field situation.

**Results**

**SPECIES IDENTIFICATION**

A total of 305 potential snow leopard scats were collected across the seven sites out of which 191 (62.62%) amplified with our snow leopard specific primer. The rest were possibly too old and degraded or were other sympatric carnivores. Site-wise details are included in table 4.1.

**INDIVIDUAL IDENTIFICATION**

We were able to genotype 53 (34%) snow leopard positive samples on all seven loci. The number of alleles per locus varied from 2 to 4. Our analysis with the program CERVUS resulted in the probability of identity or PID values which was calculated to be 0.000089 (Unbiased) and 0.012 (Siblings). Site-wise details included in Appendix S4.2.
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Table 4.1: Total effort for collecting scat samples at the seven study sites and amplification success with species specific primer and microsatellite loci

<table>
<thead>
<tr>
<th>Site</th>
<th>Area (km²)</th>
<th>Distance walked (km)</th>
<th># transects</th>
<th>Scats collected</th>
<th>Snow leopard (UNC1)*</th>
<th>Amplification for all seven loci</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lingti</td>
<td>186</td>
<td>122</td>
<td>24</td>
<td>53</td>
<td>41</td>
<td>15</td>
</tr>
<tr>
<td>Lossar</td>
<td>219</td>
<td>106</td>
<td>21</td>
<td>50</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td>Kibber</td>
<td>411</td>
<td>133</td>
<td>28</td>
<td>44</td>
<td>30</td>
<td>15</td>
</tr>
<tr>
<td>Pin</td>
<td>270</td>
<td>110</td>
<td>22</td>
<td>24</td>
<td>16</td>
<td>2</td>
</tr>
<tr>
<td>Tabo</td>
<td>341</td>
<td>131</td>
<td>26</td>
<td>46</td>
<td>31</td>
<td>10</td>
</tr>
<tr>
<td>Rumtse</td>
<td>300</td>
<td>117</td>
<td>23</td>
<td>43</td>
<td>28</td>
<td>8</td>
</tr>
<tr>
<td>Tost</td>
<td>250</td>
<td>132</td>
<td>27</td>
<td>45</td>
<td>35</td>
<td>NA</td>
</tr>
</tbody>
</table>

* species specific primer used to identify snow leopard samples

Table 4.2: Percent contribution of prey species to snow leopard diet (measured as relative occurrence in %) at seven different sites across Central Asia. NA indicates that the species was not available.

<table>
<thead>
<tr>
<th>Site</th>
<th>Blue sheep</th>
<th>Ibex</th>
<th>Argali</th>
<th>Yak</th>
<th>Horse</th>
<th>Camel</th>
<th>Shoat</th>
<th>Unid</th>
<th>Cattle</th>
<th>Donkey</th>
<th>Small mammals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lingti</td>
<td>95</td>
<td>NA</td>
<td>NA</td>
<td>0</td>
<td>0</td>
<td>NA</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Lossar</td>
<td>NA</td>
<td>34.6</td>
<td>NA</td>
<td>0</td>
<td>23</td>
<td>NA</td>
<td>0</td>
<td>3.4</td>
<td>10</td>
<td>26.9</td>
<td>2.3</td>
</tr>
<tr>
<td>Kibber</td>
<td>48</td>
<td>18</td>
<td>NA</td>
<td>10</td>
<td>10.6</td>
<td>NA</td>
<td>10.2</td>
<td>3.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pin</td>
<td>NA</td>
<td>55.9</td>
<td>NA</td>
<td>0</td>
<td>14.2</td>
<td>NA</td>
<td>12.4</td>
<td>4.3</td>
<td>6.2</td>
<td>6.8</td>
<td>0</td>
</tr>
<tr>
<td>Tabo</td>
<td>83</td>
<td>NA</td>
<td>NA</td>
<td>0</td>
<td>6.5</td>
<td>NA</td>
<td>6.5</td>
<td>1</td>
<td>3.3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rumtse</td>
<td>51.5</td>
<td>NA</td>
<td>NA</td>
<td>0</td>
<td>3.5</td>
<td>NA</td>
<td>40</td>
<td>1.5</td>
<td>0</td>
<td>0</td>
<td>3.5</td>
</tr>
<tr>
<td>Tost</td>
<td>NA</td>
<td>65</td>
<td>4.4</td>
<td>NA</td>
<td>1.8</td>
<td>3.7</td>
<td>20.6</td>
<td>3.8</td>
<td>0</td>
<td>NA</td>
<td>2.9</td>
</tr>
</tbody>
</table>

