



## Wild versus domestic prey: Variation in the kill-site behavior of two large felids

Aimee Tallian<sup>a,b,\*</sup>, Jenny Mattisson<sup>a</sup>, Gustaf Samelius<sup>c,d</sup>, John Odden<sup>e</sup>,  
Charudutt Mishra<sup>c,f</sup>, John D.C. Linnell<sup>a,g</sup>, Purevjav Lkhagvajav<sup>h</sup>,  
Örjan Johansson<sup>b,c</sup>

<sup>a</sup> Norwegian Institute for Nature Research, PO Box 5685 Torgarden, NO-7485 Trondheim, Norway

<sup>b</sup> Grimsö Wildlife Research Station, Department of Ecology, Swedish University of Agricultural Sciences, SE-739 93 Riddarhyttan, Sweden

<sup>c</sup> Snow Leopard Trust, 4649 Sunnyside Avenue North, Seattle, USA

<sup>d</sup> Nordens Ark, Åby säteri, 456 93 Hunnebostrand, Sweden

<sup>e</sup> Norwegian Institute for Nature Research, Sognsveien 68, NO-0855 Oslo, Norway

<sup>f</sup> Nature Conservation Foundation, 3076/5, IV Cross, Gokulam Park, Mysore, India

<sup>g</sup> Inland Norway University of Applied Sciences, Department of Forestry and Wildlife Management, Anne Evenstads vei 80, NO-2480 Koppang, Norway

<sup>h</sup> Snow Leopard Conservation Foundation, Khan-Uul Tower, 6th floor, room 602, Khoroo 3, Khan-Uul District, Ulanbaatar, Mongolia

### ARTICLE INFO

#### Keywords:

Eurasian lynx  
Handling time  
Landscape  
Livestock  
Predation  
Snow leopard

### ABSTRACT

Livestock depredation is an important source of conflict for many terrestrial large carnivore species. Understanding the foraging behavior of large carnivores on domestic prey is therefore important for both mitigating conflict and conserving threatened carnivore populations. Handling time is an important, albeit often overlooked, component of predatory behavior, as it directly influences access to food biomass, which can affect predator foraging efficiency and subsequent kill rates. We used long-term data on snow leopards (*Panthera uncia*) in Mongolia (Asia) and Eurasian lynx (*Lynx lynx*) in Norway (Europe) to examine how large carnivore foraging patterns varied between domestic and wild prey, and how the different landscape characteristics affected those patterns. Our results suggest handling time was generally shorter for domestic compared to wild prey. For snow leopards, rugged terrain was linked to increased handling time for larger prey. For lynx, handling time increased with terrain ruggedness for domestic, but not wild, prey, and was greater in closed compared to open habitats. There were also other differences in snow leopard and lynx foraging behavior, e.g., snow leopards also stayed longer at, and remained closer to, their kill sites than lynx. Shorter handling time suggests that felids may have utilized domestic prey less effectively than wild prey, i.e., they spent less time consuming their prey. This could a) result in an energetic or fitness cost related to decreased felid foraging efficiency caused by the risk of anthropogenic disturbance, or b) exacerbate conflict if reduced handling time associated with easy prey results in increased livestock depredation.

