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ORIGINAL RESEARCH

Snow leopard prey selection on the mountain-adapted ibex: seasonal switching between prime-aged males and newborn kids

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Abstract

Predator–prey interactions occur within the context of relative prey abundance, the nutritional value of prey individuals, and their specific vulnerability to predation. Predation patterns can therefore be expected to vary between seasons, age and sex categories, with this variation important for understanding predator–prey ecology. We examined seasonal prey selection by snow leopards (*Panthera uncia*) on different age and sex categories of Siberian ibex (*Capra sibirica*) using data collected from 150 kill sites. These were analysed in relation to known ibex population composition using Jacobs' index, which estimates the strength and direction of prey preference or avoidance. Although solitary felids typically select prey of similar or smaller size than themselves, both male and female snow leopards selected for prime-aged ibex males (>5 years old), despite these being at least twice their body mass. Female ibex, yearlings and medium-sized males, which are similar in size to snow leopards, were preyed upon less than expected. In spring, snow leopards increased their prey selection of females and newborn kids, and reduced their selection of prime males. Our results suggest that the vulnerability of ibex to snow leopard predation is related to their agility in negotiating steep mountain terrain. We propose that the much larger body size of prime-aged ibex males reduces their ability to evade snow leopard ambushes on mountain slopes. In spring, the switch to predation on kids likely relates to the ease of hunting because of their lower agility, with a similar explanation for increased predation on females in late gestation. This seasonal switching between different prey categories, and the snow leopard's specialisation to hunt in steep mountainous terrain, may impose limits on sexual size dimorphism commonly seen in other large felids. In contrast, the vulnerability of prime-aged ibex males to snow leopard predation may reflect a sexually selected handicap, imposed by high sexual size dimorphism.

Introduction

Predator–prey relationships are central to the ecology and conservation of species due to the potential impact each has on the individual fitness and population dynamics of the other (Taylor, 1984). The starting point for understanding such relationships is the abundance of prey, which governs the probability of a predator–prey encounter (Lima & Dill, 1990; Stephan et al., 2016). In addition is the prey's vulnerability during an encounter, determined by factors such as spatiotemporal location, age, size, behaviour, pregnancy status and defence weapons, which will likely influence the predator's decision to attempt capture and its capture success (Lima & Dill, 1990; Metz et al., 2018; Sunquist & Sunquist, 1989). For many predator–prey systems, the relative vulnerability of the prey, or the prey preference of the predator, can be inferred by comparing the proportional abundance of different prey species to the observed kills made by a predator (e.g. Hayward, Henschel, et al., 2006; Murdoch, 1969). When predators take prey more frequently than predicted by relative prey abundance, this suggests a preference or specific vulnerability of that prey; when predation pressure is lower in relation to relative prey abundance, it suggests predator avoidance or some prey characteristic that reduces its vulnerability (Boukal et al., 2008; Hoy et al., 2021). Such relationships between predator and prey need not be static, with the strength of prey selection potentially changing in relation to individual developmental and seasonal effects (e.g. prey switching: Murdoch, 1969). Prey selection analyses are of interest because they: (1) help identify important predator–prey interactions in the context of prey abundance, and assess the importance of prey species from the perspective of the predator (Sinclair et al., 2003) and (2) provide a basis for understanding how prey behaviour or morphology influence prey vulnerability (Metz et al., 2018; Tallian et al., 2017).

Large felids are capable of killing prey larger than themselves (Sunquist & Sunquist, 1989). However, the generally observed pattern is that they select for prey of similar or smaller size than themselves, with many large prey species avoided completely (e.g. Hayward et al., 2012; Hayward, Henschel, et al., 2006; Hayward, Hofmeyr, et al., 2006; Jędrzejewski et al., 1993; Packer, 1986). This selection for smaller prey likely relates to the high risk posed to predators from prey with very large body sizes, the low probability of capturing such prey (i.e. reduced vulnerability) successfully, or the diminishing marginal benefit of increased prey biomass beyond a certain size (Mukherjee & Heithaus, 2013; Sunquist & Sunquist, 1989). Despite this, under specific conditions, large felids do show selection for prey much larger than themselves, demonstrating that these cost–benefit relationships related to prey body size are not uniform nor static. For example, mountain lions (*Puma concolor*: 40–70 kg) show a selection for elk (*Cervus canadensis*: 175 kg) when seasonal conditions force elk into terrain that increases their vulnerability (Hornocker, 1970); and male Eurasian lynx (*Lynx lynx*: 20–28 kg) select semi-domestic reindeer bulls (*Rangifer tarandus*: 80–120 kg) during late winter when they have shed their antlers (Mattisson et al., 2014). Thus, to better understand the ecological conditions that influence predation risk from large felids, it is not enough to catalogue which species are selected or avoided, but also the conditions under which prey selection changes or where common predator–prey selection patterns are violated.

Variation in the patterns of selection for specific prey may be associated with: (1) prey age, where juveniles and senescent individuals commonly are most vulnerable, (2) prey sex, which may be related to body size, morphology or behaviour and (3) season, which is often related to spatial distribution, birth season or variation in prey body condition following periods of heavy reproductive investment or food limitation (Christe et al., 2006; Hornocker, 1970; Hoy et al., 2021; Metz et al., 2012; Owen-Smith, 2008). In seasonal environments, most large herbivores feature a phenological birth pulse where neonates are expected to represent an important food source for predators in the months following birthing (Annear et al., 2023; Sand et al., 2008). However, whether the predators exhibit an intraspecific prey switch *sensu* Murdoch (Murdoch, 1969: selection for a prey strengthens or weakens in response to its relative frequency among the available prey) or simply opportunistically hunt juveniles is rarely examined (but see Reimer et al., 2019). Discerning how demographic groups in prey species are selected and avoided, and if predators switch among groups not only provides information about which prey are most important for the predators but also which demographic prey groups are most vulnerable (and what specific conditions make an age or sex class vulnerable relative to another; Annear et al., 2023). If predators select for specific demographic classes, this may have a significant impact on prey population dynamics, as vital rates and reproductive output typically vary with age and sex across most species (Boukal et al., 2008; Ginsberg & Milner-Gulland, 1994).