NUMERICAL RESPONSE

Snow leopard abundance ranged from 0.46 to 3.3/100 km² and increased linearly with wild prey availability ($R^2 = 0.76, P = 0.01$; figure 4.1a). Snow leopard density increased by 1.01 individuals/100 km² for a unit increase in wild-prey density/ km². Snow leopard density did not show any discernible relationship with herded-stock (slope = -0.006, $P = 0.93$; figure 4.1c), large-stock (slope = -0.66; $P = 0.32$; figure 4.1b) or total livestock (slope =
Snow leopard density did not show a relationship with wild prey and large-stock density together (slope = 0.46; \( P = 0.32 \); figure 4.1d).

**FUNCTIONAL RESPONSE**

Based on snow leopard diet data from the seven sites, wild herbivore prey was most preferred, followed by large-bodied free-ranging livestock. Small-bodied herded stock was largely avoided (Table 4.3).

**Table 4.3.** Jacobs Index (D) of prey selection of snow leopard at seven sites. Strong positive and negative values indicate selection and avoidance, respectively.

<table>
<thead>
<tr>
<th>Site</th>
<th>Wild-herbivores</th>
<th>Free-ranging stock</th>
<th>Herded stock</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lingti</td>
<td>0.99</td>
<td>-1</td>
<td>-1</td>
</tr>
<tr>
<td>Kibber</td>
<td>0.88</td>
<td>0.83</td>
<td>-0.75</td>
</tr>
<tr>
<td>Tabo</td>
<td>0.99</td>
<td>0.55</td>
<td>-0.81</td>
</tr>
<tr>
<td>Pin</td>
<td>0.84</td>
<td>-0.09</td>
<td>0.024</td>
</tr>
<tr>
<td>Lossar</td>
<td>0.51</td>
<td>0.92</td>
<td>0.27</td>
</tr>
<tr>
<td>Rumtse</td>
<td>1</td>
<td>-0.16</td>
<td>-0.75</td>
</tr>
<tr>
<td>Tost</td>
<td>0.99</td>
<td>0.51</td>
<td>-0.94</td>
</tr>
</tbody>
</table>

The proportion of wild-prey in snow leopard diet increased as an asymptotic function of the proportionate availability with a power of \( m = 0.33 \). The equation of the form \( \frac{F_{wp}}{F_l} = 1.29(N_{wp} / N_l)^{0.33} \) best fit the data (\( R^2 = 0.80; \) Adjusted \( R^2 = 0.76; \) \( P = 0.006 \)) where \( wp \) represents wild-prey, and \( l \) represents total livestock. The above equation suggests a type II functional response to wild prey (figure 4.2a). Proportion of large-stock in snow leopard diet increased as a power function of availability with \( m = 2.26 \) suggesting a strong type III or switching response to large-stock (figure 4.2b). Equation of the form \( \frac{F_{lr}}{F_{wp}} = 0.40(N_{lr} / N_{wp})^{2.26} \) best explained the data (\( R^2 = 0.80; \) Adjusted \( R^2 = 0.76; \) \( P = 0.007 \)); where \( lr \) represents large-stock. Proportion of herded-stock in snow leopard diet increased as a power function of proportion availability with \( m = 4.16 \) Suggesting a strong type III functional response to herded-stock (figure 4.2c). The equation \( \frac{F_{hs}}{F_{wp}} = 0.36(N_{hs} / N_{wp})^{4.16} \) (\( R^2 = 0.95; \) Adjusted \( R^2 = 0.94; \) \( P < 0.005 \)); where \( hs \) represents herded-stock.
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Proportion of total livestock ($l$) increased as a power function of proportion availability with $m = 4.84$ suggesting a strong type III functional response to total livestock (figure 4.2d). The equation $\frac{F_l}{F_{wp}} = 0.55(\frac{N_l}{N_{wp}})^{4.84}$ best explained the data ($R^2 = 0.95$; Adjusted $R^2 = 0.94$; $P < 0.005$).