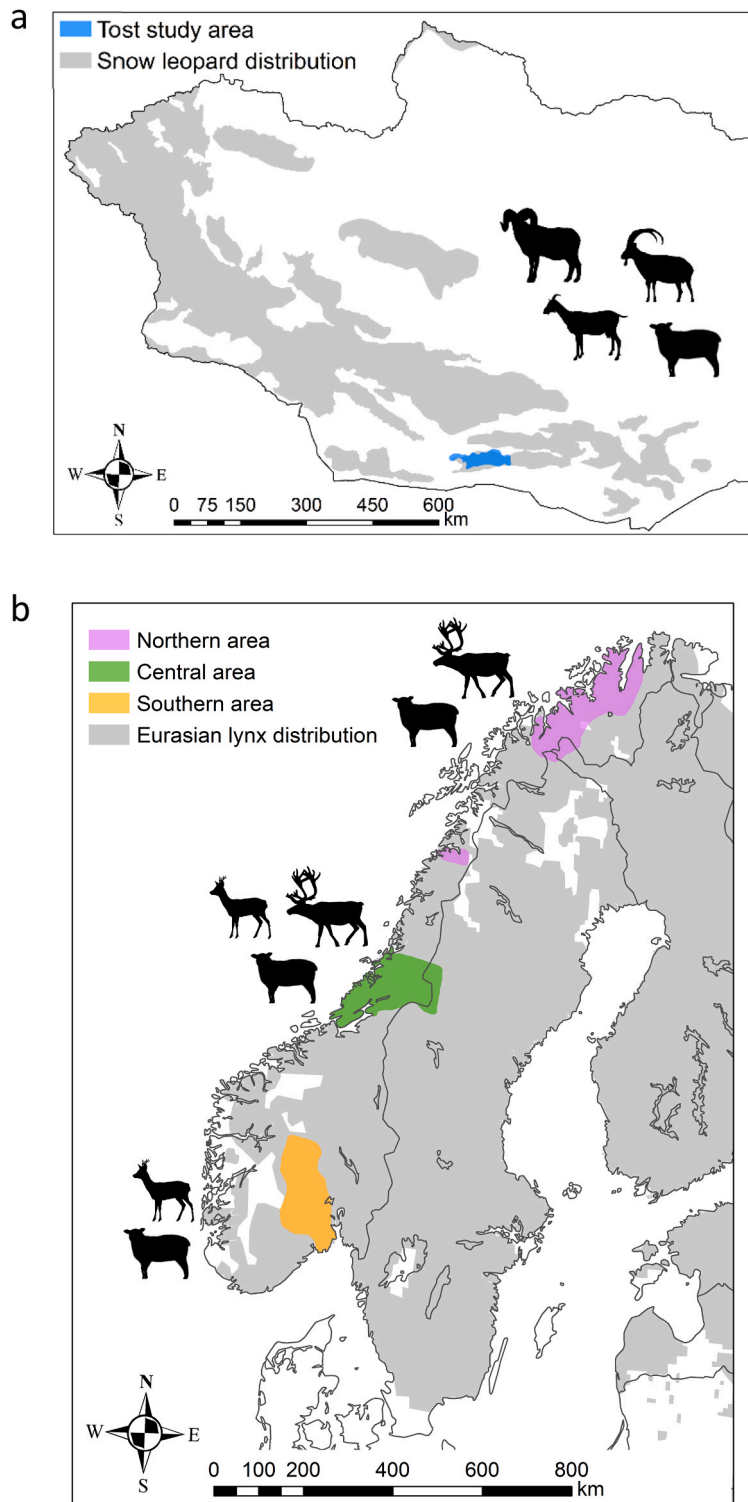
\* Corresponding author at: Norwegian Institute for Nature Research, PO Box 5685 Torgarden, NO-7485 Trondheim, Norway  
E-mail address: [aimee.tallian@nina.no](mailto:aimee.tallian@nina.no) (A. Tallian).

<https://doi.org/10.1016/j.gecco.2023.e02650>

Received 11 January 2023; Received in revised form 19 September 2023; Accepted 19 September 2023

Available online 20 September 2023

2351-9894/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).



**Fig. 1.** Maps of the study areas in Mongolia (a) and Norway (b) with snow leopard and Eurasian lynx distributions shown in grey, respectively. The northern (purple: reindeer/sheep), central (green: reindeer/sheep/roe deer), and southern (orange: sheep/roe deer) study areas Scandinavia (a), and the Tost Mountain study areas (blue: Argali sheep/ibex/sheep/goat/other livestock) are shown alongside the prey species available in the area.

## 1. Introduction

Although some large carnivore populations have recovered in certain parts of the world (Bruskotter and Shelby, 2010; Chapron et al., 2014), many remain severely threatened largely due to habitat loss, the depletion of wild prey, and negative human-wildlife interactions, i.e., often stemming from diverse conflict (Ripple et al., 2014). Livestock depredation remains one of the most important sources of conflict for most terrestrial large carnivore species (Kaczensky, 1999; Linnell et al., 2012). Thus, understanding the foraging patterns of large carnivores on domestic prey is important for both conflict mitigation and long-term carnivore management and conservation. It is well understood that preference for domestic prey varies with ecological context. For example, preference for domestic prey may increase with their relative availability on the landscape or decrease in areas that employ effective herding and guarding techniques (Linnell et al., 1999; Khorozyan et al., 2015; Ghoddousi et al., 2016). Yet, less is known about how carnivores handle domestic prey once they have killed them. This is important as the ability of carnivores to access their kills is key to individual survival and population-level growth.

Handling time, or “the sum of time spent attacking and capturing a prey and consuming and digesting the kill” (Mukherjee and Heithaus, 2013; Tallian et al., 2021), is an important, yet often overlooked, component of predation. Handling time partially drives predator kill rate, which is a fundamental measure of predation across taxa and systems. Furthermore, the amount of time carnivores spend handling their prey directly influences their access to food biomass. Large carnivores invest a vast amount of time and energy searching for and killing prey (Mukherjee and Heithaus, 2013), and unrestricted access to their kills is needed to make their energetic investment worthwhile (Elbroch et al., 2014b). For example, kleptoparasitism, or the loss of kills to other predators/scavengers, has been shown to have serious energetic consequences for several species (van der Meer et al., 2011; Hilborn et al., 2018). Handling time is thus a key measurement of predation, as the ability of carnivores to acquire food can alter overall foraging efficiency and predation patterns (Krofel et al., 2012; Elbroch et al., 2014a; Tallian et al., 2021) as well as influence individual body condition and reproductive success (Walton et al., 2017), key factors influencing long-term population growth and survival.