One predator–prey system suitable for studying intraspecific prey vulnerability, and if this changes seasonally, is the snow leopard (*Panthera uncia*) and its Siberian ibex (*Capra sibirica*, hereafter ibex) prey. Ibex exhibit large sexual dimorphism and grow slowly, with males reaching their full size at 8–9 years; this creates a wide range of prey sizes for snow leopards to select from within the species. Male ibex can range from half the size (yearlings: 20–30 kg) to more than twice the size (full-grown males: 80–100 kg) of an average-sized adult snow leopard (mean body mass of female and male snow leopards is 36 ± 3 and 42 ± 4 kg, respectively), with female ibex being approximately the same weight (35–45 kg) as an adult snow leopard (Fedosenko & Blank, 2001; Johansson et al., 2022; Mahato & Raziuddin, 2012). Both ibex sexes have horns that grow throughout their lives (male horns are much larger), allowing animals in the standing population to be reliably classified into sex and age categories. Ibex biology is governed by the highly seasonal systems where they occur, with the rut taking place in autumn and kids born in the following spring (Fedosenko & Blank, 2001; Willisch & Neuhaus, 2009).

In this study, we examine the preferences of snow leopards towards various age-sex classes of ibex using data from 150 ibex kills made by 22 GPS-collared snow leopards in Mongolia. We analyse seasonal preferences in prey selection relative to ibex demographics and if this differs between snow leopard males and females. Snow leopards have been observed ambushing from above, pursuing prey downhill along slopes and cliffs (Johansson et al., 2024). Ibex use the same terrain to escape predators, and hence, the agility of the individual ibex is expected to be critical in determining its vulnerability to snow leopard predation. Based on the behaviour of other felids, we expected that snow leopards should select for ibex size categories similar to or smaller than themselves: that is, kids, yearlings and ibex females to be preferred, with young males killed relative to their abundance and prime-aged ibex males avoided.

Materials and methods

Study area

The study was conducted in the Tost Mountains of Southern Mongolia (43° N, 100° E) from September 2008 to February

2020. The Tost Mountains consist of several rugged mountain massifs, rising steeply from the surrounding steppe to a maximum elevation of 2517 m above mean sea level. The climate is windy and dry with <130 mm of precipitation annually, most of it falling as rain from June to August. The environment is highly seasonal with cold winters and warm summers; mean daily temperature ranges from −14°C in January to 23°C in July. Vegetation is sparse and dominated by short grasses, mostly *Stipa* spp., herbs and small shrubs such as *Amygdalus mongolica, Caragana leucophlae, Eurotia ceratoides* and *Artemisia* spp. The area greens up following spring/summer rains, and by early autumn, the vegetation has dried. The snow leopards in our study area prey mainly on Siberian ibex (65–70%), domestic goats (*Capra aegagrus*) and sheep (*Ovis aries*: 20%), and Argali sheep (*Ovis ammon*: 8–9%) (Johansson et al., 2015; Shehzad et al., 2012).

Ibex biology and population demography

Ibex occur in loosely formed groups. Outside of the rut, females with kids and yearlings tend to occur together, with prime-aged males commonly associating in smaller bachelor herds. Younger adult males occur in both female (mixed) and bachelor herds (Mahato & Raziuddin, 2012). Ibex in Tost rut in late October to early November, and kids are born in mid-April to late May. Ibex appear to have a conservative life history compared to many ungulates; in Alpine ibex (*Capra ibex*) primiparity occurs at three to 4 years of age, whereafter approximately only half of the females reproduce in a given year (Rughetti et al., 2015). Males do not start exerting dominance in the rut before 7 years of age (Mahato & Raziuddin, 2012; Willisch & Neuhaus, 2009). Annual survival in a population of Alpine ibex was ~98% for animals aged 2–-8 years (Toigo et al., 2007), whereas all kids survived until autumn, and 92% survived until 1 year of age (Rughetti et al., 2015). We surveyed ibex and classified them into sex and age categories using the double-observer method in a systematic sampling across the study area (Tumursukh et al., 2016) during 2 weeks in late October to early November of 2012, 2013, 2014, 2017, 2019 and 2020. We combined both observers' classifications for groups where the observers were able to classify all individuals while controlling that the total number of ibex did not exceed the group size. Ibex were classified as kids (0–1 year), yearlings (1–2 years), adult females, young males (2–5 years) and prime males (≥6 years) (Han et al., 2020). Males were aged using the approximate length of the horn as assessed in the field and divided into age classes following Schaller (1977), where Classes I–III were grouped as young males and Class IV as prime males. We set the date when ibex changed age class to April 15 based on the first observations of newborn kids in the study area.

Snow leopard captures and kill site visits

We captured 22 snow leopards (12 males and 10 females) in foot-snares and immobilised them with a combination of medetomidine and tiletamine-zolazepam (see Johansson et al., 2013 for details). Captured animals were equipped with GPS collars (North Star King George, Virginia, USA) in 2008–2009 and with GPS-Plus and Vertex Lite collars (Vectronic Aerospace, Berlin, Germany) from 2010 to 2020. The collars were programmed to take a GPS location every 7 h for the North Star and every 5 h for the Vectronic collars. Locations were uplinked via Globalstar or Iridium satellite communication.

We visited clusters of GPS locations (≥2 locations acquired within 24 h and within 100 m distance of each other) and searched for prey remains (see Johansson et al., 2015 for details). The data were collected over 12 periods of cluster visits with a mean length of 104 days (range 21–216 days), yielding a total of 1249 days. The median time between the snow leopard leaving the kill site and our cluster visit was 12 days (mean 18 days, range 1–132 days). To assess whether there were biases in the classification of ibex remains based on the time to cluster visit (i.e. were some categories of ibex likely to be under- or over-represented in our data because of the time taken between the kill and our observation of the kill site), we used a multinomial regression analysis. We likely underestimated the number of kids killed in spring because: (1) it is possible that kids were fully consumed and the snow leopard moved on before at least two GPS locations were acquired to generate a 'kill' cluster; (2) kids still nursing would not leave any significant rumen plant content that was one of the variables typically used for kill detection at a cluster; (3) the young kids we found at clusters were killed in steep, rugged sites that are difficult to search systematically in a safe way, and thus more likely to be overlooked. All ibex carcasses encountered within a cluster area that matched the dates of the cluster, and where there were no indications that the animal had died of other causes, were considered killed by the respective GPS-collared snow leopard. We removed one ibex that was thought to have died of unknown causes because its level of deterioration indicated that it may have died well before the GPS cluster was generated by the collared snow leopard. The sex of the killed ibex was determined using the shape of horns, whereas age was estimated by tooth eruption and wear, the number of horn segments for males, and from horn segments and horn length for females (Schaller, 1977).