![Graphs](image)

**Figure 4.1:** Relationship between snow leopard and a) wild prey, b) large-stock, c) herded-stock, and d) total livestock density across seven site in Central Asia. Linear relationship between snow leopard and wild-prey density is the only significant relationship (Slope = 1.01; $R^2 = 0.76$; $P = 0.01$). Error bars in a) represent 95% CI. Wild-prey density was estimate using the double-observer survey (Chapter 3; Suryawanshi et al. 2012). All livestock densities were arrived using total census.
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Figure 4.2. Relationship between ratio of prey type in diet versus availability across seven sites in Central Asia. Best fit a) $y = 1.29x^{0.33}$; ($R^2 = 0.80$; Adjusted $R^2 = 0.76$; $P = 0.006$). Best fit b) $y = 0.40x^{2.26}$; ($R^2 = 0.80$; Adjusted $R^2 = 0.76$; $P = 0.007$). Best fit c) $y = 0.36x^{4.16}$; ($R^2 = 0.95$; Adjusted $R^2 = 0.94$; $P < 0.005$). Best fit d) $y = 0.55x^{4.84}$ ($R^2 = 0.95$; Adjusted $R^2 = 0.94$; $p<0.005$) Error bars represent 95% CI calculated using 1000 bootstraps with each scat as a sampling unit.

MODEL PREDICTIONS

The model (figure 4.3) makes two key predictions, 1) the number of livestock killed by snow leopards over unit time will increase as a sigmoidal function of livestock abundance for any given value of wild prey abundance. However, the saturation value of this relationship will depend on the abundance of the wild-prey. 2) The model also predicted
that for a given value of livestock abundance, the number of livestock killed by snow leopards over unit time would have a hump-shaped relation with wild-prey abundance, ie., as wild-prey increases, livestock depredation by snow leopard will first increase and then decrease. Thus when expressed as proportions, the proportion of livestock killed by the snow leopard first increases and then decreases with increasing ratio of wild-prey to livestock abundance. We define the point at which the increase in livestock killing stops and the decline starts as the 'critical ratio'.

**Figure 4.3:** The predicted relationship between rate of livestock depredation by snow leopards along densities of wild and domestic prey. The relationship was modeled as a product of snow leopard abundance ($Pr$) as a function of wild-prey abundance and snow leopard functional response towards livestock ($F$) as a ratio-dependent multi-species functional response.
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LIVESTOCK DEPREDATION

The total number of herded stock killed by snow leopard ranged from zero at Lingti in 2012 to 101 at Tabo in 2011. The total number of large stock killed by snow leopard in a year ranged from zero at Lingti in 2011 to 60 at Kibber in 2010. The proportion of livestock killed by snow leopard showed a hump-shaped pattern along ratio of wild-prey to livestock density. The proportion of large-stock killed by snow leopard peaked at equal number of large-stock and wild-prey while the proportion of herded-stock killed peaked at 1:7 ratio of wild-prey to herded stock (figure 4.4). The number of livestock killed by snow leopards declined on either side of these critical ratios as expected from our model.

![Figure 4.4: Proportion of a) large-bodied free-ranging and b) small-bodied herded livestock killed by snow leopard along an increasing ratio of wild-prey to livestock. The line represents a smoothing interpolation performed using function 'loess' in R.](image)

Discussion

We examined the numerical and functional responses of the snow leopard to assess the impact of increased wild-prey availability on the extent of livestock depredation by this endangered large carnivore. Specifically we tested whether wild-ungulates compete or facilitate livestock rearing through their impact on the population and foraging behaviour of the snow leopard.