Large carnivores may handle domestic prey differently than wild prey. For example, handling domestic prey may be riskier due to the increased potential, or increased perceived potential, for human disturbance and retaliation. Mountain lions (*Puma concolor*) are more likely to flee, and take longer to return to, a kill site when people are nearby, which reduces their feeding time and increases subsequent kill rates (Smith et al., 2015; Smith et al., 2017). Amur tigers (*Panthera tigris altaica*) also reportedly abandon their kills more quickly in response to human disturbance, resulting in overall reduced foraging efficiency (Kerley et al., 2002). Alternatively, handling times may be shorter in environments with a high density of domestic prey (Cook and Cockrell, 1978), as domestic livestock are often easier to kill than wild prey species. Furthermore, landscape characteristics provide escape terrain and refugia that can reduce disturbance for predators and moderate risk for prey (Gorini et al., 2012). While a wealth of research addresses the trade-off between foraging and mitigating landscape-specific risk for prey (e.g., Brown, 1999; Atwood et al., 2009; Atwood et al., 2018; Kohl et al., 2019), we still know little about how landscape features drive the foraging behavior of large carnivores. Our goal was to explore whether handling time was different for domestic versus wild prey and see how the landscape affected that relationship.

The snow leopard (*Panthera uncia*) occurs in the mountain ecosystems of Southern and Central Asia, while the Eurasian lynx (*Lynx lynx*) is distributed across the temperate northern hemisphere in Eurasia. Long-term data on the predatory behavior of these two species in Mongolia and Norway, respectively, represent an opportunity to compare how two felids, occurring in different habitats in which free-ranging livestock occur, adjust their foraging behavior when preying on domestic versus wild prey. A deeper understanding of how foraging patterns vary between wild and domestic prey will advance predator-prey theory, and improve predictions of interactions between felids, prey, and competitors in human-dominated landscapes, helping inform conservation and management decisions.

We used GPS-derived movement and predation data from two long-term studies on snow leopard in the Tost Mountains of Mongolia (2010–2020) and lynx across Norway (2009–2016) to examine how felid foraging behavior varied between domestic and wild prey species. We expected snow leopards and lynx would spend less time handling domestic compared to wild prey due to the potentially increased risk of human disturbance near domestic prey. We also expected landscape characteristics would be important drivers of prey handling time for both species. Because rugged terrain provides better escape routes and more refugia than flat terrain (Rauset et al., 2013; Kusler et al., 2017), we expected snow leopards and lynx handling time would increase as the terrain became more rugged. Compared to the mostly open, barren, and roadless terrain of the Tost Mountains, lynx in Scandinavia persist in a mixed landscape of open alpine tundra and boreal forest. Cover is known to increase felid handling time (Mattisson et al., 2011a; Leighton et al., 2021), while proximity to roads is linked to increased risk of mortality (Sunde et al., 1998; Basille et al., 2013). We therefore also expected lynx handling time would be greater in closed compared to open habitats, and when kill sites were farther from roads.

## 2. Materials and methods

### 2.1. Study areas

#### 2.1.1. Mongolia

The study on snow leopards was conducted in the Tost Mountains (~1700 km<sup>2</sup>) in southern Mongolia (Fig. 1a). The Tost Mountains consist of several rugged mountain massifs traversed by valleys and canyons, and the elevation ranges between 1800 and 2500 m. While the elevation range is modest, the mountains rise steeply from the surrounding desert steppe (Sheehy and Damiran, 2012) and the many crisscrossing crevices and canyons create highly rugged terrain. Annual precipitation measures less than 130 mm per year, and the temperature ranges between -35 °C in winter and 40 °C in summer. Approximately 90 semi-nomadic herder families live in

the study area. Local nomadic herders relocate their camps 2–4 times per year, with most herders staying in the mountains during winter (early November to late March), and in the surrounding desert steppes during the rest of the year (Mijiddorj et al., 2018). The sparse vegetation consists mainly of short grasses, dwarf shrubs, and patches of shrubs dominated by *Amygdalus mongolica*, *Stipa* spp., *Caragana leucophlaea* and *Eurotia ceratoides*.

Wild prey include Siberian ibex (*Capra sibirica*), Argali sheep (*Ovis ammon*), black-tailed gazelle (*Gazella subgutturosa*), and various lagomorphs, rodents, and birds. The domestic prey available include livestock whose abundance may vary seasonally; ~32,000 goats (*Capra aegagrus*) and domestic sheep (*Ovis aries*), ~1100 camels (*Camelus bactrianus*), and ~300 horses (*Equus ferus caballus*). Sheep and goats are herded by their owners during the day, and are enclosed in holding pens during night, while camels and horses free-range across the landscape. Snow leopard diets here are dominated by ibex (~65%), but also include argali (~10%) and goats and sheep (~20%) (Johansson et al., 2015). Snow leopards in the Tost Mountains co-occur with wolves (*Canis lupus*), Eurasian lynx, red foxes (*Vulpes vulpes*), martens (*Martes* spp.), and a host of obligate and facultative avian scavengers.