Analyses

We estimated snow leopard prey selection of different ibex classes across seasons using Jacobs' index:

$$D = (r_i - p_i)/(r_i + p_i - 2r_i p_i)$$

where r_i is the proportion of the category i among all kills and p_i is the proportion of category i within the population (Hayward, Henschel, et al., 2006; Jacobs, 1974). The resulting values (D) range from −1 to 1 where −1 indicates maximum avoidance and 1 indicates maximum selection preference. To account for uncertainties in these estimates and to assess the probabilities that different age and sex categories of ibex encountered different prey selection strengths, we implemented the model in a Bayesian framework using JAGS (Plummer, 2003), called from R (R Development Core Team, 2023). For this, we generated posterior distributions for different age and sex categories (i.e. kids, yearlings, adult females, young males and prime males) using a multinomial likelihood and weakly informative prior for both the observed ibex kills (r_i) and observed ibex population (p_i) (see Appendix S1 for full model descriptions). Using these posterior distributions, we could directly calculate the Jacobs' index for each ibex age and sex category, and the result was a posterior distribution that included estimation uncertainties and could be used to determine the probability of one index being different from another and the direction and magnitude of this difference (i.e. by calculating the proportion <0 for the between-group posterior distributions).

We first looked at Jacobs' index across the entire year (pooled samples for each category) and for male and female snow leopards separately, before investigating whether there was evidence for seasonal changes in ibex prey selection. For the seasonal analysis, we divided the year into four seasons based on ibex biology: (1) Winter, cold and scarce food supply (Jan-Mar), (2) Spring, here vulnerability may change among categories because females are in late gestation, kids are born and yearlings, with limited experience, are no longer protected by their vigilant mothers as females presumably shift their focus from the yearlings towards optimising neonate security (April to June), (3) Summer, warm temperatures and highest food supply (July to September) and (4) Autumn, ibex congregate in large groups for rutting activities; prime-aged males may be more vulnerable to predation because of reduced vigilance during rut (October to December). To account for an assumed higher proportion of kids in spring than we observed later in the year during our population surveys, we assumed that 50% of the adult ibex females gave birth (based on Rughetti et al., 2015 and our own field observations), yielding a slightly higher proportion of the ibex population being kids than was observed in our autumn population surveys (i.e. 20% in spring and 18.5% in summer). Here, we adjusted our ibex population estimates based on this assumed change in the proportion of kids in the ibex population throughout the year when calculating the Jacobs' index (by directly adjusting the estimated proportion of kids and then rescaling the remaining categories using a correction factor [(1−new kid-proportion) / (1−old kid-proportion)] so they remained in the same relative proportions to each other but all categories summed to 100%); this had some minor influence on the seasonal estimates but did not change the overall prey selection patterns reported.

Results

Ibex population demography

We observed 714 ibex groups during the 6 years of population surveys, totalling 3761 animals (mean group size = 5 ± 4.2 animals; group size range 1–26; summarised in Table 1; raw data in Table S1). Of these, 3545 (94%) could be classified according to age and sex, with 39.3% females, 23.6% young males, 17.7% kids, 11.6% yearlings and 7.8% prime males. The proportions of observed age and sex classes remained relatively stable during the survey years (Fig. S1).

Ibex killed by snow leopards

We recorded 195 ibex killed by snow leopards, and of these, 150 (77%) could be classified according to the age and sex categories used for the ibex population demography surveys (Table 1). The possibility of systematic bias in our ability to classify a carcass in relation to the time elapsed since it was killed was low. Of the carcasses found, 75% were visited within 21 days of the kill (Fig. S2a), and during this time, there was no evidence of changing proportions in the age, sex or unknown carcass classification categories (Fig. 1). The absolute majority, 95% of all carcasses were visited within 50 days of the kill (Fig. S2a), and during this time there were only minor changes in the proportions of kill categories: with a small increase in the number of 'unknown' carcasses and a corresponding decrease in the number of 'prime males' being classified (Fig. S2b). There was no evidence that the smaller categories (kids, yearlings and females) became more difficult to identify at kill sites as time progressed (Fig. S2b).

Table 1 (a) Number and proportion of ibex *Capra sibirica* in different age and sex categories observed in 714 groups in October–November over 6 years in Tost Mountains of Mongolia (kid <1 year-old, yearling 1–2 years old, females ≥2 years old, young males 2–5 years old, prime males ≥6 years). (b) Number of ibex killed by GPS-collared snow leopards *Panthera uncia* that could be classified into the sex and age categories used in population surveys (77% of all kills), the proportions of kills in each category based on the total number of identified kills, and the observed kills disaggregated by season

	Kids	Yearlings	Females	Young males	Prime-age males
(a) *Ibex population surveys*					
Total observed	628	410	1393	837	277
Proportion of population	0.18	0.11	0.39	0.24	0.08
(b) *Ibex carcasses classified*					
Total *n* identified	35	7	44	18	46
Proportion of killed	0.23	0.05	0.29	0.12	0.31
Winter (*n*)	0	0	4	1	3
Spring (*n*)	22	4	27	5	9
Summer (*n*)	8	2	11	6	16
Autumn (*n*)	5	1	2	6	18