Firstly, we find that wild-prey availability is a fundamental determinant of snow
leopard abundance and critical for snow leopard conservation. Snow leopard population increased linearly with wild-prey availability (figure 4.1a) while snow leopards did not show any numerical response towards availability of large-bodied free-ranging or small-bodied herded livestock. Although snow leopard population density is ultimately expected to reach an asymptote with wild prey abundance as other resources such as denning sites, resting sites etc. become limited, we did not find any evidence for density saturation. This finding is consistent with other studies on carnivore population densities (Carbone & Gittleman 2002; Karanth et al 2004).

The numerical response of snow leopards is consistent with their prey selection. Snow leopard showed a strong selection for wild-prey followed by a proportionate use of large-bodied free-ranging livestock and avoidance of herded livestock. It is surprising that snow leopards did not show a numerical response to livestock availability despite utilizing livestock for up to 40% of their diet requirements at four of the seven sites. This could possibly be due to the uncertainty in livestock availability. Livestock herders are expected to be more vigilant for at least a few days following a predation event by the snow leopard. Even in the case of free ranging-livestock, villagers often round up all the dispersed animals to one location in one group after serious predation events. This presumably reduces livestock predation events by snow leopards temporarily.

We found a type II functional response of the snow leopard towards wild-herbivore prey and a strong switching response towards both the large-bodied free-ranging and small-bodied herded livestock. This suggests that snow leopard attacks on livestock will be disproportionately small when livestock is relatively rare. The model (product of numerical and functional response) suggests that increasing wild-prey will first lead to a rapid increase in livestock depredation per unit time followed by a gentle decline (figure 4.3). Increasing livestock population will lead to an increase in livestock depredation but it will plateau after some time. Our data suggest that the depredation of large-bodied free-ranging livestock peaks at 1:1 ratio of wild-prey to large-stock (figure 4.4a). Depredation of herded-stock peaks at 1:7 ratio of wild-prey to herded-stock (figure 4.4b). However, we could not fit our model to this dataset due to low sample size. The ratio-dependent functional response includes two attack-rate parameters ($a_l$ & $a_w$), two
handling-time parameters ($T_l$ & $T_w$) and the switching parameter (m). Data from just five sites was inadequate to estimate five parameters. The total number of livestock lost to snow leopards is predicted to decline beyond these critical ratios. However, the rate of this decline cannot be ascertained with the current data. Such a hump-shaped pattern between the density of wild-prey and number of livestock killed by the snow leopard suggests apparent competition mediated via the snow leopard when wild prey populations improve from relatively low densities typical of multiple-use landscapes, which changes to facilitation beyond the critical ratios.

Our results reiterate that facilitating an increase in wild ungulate populations is a critical measure for increasing carnivore abundance (Carbone & Gittleman 2002; Karanth et al. 2004). However, this is likely to lead to an increase in livestock depredation due the increasing population of the carnivore, up to a point where the ratio of wild-ungulate prey to livestock reaches a critical ratio. Beyond which, further increase in wild-ungulate prey will lead to a reduction in livestock damage. Our results suggest that the interactions between wild ungulates, livestock and carnivores could be complex and often non-linear. Furthermore, livestock are known to compete with wild-ungulates for limited resources (Mishra et al. 2004; Madhusudan 2004). Thus, reduction in livestock density is a recommended strategy for increasing wild-ungulates populations. Improving wild ungulate populations could also be an effective strategy in reducing livestock damage by carnivores in areas where the population of wild-ungulates and livestock are already close to the critical ratio. Facilitation of wild-prey could be an effective strategy also in areas with low livestock density, as wild-prey to livestock ratio is likely to cross the threshold ratio much sooner than in areas with high livestock stocking density.

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Population density of the snow leopard (*Panthera uncia*) was primarily determined by the density of wild ungulates such as the blue sheep (*Pseudois nayaur*) & ibex (*Capra sibirica*).

**Picture 7.** Population density of the snow leopard (*Panthera uncia*) was primarily determined by the density of wild ungulates such as the blue sheep (*Pseudois nayaur*) & ibex (*Capra sibirica*).