### 2.1.2. Norway

The study on lynx was carried out in three regions in Norway; hereafter the northern (Troms og Finnmark and Nordland counties), central (northern part of Trøndelag county), and southern (Buskerud, Vestfold and Telemark counties) study areas (Fig. 1b). The climate in the northern study area is generally coastal alpine, while a more continental climate prevails in the central and southern study areas. The northern study area is dominated by alpine tundra, with mountain birch forest (*Betula pubescens*) dominating below tree line and patches of pine forest (*Pinus sylvestris*) interspersed throughout. The central and southern regions are conifer (*Pinus sylvestris*, *Picea abies*) dominated boreal forest, which is interspersed with bogs, mires, and open cultivated land. Snow persists across all regions from November through May, and clear-cut forestry practices create a mosaic of even-aged stands throughout the forested study areas in Norway.

Ungulate prey species in Norway are a mix between wild and domestic prey at varying densities. In Norway, most livestock are free ranging. Sheep are released from farms around June, and they roam with very limited supervision, no guardian animals, and few constraints on their movements, until they are rounded up around September and corralled for winter (Kaczensky, 1999; Mabile et al., 2015). However, the density and distribution of sheep varies considerably between and within the study areas. In the north and central part of Norway, reindeer (*Rangifer tarandus*) are semi-domestic, while several wild reindeer populations can be found in the mountain areas of southern Norway. Semi-domestic reindeer are free-ranging year-round, but are actively herded between winter and summer ranges, as well as gathered by their owners several times a year for calf marking and slaughtering events. Herding is not intensive between these events, although there is irregular supervision of the herds.

Ungulate prey species composition differed between the three study areas. In the northern study area, only semi-domestic reindeer persist on the tundra year around, although the western (coastal) parts of this area are almost completely devoid of reindeer during winter (Mattisson et al., 2011b). Sheep are present during summer in some areas. In the central study area, semi-domestic reindeer and domestic sheep co-occur with roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). The southern study area has domestic sheep, roe deer, red deer, and some wild reindeer near the western boundary. Other prey for lynx in all areas include mountain hare (*Lepus timidus*), black grouse (*Lyrurus tetrix*), capercaillie (*Tetrao urogallus*), ptarmigan (*Lagopus* spp.), other small birds and mammals, and more rarely, moose calves (*Alces alces*). In Norway, lynx co-occur with wolverines (*Gulo gulo*), wolves, occasionally brown bears (*Ursus arctos*), and other smaller terrestrial and facultative avian scavengers.

## 2.2. Data collection

### 2.2.1. Snow leopard

Snow leopard predation studies were conducted in the Tost Mountains between 2010 and 2020. Snow leopards were captured using modified foot-snares, and anaesthetized and fitted with a GPS-Plus or Vertex Lite collar (Vectronic Aerospace, Berlin, Germany). We obtained all relevant permits for conducting research and capturing and collaring snow leopard from Mongolia's Ministry for Environment and Green Development. Animal handling followed appropriate ethical standards, and was approved by the Board for Animals in Research and Teaching at the Swedish University of Agricultural Sciences (permit SLU-ua-2020.4.1–2295). Collars were programmed to take locations every 5 h. We followed 18 individual snow leopards (M = 9, F = 9) over multiple years (Table S1a). Field crews searched intensively for carcasses at all 'clustered' GPS points (defined as >2 positions within 100 m in 24 h) and recorded cause of death, species, age (calf, yearling, adult), and sex (see Johansson et al., 2015 for further methodology). Ungulate prey species were identified based on prey remains such as fur, feet, and skulls. Age was estimated by counting annular rings of the horns for ibex and argali > 2 years, from horn-length for ibex and argali (<2 years), and tooth wear and eruption for all species. We calculated a terrain ruggedness index (TRI) at each kill site using 6 × 6 m resolution digital elevation models (Intermap Technologies) and the 'terrain' function in the 'raster' package in R version 3.6–20 (Hijmans et al., 2023). The terrain 'TRI' function estimates the mean of the absolute differences between the value of a cell and the values of its 8 surrounding cells, which resulted in a point estimate of variation in terrain around snow leopard kill sites measured within 64 m<sup>2</sup>. For double kills, we used the median point between kill sites.

### 2.2.2. Lynx

Lynx predation studies were conducted in Norway between 2009 and 2016. Lynx were captured and immobilized via darting from a helicopter, using walk-through box-traps, or using foot snares placed at carcass sites, and handled according to established protocols (Armeno et al., 2011) which were approved by the Norwegian National Animal Research Ethics Committee. Lynx were fitted with GPS collars that transferred data via the Global System for Mobile Communication network (GPS plus mini, Vectronic Aerospace GmbH,

Berlin, Germany). We followed 39 individual lynx (F = 20; M = 19) over 88 study periods, totaling 2309 monitoring days (Fig. S1b). Collars were programmed to take GPS points at one-hour (N = 25) or two-hour (N = 39) intervals, or one-hour intervals at night (2000–0800) and two-hour intervals during the day (N = 18). To make the GPS data comparable across lynx, we subsampled the one-hour GPS data to a two-hour fix interval. During each study period, field crews searched for carcasses at all ‘clustered’ GPS positions (defined as  $\geq 2$  positions within 100 m) and recorded the cause of death, species, age, and sex (Mattisson et al., 2011b; Gervasi et al., 2014).