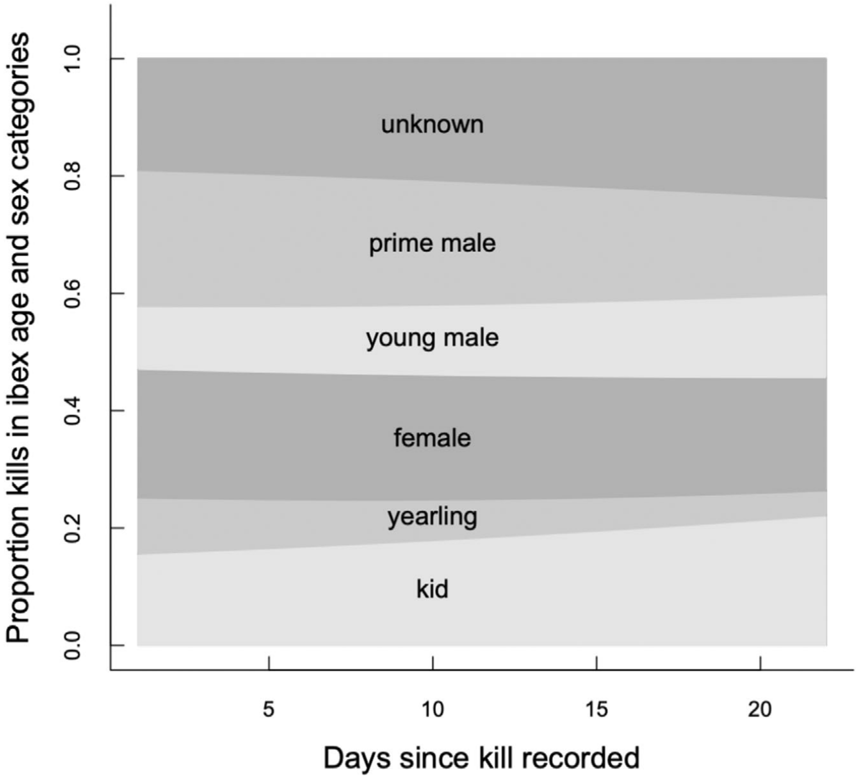

Figure 1 Results from a multinomial regression analysis examining how the proportions of sex and age categories (and unknown) of ibex *Capra sibirica* killed by GPS-collared snow leopards were affected by the time elapsed between the kill and their actual on-site identification. Seventy-five per cent of kill sites were visited within the first 21 days, as shown here, with minimal evidence of systematic bias in identifying and categorising ibex carcass remains (for additional information and analyses, see also Fig. S2).

Snow leopard prey selection for ibex age and sex classes

There was a clear deviation between the observed kills and what would be expected based on prey availability (chi-square [d.f. = 4, $N = 150$] = 121.45, $P < 0.0001$). Based on the Jacobs' index for prey selection, there was a clear selection by snow leopards for prime-aged ibex males (Table 2). The number of prime-aged males identified from kill remains was 46 out of the 150 classified remains (31% of the total), despite them comprising only 7.8% of the ibex population observed during surveys. None of these males were senescent (>13 years old; Toigo et al., 2007; Willisch & Neuhaus, 2009), and the majority (44) were 6–11 years old. Adult females were killed in roughly equal numbers to prime-aged males (approx. 30% of the kills were from each category with the two groups making up about 60% of all the kills), demonstrating the importance of both groups, albeit with varying preferences, as a food source for snow leopards (Table 1). Females, yearlings and young males were hunted at a rate lower than expected based on their proportion in the population, with kids being taken at a rate slightly higher than expected (Table 2).

Seasonal analyses showed that the selection for some age and sex categories changed during the year (Fig. 2, Fig. S3, Table 2). Seasonal selection did not dramatically change within age and sex categories between the summer, autumn and winter (e.g. prime males selected, females and yearlings avoided); however, during spring, prey selection shifted in most categories (Fig. S3, Table 2). Kids were clearly selected for in spring, while in other seasons they were taken in proportion to their abundance in the population. Females were slightly selected for or taken at a rate relative to their population in spring, while they were avoided in other seasons. Young males were clearly avoided in spring and hunted at a rate relative to their population (or slightly lower) in other seasons. Prime-aged males were only slightly selected for in spring, while being strongly selected for in other seasons (Fig. 2, Figs S3 and S4, Table 2). Yearlings were the only group that did not show any obvious change in snow leopard prey selection during the spring relative to other periods (Fig. 2) and showed negative prey selection during all time periods of the year (Fig. S3). The magnitude and probability of a difference in the strength and direction of prey selection between spring and the other seasons for the ibex age and sex categories are shown in Table 2. Snow leopard males and females showed similar strong selection patterns for prime-age male ibex, some evidence of avoidance for females and young male ibex, whereas yearlings were killed in accordance with their relative abundance by snow leopard males and avoided by

Table 2 Selection of different age and sex categories of ibex *Capra sibirica* by snow leopards *Panthera uncia* calculated using Jacobs' index as means ± SD, calculated from the posterior distribution of Bayesian multinomial models for yearly and seasonal estimates. Selection of ibex categories in spring is compared to the other (winter, summer and autumn) seasons, together with the probability of a difference in selection between spring and the other seasons (calculated directly from the Bayesian posterior distribution of the difference between spring and other seasons: that is, the proportion <0)

Jacobs' Index	Kids	Yearlings	Females	Young Males	Prime-age Males
Yearly	0.16 ± 0.09	−0.46 ± 0.15	−0.22 ± 0.08	−0.39 ± 0.1	0.67 ± 0.05
Seasonal					
Winter	−0.91 ± 0.21	−0.88 ± 0.25	0.14 ± 0.31	−0.43 ± 0.37	0.67 ± 0.21
Spring	0.35 ± 0.11	−0.36 ± 0.21	0.02 ± 0.12	−0.58 ± 0.14	0.27 ± 0.16
Summer	−0.02 ± 0.19	−0.47 ± 0.25	−0.30 ± 0.15	−0.31 ± 0.19	0.73 ± 0.07
Autumn	−0.11 ± 0.23	−0.61 ± 0.27	−0.81 ± 0.12	−0.16 ± 0.21	0.87 ± 0.04
Spring versus other seasons					
Other seasons	−0.08 ± 0.14	−0.56 ± 0.19	−0.43 ± 0.11	−0.26 ± 0.14	0.80 ± 0.04
Spring	0.35 ± 0.11	−0.36 ± 0.21	0.02 ± 0.12	−0.58 ± 0.14	0.27 ± 0.16
Diff spring versus other	0.43 ± 0.18	0.20 ± 0.28	0.45 ± 0.16	−0.32 ± 0.20	−0.54 ± 0.17
Probability of difference	0.99	0.75	0.99	0.94	1