We classified open versus closed habitats at kill sites using  $30 \times 30$  m resolution vegetation maps derived from satellite imagery of Norway (Johansen et al., 2009); open habitats included open areas (mountain and lowlands), bogs, and human-dominated areas (agricultural land and built up areas), whereas closed habitats included forests. We recorded only 2 kills made in human-dominated areas. We calculated TRI at carcass sites using  $10 \times 10$  m resolution digital elevation models from the Norwegian Mapping Authority (www.geonorge.no), which resulted in a point estimate of variation in terrain around lynx kill sites measured within 100 m<sup>2</sup>. We also calculated the distance to the nearest paved or gravel road (m) from each kill site.

### 2.3. Defining behavior at kill sites

We defined the location of the rumen as the kill-site for both snow leopard and lynx kills. Time of death (TOD) was estimated as the first position of the focal predator within 200 m of the kill site. Time of death was categorized as summer (1 May to 31 October) or winter (1 November to 30 April). We restricted our data to ungulate kills only, as we were interested in examining felid behavior around kill sites of comparably sized wild and domestic prey. Carcasses considered not killed by the focal individual (i.e., scavenged carcasses, assessed based on field signs) were also removed from the data set. Prey biomass (kg) per kill was estimated using the known mean body mass of prey species based on age and sex (see Table S2). For adult ungulates of unknown sex, we used the mean of adult male and female body mass. When age was unknown, body mass was estimated using the mean body mass for all age/sex groups; for adult reindeer of unknown sex, we used adult female body mass as males were rarely killed by lynx. For neonates killed during summer, we estimated body mass using linear growth curves extrapolated to the date of death from a mean birth date.

We used space-time cluster methodology to estimate time spent at kill sites (Tallian et al., 2021), thus restricting our definition of handling to time spent near killed prey after the kill occurred (e.g., Merrill et al., 2010; Tallian et al., 2022). Lynx GPS collars stopped intensive fix intervals at the end of each study period, so lynx GPS data were cut short for kills made closer to the end of each study period. In order to maximize our sample size with minimal information loss, we therefore examined handling time for both felids within the first 7 days following TOD, when the majority of activity near kill sites occurred (Fig. S1). Space-time clusters were defined as a set of GPS positions where each location was  $\leq 200$  m from the next sequential position, which generated a set of space-time clusters within each 7-day window. Our definition of handling time, and thus our response variable, included all GPS positions within any space-time cluster where  $\geq 1$  position within the cluster was within 200 m of the kill site within 7 days after TOD. Double/triple kills were defined as any kill where the TOD was  $< 7$  days and the distance between kill sites was  $< 400$  m. This measure was to avoid double counting positions that were located within similar kill buffers (i.e., 200 m) within our time frame of interest (7 days post kill). The biomass of carcasses classified as a double/triple kill were added together, and we included all space-time cluster GPS positions within 7 days after the last possible time of death (i.e., if kills were not made on the same date, we included positions up to 7 days after the last kill).

To examine kill-site fidelity, we quantified the number of independent visits snow leopards and lynx made to each kill site, and the proportion of time spent at kills. First, we calculated the total number of independent space-time clusters that were generated at each kill site within the first 7 days of TOD. Visits were defined as independent space-time clusters at the kill, i.e., if the animal moved away from the kill and then came back. Then, we calculated the proportion of time spent at the kill while the kill was ‘active’, i.e., between the first and last position of the focal individual within the same 7-day timeframe.

### 2.4. Data analyses

Our goal was to evaluate the effect of prey type (domestic or wild) and landscape characteristics (i.e., terrain ruggedness, distance to the nearest road, and habitat openness) on time spent at kill sites, i.e., prey handling time. We used an Akaike information criterion (AIC) model selection framework (Burnham and Anderson, 2002) to test our main predictions; the best-fit model had the lowest AIC score, adjusted for small sample size (AIC<sub>c</sub>). To determine the relative importance of our variables of interest, we examined whether they were retained in models that could be considered substantially or moderately supported (models with a  $\Delta\text{AIC}_c < 2$  or  $\Delta\text{AIC}_c 2\text{--}7$ , respectively; Burnham and Anderson, 2002; Burnham et al., 2010). We examined whether 90% and 95% CIs overlapped zero in our top models to evaluate the weight of evidence for variable effects (Muff et al., 2021).

The unit of analysis for the response variable was the number of GPS positions at a kill site, which was estimated using space-time cluster methodology as previously described, and were at five-hour intervals for snow leopards and two-hour intervals for lynx. Variables in the candidate model set included prey type (wild or domestic), terrain ruggedness (range snow leopard = 0.13–6.65; lynx = 0.03–9.2), distance to the nearest road (lynx = 3.7–15,979 m), and habitat openness (lynx = open/closed), prey biomass (snow leopard = 3–150 kg; lynx = 2.5–160.5 kg), cat type (male/female/female with cubs), and season (winter/summer). We considered potential interactions between prey type and prey biomass, prey biomass and terrain ruggedness, prey type and terrain ruggedness, and openness and terrain ruggedness (lynx only). To simplify the model set, we used likelihood ratio tests to compare full models to models that included interaction terms, and only included interactions in the model set if they improved model fit. We were unable to test for an interaction between prey type and openness for lynx due to the uneven spread of the data, i.e., there were very few instances

of wild prey killed in the open. To assess the relative importance of our variables of interest and potential interactive effects, we compared all possible combinations of our variables of interest and interaction terms; prey biomass, cat type (i.e., sex and reproductive status), and season were included in all models except the null. To explore potential variation between the handling times of different domestic prey types and wild prey for lynx, we performed a secondary analysis where we split domestic prey into two categories where reindeer were considered semi-domestic and sheep domestic (Mattisson et al., 2014). We then substituted this new categorization of prey type into all models and re-ran our candidate model set, excluding double kills.

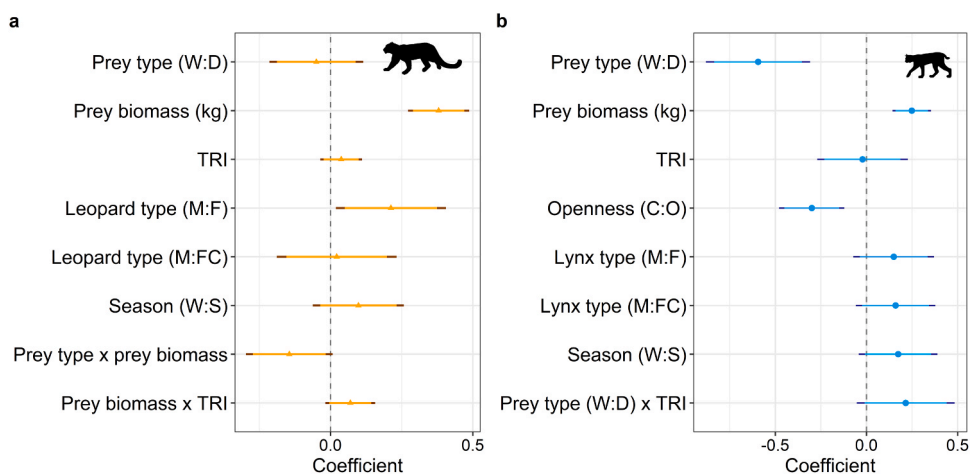
Analyses were conducted in R version 4.0.2 using generalized linear mixed models (GLMMs) using the 'glmer.nb' function in the 'lme4' package version 1.1–23 (Bates et al., 2015). To control for potential variation in handling time due to GPS collar fix success, we limited our analysis to kills that included  $\geq 70\%$  of the GPS positions within the 7-day interval. All models included a negative binomial distribution to correct for overdispersion. Year and cat ID were included a priori as crossed random effects in all models, and study area was also included in models for lynx; we divided the northern study area in two as there was a large geographical distance between the two northern study regions (Fig. 1b), which resulted in four study areas included in the lynx models. We sequentially removed random effects that did not contribute to model fit, i.e., the variance of the random effect was 0. To assess goodness of fit for our top models, we calculated the pseudo- $R^2$  for the conditional and marginal effects (Nakagawa and Schielzeth, 2013) using the 'r.squaredGLMM' function in the 'MuMIn' package (Bartoń, 2023). The correlation coefficients between variables in each model set were all less than 0.34. All variables were centered and scaled. Population-averaged fitted values and 95% confidence intervals (95% CIs) for graphs were calculated from best-fit models using the 'predict' and 'bootMer' functions in lme4.