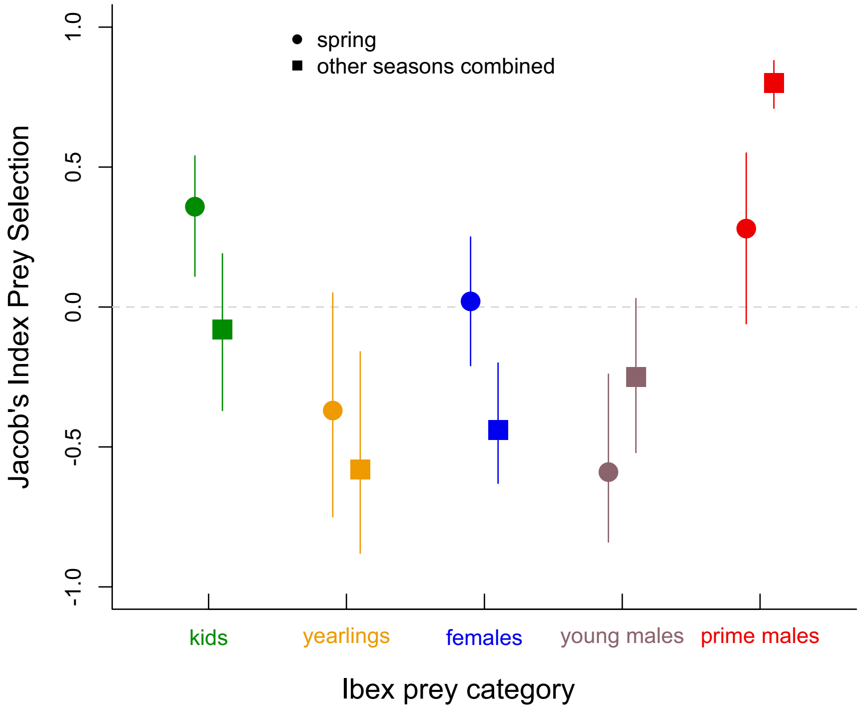

Figure 2 Seasonal variation (spring [filled circles] vs. other seasons [squares]) in the Jacobs' prey selection index for snow leopards *Panthera uncia* as determined for sex and age categories (kids, yearlings, adult females, young males and prime-aged males) of ibex *Capra sibirica* in relation to their observed proportions in the ibex population of the study area. Spring is examined separately because other seasons tended to be similar, with spring as the 'outlier' season (see Fig. S3 for an expanded version of this analysis showing estimates for all four seasons). Here a selection of 0 (grey dotted line) indicates that prey were taken in proportion to their relative abundance in the population. Positive values (0 to 1) demonstrate increasing degrees of prey selection by snow leopards, while negative values (0 to −1) show increasing degrees of prey avoidance. Points represent medians with 95% Bayesian credible intervals. The magnitude of differences in Jacobs' index between seasons for each age and sex class, and the probability that estimated prey selection differs between spring and other seasons, is shown in Table 2.

snow leopard females in the yearly patterns of prey selection (Fig. 3). When looking at seasonal changes (i.e. spring vs. rest of the year), female snow leopards selected for newborn kids in spring, whereas male snow leopards tended to select more for yearlings and female ibex rather than kids during this period (Fig. 3, Fig. S4).

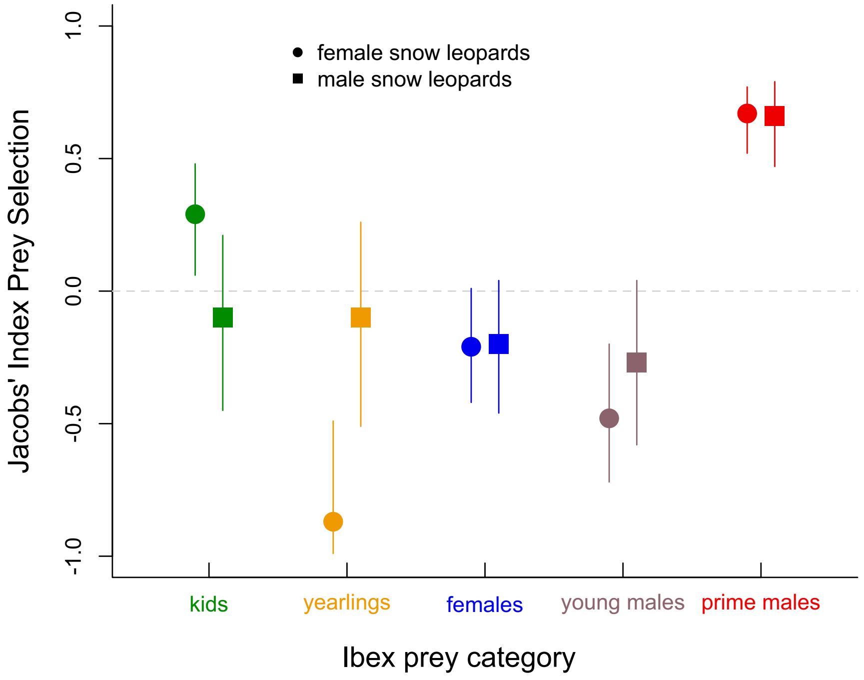

Figure 3 Variation in the Jacobs' prey selection index for male (squares) and female (filled circles) snow leopards, for the different sex and age categories of their ibex prey (kids, yearlings, adult females, young males, prime-aged males) in relation to their observed proportions in the ibex population of the study area. Here, a selection of 0 (grey dotted line) indicates that prey were taken in proportion to their relative abundance in the population. Positive values (0 to 1) demonstrate increasing degrees of prey selection by snow leopards, while negative values (0 to −1) show increasing degrees of prey avoidance. Points represent medians with lines representing 95% Bayesian credible intervals.

Discussion

Snow leopards showed strong positive prey selection for the largest of all ibex categories, prime-aged males, which are at least twice their own body mass. During spring, the prey preference of female snow leopards shifted towards the smallest ibex category, kids, while male snow leopards increased their preference for female ibex. This general pattern of preferring prey much larger than themselves is in contrast to the general patterns observed in other large felids that typically select prey that is smaller than or similar to their own body mass. These results show that snow leopards are dynamic predators that adjust their prey selection seasonally and that this may be driven by seasonal variation in prey vulnerability.