### 3. Results

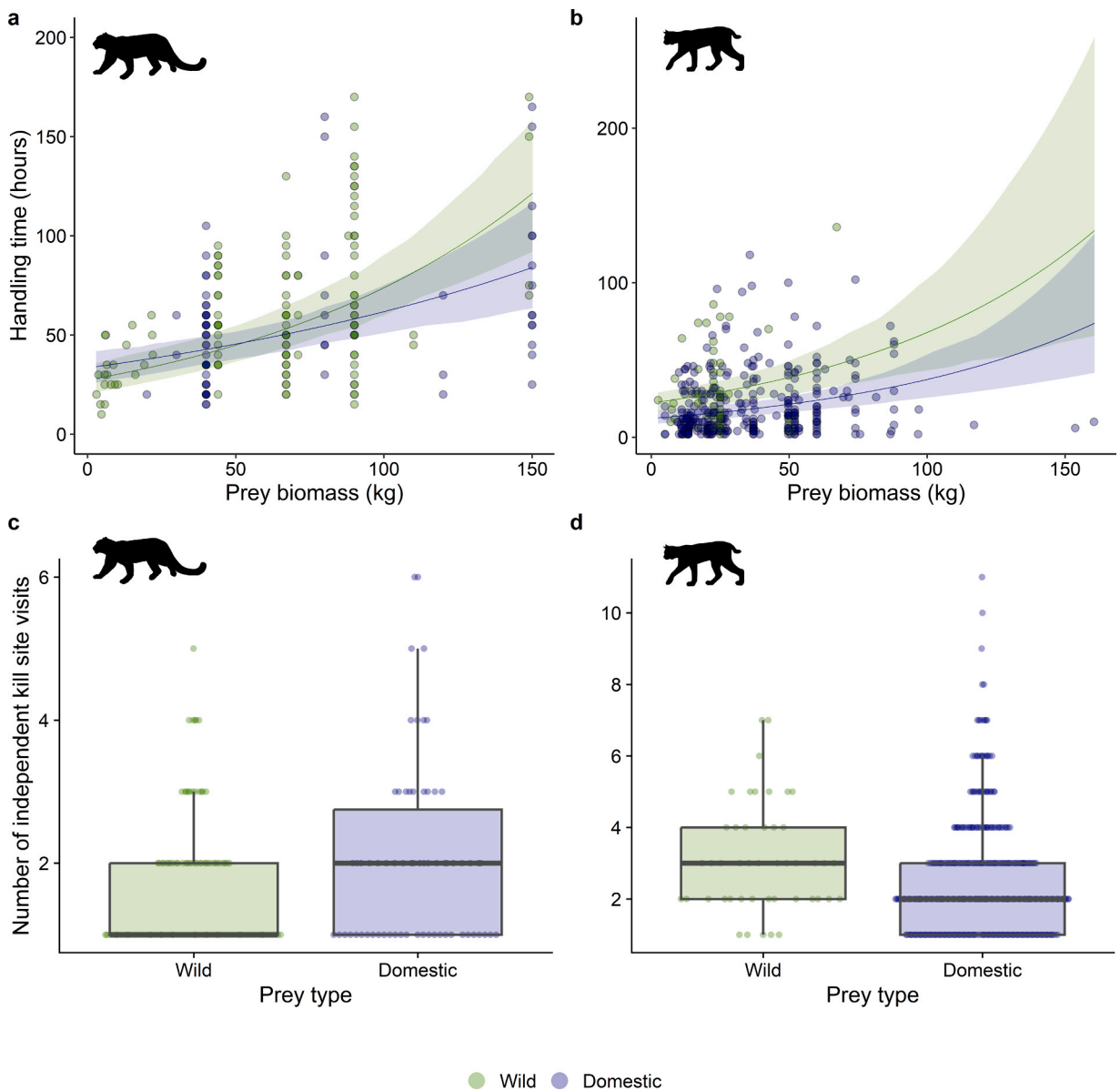
#### 3.1. Snow leopard

GLMMs included 188 observations (203 total kills including 176 single, 11 double, and 1 triple kills) from 18 individual snow leopards over 8 different years (Table S3a). Prey type was retained in four of the five top models (combined  $W_i = 0.72$ ; Table S4a), and terrain ruggedness three of the five (combined  $W_i = 0.62$ ; Table S4a), that showed substantial support (i.e.,  $\Delta AIC_c < 2$ ), and interaction terms for prey type and prey biomass (combined  $W_i = 0.48$ ) and prey biomass and terrain ruggedness (combined  $W_i = 0.39$ ) were each included in two of the top five models (Table S4a). All models except the null showed moderate support (i.e.,  $\Delta AIC_c 2-7$ ; Table S4a). The 90% CI for the interaction between prey type and prey biomass did not overlap 0 in the top model, and the 95% CI did not overlap 0 in the other top model it was included in (Table S4a). The 90% CI for the interaction between prey biomass and terrain ruggedness overlapped 0 in the top model, but the 95% CI did not overlap 0 in the other top model it was included in (Table S4a). The marginal and conditional pseudo- $R^2$  values (lognormal) for the top model were 0.30 and 0.32, respectively.

Snow leopard handling times were similar across both types of smaller prey, but with larger prey, handling time was greater at the kill sites of wild versus domestic ungulates (Figs. 2a-3a). On average, snow leopards spent an extra  $\sim 38$  h handling the largest wild ( $\bar{x} = 122.3$ ; 95% CI = 89.2, 156.21) compared to the largest domestic ( $\bar{x} = 84.0$ ; 95% CI = 63.1, 104.7) prey of similar body mass (estimated at the maximum comparable biomass of 150 kg). The handling time of domestic prey increased as terrain became more rugged with large prey but remained relatively constant across terrain ruggedness with medium and small sized prey (Fig. 4a). There was also evidence that solitary female snow leopards spent more time handling prey than males; the 95% CI did not overlap 0 in four of the five top models (Table S5a). Season was included in all top models, however, the 90% CIs overlapped 0 in all cases (Table S4a-S5a).



**Fig. 2.** Parameter estimates and 90% CI (light orange/blue) and 95% CI (black/dark blue) from the top models predicting snow leopard (a) and lynx (b) handling time (Table S4-5). Continuous variables were scaled in all models. Continuous variables include prey biomass (kg) and terrain ruggedness index (TRI), categorical variables include prey type (W:D= wild:domestic), cat type (M:F:FC= male:female:female with cubs), season (W:S= winter:summer), and habitat openness (C:O= closed:open).