Selection patterns and prey agility

Predators are expected to select the prey that provides the highest energetic exchange; energy gained from consumption minus energy expended searching for and handling the prey (Stephens & Krebs, 1986; Sunquist & Sunquist, 1989). While the prime-aged male ibex provide more biomass than the young males (average weights 90 kg vs. 55 kg respectively) there is a relatively small difference in handling time at the carcass (66 h vs. 51 h on average for prime aged and young males respectively; Tallian et al., 2023), implying that the snow leopards only utilise parts of the extra energy available. Young male ibex provide the second highest biomass of all prey categories, and despite this, prey selection was negative or neutral for this category and consistently lower than prey selection for prime males in all seasons. This suggests that prime-aged ibex males are selected for (i.e. they are a desired prey) not because they offer more biomass, but because they are more vulnerable to the hunting strategies of the snow leopard. Wolves hunting large prey such as moose (*Alces alces*) commonly select the more vulnerable juvenile and senescent prey, with selection primarily being driven by intrinsic differences in vulnerability rather than maximising intake rate per kill (e.g. Hoy et al., 2021). Several large carnivores have been reported to select for male ungulates during the rut when the males are exposed, or after mating when they are in poor body condition (Knopff et al., 2010; Owen-Smith, 2008). However, this does not appear to explain the selection of ibex males by snow leopards, as they were strongly selected for in all seasons except spring (where the strength of selection was still positive but weaker for female snow leopards). In contrast to general reproductive behavioural patterns in ungulates, ibex males engage in a lower effort reproductive strategy where most fights occur prior to the rut, thereby establishing social dominance (Willisch & Neuhaus, 2010). This allows males not to deplete reserves prior to winter, which may be a necessary adaptation to the low primary production in dry alpine habitats, and perhaps also allows the males to maintain a higher vigilance during the rut compared to males in other species. During the rut, ibex congregate in large herds for a couple of weeks, where access to receptive females is determined by social dominance; here, sexual selection favours males with the largest body sizes and horns (Willisch & Neuhaus, 2010).

Ibex utilise crags and steep slopes as escape terrain where they can outmanoeuvre predators (Fox et al., 1992; Schaller, 1977). However, snow leopards are adapted to hunt in such terrain. Therefore, the agility of individual ibex is expected to play a crucial role in determining whether it can escape from a snow leopard ambush and chase. Sexual selection pressure resulting in relatively large body and horn sizes in male ibex presumably imposes costs in terms of reduced agility in the mountains (possibly even a sexually selected 'handicap'; Zahavi, 1975). This likely makes prime males more vulnerable to snow leopard predation than the other age and sex categories, resulting in the high selection of prime males we observed in our study. Thus, while large body size and weapons in males may limit predation risk in some species (Mattisson et al., 2014; Metz et al., 2018), these traits appear to increase the vulnerability of prime-age male ibex to snow leopard predation.

While females were never strongly selected for, they did experience higher selection in spring compared to the rest of the year, especially from male snow leopards (Table 2, Fig. 2, Fig. S4). This could be explained using the agility hypothesis as resulting from decreased agility of gravid female ibex during late gestation (and can also be seen in the 'winter' results in Fig. 2, where the higher kills on female ibex occurred in March, just before the calving). Our results also showed a seasonal change in prey preference by female snow leopards selecting for ibex kids during and immediately after the birthing season, and male snow leopards showing higher prey preferences for yearlings and adult females. This change of hunting preference is likely related to the reduced preference observed for prime males during the same time period (Fig. 2, Fig. S4). While it is common that predators hunt neonates, not many studies have found a positive frequency selection for them as seen in our spring results (but see Reimer et al., 2019). Ibex kids are highly vulnerable in the first months, perhaps because they are not fast and experienced enough to escape snow leopards in steep terrain, increasing the profitability for the predator in hunting them despite their low biomass. It appears that once the kids are 2–3 months old (63% of the kids found at clusters were killed in April to June), they are no longer as vulnerable and selection for them decreases to neutrality.

It should be noted that we did not have perfect knowledge of the ibex population across all seasons, and here we have had to make some assumptions. The proportions of ibex age classes are likely to show some annual variation, which we could not capture with our yearly population assessments in October to November. We expect that this variation largely occurs between spring and the other seasons, when kids are born and individuals shift into new age classes (e.g. kids to yearlings, yearlings to adults). We attempted to account for these shifts by looking at what is known about ibex reproduction to adjust the proportion of kids in the spring population upwards (Rughetti et al., 2015); however, this did not have any appreciable effect on our results as compared to when we used a single population structure across the year.

Implications for snow leopard morphology and ibex demography

Sexual selection is typically invoked as an explanation for the size difference between males and females in mammal species (Lande, 1980). Even though snow leopard males are larger than females (42 ± 4 kg and 36 ± 3 kg respectively with similar sizes throughout their distribution range; Johansson et al., 2022) the species show relatively lower sexual dimorphism compared to other large felids (Sunquist & Sunquist, 2002). A possible limit to sexual size dimorphism in snow leopard males may result from the need to maintain agility to hunt effectively in mountainous terrain. This would explain why female snow leopards showed the same positive selection for the prime-age ibex males, a prey almost three times their weight. Snow leopards use ambush direction (from above) and the topography of the landscape to their advantage when hunting large prey (Johansson et al., 2024). Here, the downward momentum likely helps knock the prey off balance, and predator body mass is less influential for hunting success compared to predators hunting in flatter landscapes. Thereby, the mountainous terrain imposes the same body mass constraints on ibex and snow leopards, although their mating systems differ; snow leopards require agility to hunt, while ibex males trade off the agility needed to escape snow leopard predation with sexually selected body and horn size to dominate other males and secure matings.

Slow life-history species such as the ibex, characterised by a lower fecundity, older age at first reproduction and longer life expectancy, are often sensitive to changes in adult survival (Gaillard et al., 1998). Thus, snow leopard preferences for prime-age males (year round) and females (somewhat in spring) may play a significant role in regulating ibex populations. It is also possible that disproportionate predation on prime-age male ibex impacts their social system, with fewer prime-aged males co-occurring with females during the rut. There are trophy hunting programmes involving ibex in snow leopard habitats of countries such as Mongolia, Kyrgyzstan and Tajikistan (Michel et al., 2024; Reading & Amgalanbaatar, 2024). The high predation pressure of snow leopards on prime-aged males must be considered when calculating quotas for trophy hunting programmes, as the snow leopards and trophy hunters prefer the same category of prey (Boukal et al., 2008; Reading & Amgalanbaatar, 2024).

Our results are in contrast to previous work suggesting that snow leopards avoid prime-aged males and select prey weighing 36–76 kg (corresponding to yearlings, adult females and young males) with an optimum at 55 kg (corresponding to young males) (Lyngdoh et al., 2014). We found that snow leopards avoided ibex in the 36–76 kg range, with similar negative Jacobs' index values throughout the year (Table 2). Lyngdoh et al.'s (2014) review analysed snow leopard faeces to assess diet and could not categorise ibex prey into their age and sex categories. Using average prey weights for analysis seems to have led to the incorrect conclusion that snow leopards select for intermediate-sized ibex (Lyngdoh et al., 2014), when, in fact, they select ibex of the largest and smallest weight categories.

Studies that directly calculate intraspecific prey selection are rare, not only because many species are difficult to age accurately from a distance (Annear et al., 2023) but also because predation must be assessed by classifying kills using direct observations. Our study is unusual as it provides detailed knowledge that improves our understanding of prey selection by an elusive species across both seasonal and age and sex categorisation of its prey. In addition, the mechanism we propose by which the snow leopard selects its prey based largely on agility constraints suggests it likely imposes limits on sexual selection for body size in ibex males and possibly also limits sexual dimorphism in snow leopards.

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Author contributions

ÖJ, CM and PL conceived the ideas and designed methodology; ÖJ, GS and JSA collected the data; ML and ÖJ analysed the data; ÖJ, ML and CM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest

The authors declare no conflict of interest.

References

Annear, E., Minnie, L., Andrew, K., & Kerley, G. I. (2023). Can smaller predators expand their prey base through killing juveniles? The influence of prey demography and season on prey selection for cheetahs and lions. *Oecologia*, **201**, 649–660.

Boukal, D. S., Berec, L., & Křivan, V. (2008). Does sex-selective predation stabilize or destabilize predator-prey dynamics? *PLoS One*, **3**, e2687.

Christe, P., Keller, L., & Roulin, A. (2006). The predation cost of being a male: Implications for sex-specific rates of ageing. *Oikos*, **114**, 381–384.

Fedosenko, A. K., & Blank, D. A. (2001). *Capra sibirica*. *Mammalian Species*, **675**, 1–13.

Fox, J. L., Sinha, S. P., & Chundawat, R. S. (1992). Activity patterns and habitat use of ibex in the Himalaya mountains of India. *Journal of Mammalogy*, **73**, 527–534.

Gaillard, J.-M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, **13**, 58–63.

Ginsberg, J. R., & Milner-Gulland, E. (1994). Sex-biased harvesting and population dynamics in ungulates: Implications for conservation and sustainable use. *Conservation Biology*, **8**, 157–166.

Han, L., Blank, D., Wang, M., & Yang, W. (2020). Vigilance behaviour in Siberian ibex (*Capra sibirica*): Effect of group size, group type, sex and age. *Behavioural Processes*, **170**, 104021.

Hayward, M. W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., & Kerley, G. I. H. (2006). Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology*, **270**, 298–313.

Hayward, M. W., Hofmeyr, M., O'Brien, J., & Kerley, G. I. H. (2006). Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): Morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *Journal of Zoology*, **270**, 615–627.

Hayward, M. W., Jędrzejewski, W., Jêdrzejewska, B., & Kitchener, A. (2012). Prey preferences of the tiger *Panthera tigris*. *Journal of Zoology*, **286**, 221–231.

Hornocker, M. G. (1970). An analysis of mountain lion predation upon mule deer and elk in the Idaho primitive area. *Wildlife Monographs*, **21**, 3–39.

Hoy, S. R., MacNulty, D. R., Metz, M. C., Smith, D. W., Stahler, D. R., Peterson, R. O., & Vucetich, J. A. (2021). Negative frequency-dependent prey selection by wolves and its implications on predator–prey dynamics. *Animal Behaviour*, **179**, 247–265.

Jacobs, J. (1974). Quantitative measurement of food selection: A modification of the forage ratio and Ivlev's electivity index. *Oecologia*, **14**, 413–417.

Jędrzejewski, W., Schmidt, K., Milkowski, L., Jędrzejewska, B., & Okarma, H. (1993). Foraging by lynx and its role in ungulate mortality: The local (Bialowieza Forest) and the Palaearctic viewpoints. *Acta Theriologica*, **38**, 385–403.

Johansson, Ö., Agvaantseren, B., Jackson, R., Kachel, S., Kubanychbekov, Z., McCarthy, T., Mishra, C., Ostrowski, S., Kulenbekov, R., Madad Rajabi, A., & Subba, S. (2022). Body measurements of free-ranging snow leopards across their range. *Snow Leopard Reports*, **1**, 1–6.

Johansson, Ö., Malmsten, J., Mishra, C., Lkhagvajav, P., & McCarthy, T. (2013). Reversible immobilization of free-ranging snow leopards (*Panthera uncia*) with a combination of medetomidine and tiletamine-zolazepam. *Journal of Wildlife Diseases*, **49**, 338–346.

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

Johansson, Ö., Nyam, E., Lkhagvajav, P., Alexander, J. S., & Samelius, G. (2024). Predation patterns and hunting behavior of snow leopards: Insights from an ibex hunt. *Snow Leopard Reports*, **2**, 6–9.

Knopff, K. H., Knopff, A. A., Kortello, A., & Boyce, M. S. (2010). Cougar kill rate and prey composition in a multiprey system. *Journal of Wildlife Management*, **74**, 1435–1447.

Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, **34**, 292–305.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.

Lyngdoh, S., Shrotriya, S., Goyal, S. P., Clements, H., Hayward, M. W., & Habib, B. (2014). Prey preferences of the snow leopard (*Panthera uncia*): Regional diet specificity holds global significance for conservation. *PLoS One*, **9**, e88349.

Mahato, A. K. R., & Raziuddin, M. (2012). *Handbook of the mammals of the world. 2: Hoofed mammals*. Lynx Edicions.

Mattisson, J., Arntsen, G. B., Nilsen, E. B., Loe, L. E., Linnell, J. D. C., Odden, J., Persson, J., & Andrén, H. (2014). Lynx predation on semi-domestic reindeer: Do age and sex matter? *Journal of Zoology*, **292**, 56–63.

Metz, M. C., Emlen, D. J., Stahler, D. R., MacNulty, D. R., Smith, D. W., & Hebblewhite, M. (2018). Predation shapes the evolutionary traits of cervid weapons. *Nature Ecology & Evolution*, **2**, 1619–1625.

Metz, M. C., Smith, D. W., Vucetich, J. A., Stahler, D. R., & Peterson, R. O. (2012). Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *The Journal of Animal Ecology*, **81**, 553–563.

Michel, S., Rosen, T., & Kubanychbekov, Z. (2024). Hunting of a prey species - a review of lessons, successes, and pitfalls: Experiences from Kyrgyzstan and Tajikistan. In D. M. T. McCarthy (Ed.), *Snow leopards* (pp. 265–274). Academic Press.

Mukherjee, S., & Heithaus, M. R. (2013). Dangerous prey and daring predators: A review. *Biological Reviews of the Cambridge Philosophical Society*, **88**, 550–563.

Murdoch, W. W. (1969). Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecological Monographs*, **39**, 335–354.

Owen-Smith, N. (2008). Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos*, **117**, 602–610.

Packer, C. (1986). The ecology of sociality in felids. In D. I. Rubenstein and R. W Wrangham (Eds.), *Ecological aspects of social evolution: Birds and Mammals* 429–451, Princeton University Press.

Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. The 3rd international workshop on distributed statistical computing (DSC 2003), pp. 1-8. Vienna.

R Development Core Team, R. (2023). *R: A language and environment for statistical computing*. R foundation for statistical computing.

Reading, R. P., & Amgalanbaatar, S. (2024). Argali sheep (*Ovis ammon*) and Siberian ibex (*Capra sibirica*) trophy hunting in Mongolia. In D. Mallon & T. McCarthy (Eds.), *Snow leopards* (pp. 259–264). Academic press.

Reimer, J. R., Brown, H., Beltaos-Kerr, E., & de Vries, G. (2019). Evidence of intraspecific prey switching: Stage-structured predation of polar bears on ringed seals. *Oecologia*, **189**, 133–148.

Rughetti, M., Dematteis, A., Meneguz, P. G., & Festa-Bianchet, M. (2015). Age-specific reproductive success and cost in female Alpine ibex. *Oecologia*, **178**, 197–205.

Sand, H., Wabakken, P., Zimmermann, B., Johansson, O., Pedersen, H. C., & Liberg, O. (2008). Summer kill rates and predation pattern in a wolf-moose system: Can we rely on winter estimates? *Oecologia*, **156**, 53–64.

Schaller, G. B. (1977). *Mountain monarchs. Wild sheep and goats of the Himalaya*. University of Chicago Press.

Shehzad, W., McCarthy, T. M., Pompanon, F., Purevjav, L., Coissac, E., Riaz, T., & Taberlet, P. (2012). Prey preference of snow leopard (*Panthera uncia*) in south Gobi, Mongolia. *PLoS One*, **7**, e32104.

Sinclair, A. R., Mduma, S., & Brashares, J. S. (2003). Patterns of predation in a diverse predator–prey system. *Nature*, **425**, 288–290.

Stephan, J. G., Low, M., Stenberg, J. A., & Björkman, C. (2016). Predator hunting mode and host plant quality shape attack-abatement patterns of predation risk in an insect herbivore. *Ecosphere*, **7**, e01541.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory.* Princeton University Press.

Sunquist, M. E., & Sunquist, F. C. (1989). Ecological constraints on predation by large felids. In J. L Gittleman (Ed.), *Carnivore Behavior, Ecology, and Evolution*, 283–301. Springer.

Sunquist, M. E., & Sunquist, F. C. (2002). *Wild cats of the world*. University of Chicago press.

Tallian, A., Mattisson, J., Samelius, G., Odden, J., Mishra, C., Linnell, J. D. C., Lkhagvajav, P., & Johansson, Ö. (2023). Wild versus domestic prey: Variation in the kill-site behavior of two large felids. *Global Ecology and Conservation*, **47**, e02650.

Tallian, A., Smith, D. W., Stahler, D. R., Metz, M. C., Wallen, R. L., Geremia, C., Ruprecht, J., Wyman, C. T., MacNulty, D. R., & Costa, D. (2017). Predator foraging response to a resurgent dangerous prey. *Functional Ecology*, **31**, 1418–1429.

Taylor, R. J. (1984). *Predation theory. Predation* (pp. 6–23). Springer, Boston, MA..

Toigo, C., Gaillard, J. M., Festa-Bianchet, M., Largo, E., Michallet, J., & Maillard, D. (2007). Sex- and age-specific survival of the highly dimorphic alpine ibex: Evidence for a conservative life-history tactic. *The Journal of Animal Ecology*, **76**, 679–686.

Tumursukh, L., Suryawanshi, K. R., Mishra, C., McCarthy, T. M., & Boldgiv, B. (2016). Status of the mountain ungulate prey of the endangered snow leopard *Panthera uncia* in the Tost local protected area, south Gobi, Mongolia. *Oryx*, **50**, 214–219.

Willisch, C. S., & Neuhaus, P. (2009). Alternative mating tactics and their impact on survival in adult male alpine ibex (*Capra ibex ibex*). *Journal of Mammalogy*, **90**, 1421–1430.

Willisch, C. S., & Neuhaus, P. (2010). Social dominance and conflict reduction in rutting male alpine ibex, *Capra ibex*. *Behavioral Ecology*, **21**, 372–380.

Zahavi, A. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Bayesian formal model description.

Figure S1. Observed proportions of the surveyed ibex population in relation to different age and sex categories from 2012 to 2020.

Figure S2. Time in days from when an ibex was killed (as determined by snow leopard GPS locations) to field confirmation and classification of the carcass.

Figure S3. Seasonal variation in the Jacobs' prey selection index as determined for ibex sex and age categories (kids, yearlings, adult females, young males, prime-age males) in relation to their observed proportions of the local ibex population.

Figure S4. Seasonal variation in the Jacobs' prey selection index for spring (filled circles) and other seasons combined (filled squares) for snow leopard females (panel a) and males (panel b) as determined for ibex sex and age categories (kids, yearlings, adult females, young males, prime-age males) in relation to their observed proportions of the local ibex population.

Table S1. Number of ibex seen in population surveys conducted in October and November of 2012, 2013, 2014, 2017, 2019 and 2020 in Tost Mountains divided in age and sex categories and the proportion of each category compared to total number of ibex seen.