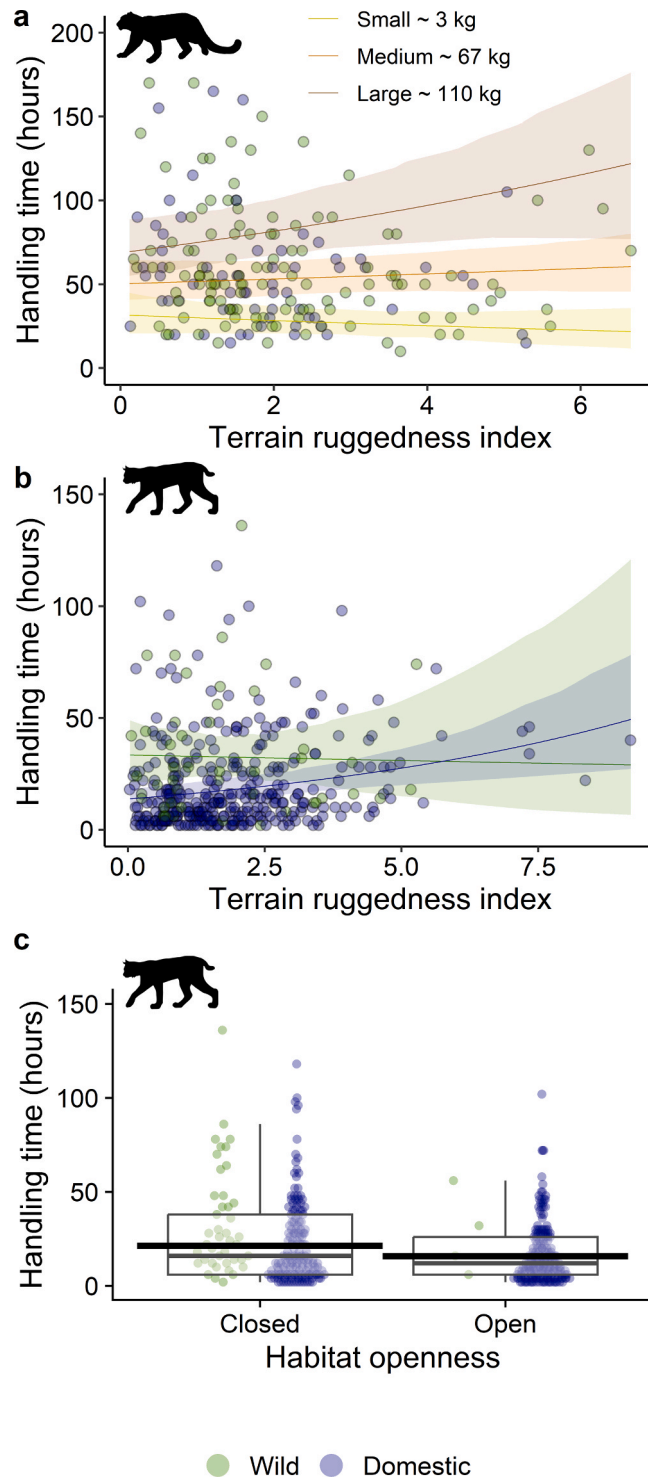


**Fig. 3.** The effect of prey type (wild vs domestic) on snow leopard (a) and lynx (b) handling time and the number of independent visits to kill sites of wild (green) and domestic (purple) prey, i.e., the number of times cats moved > 200 m away from a kill site and then came back, for snow leopard (c) and lynx (d) in Norway and Mongolia, respectively. Lines (a-b) are population-averaged fitted values with associated 95% confidence intervals representing wild (green) and domestic (blue) prey types. Circles are observed frequencies. The top models from the  $AIC_c$  model sets (Table S4) were used to generate population-averaged fitted values; season was set to winter and cat type to male. The boxplots (c-d) are based on the raw data (points), excluding double kills. Snow leopard made more visits to the kill sites of domestic prey than wild prey ( $\bar{x}=2.0$  vs.  $\bar{x}=1.6$ ;  $t(100.1)=-2.6$ ;  $p=0.01$ ), while lynx made fewer visits to the kill sites of domestic prey than wild prey ( $\bar{x}=2.6$  vs.  $\bar{x}=3.1$ ;  $t(60.8)=2.0$ ;  $p=0.05$ ).

Snow leopards generally made more visits to the kill sites of domestic ( $\bar{x}=2.0$ ) compared to wild ( $\bar{x}=1.6$ ) prey ( $t_{100.1}=-2.6$ ;  $p=0.01$ ; Fig. 3c). Snow leopards spent ~84% of the time the kill was active near the kill site, i.e., between the time of first and last position of the cat at the kill site, but there was no difference in the proportion of time spent near the kill between wild ( $\bar{x}=0.84$ ) and domestic ( $\bar{x}=0.84$ ) prey ( $t_{112.2}=-0.16$ ;  $p=0.88$ ; Fig. S2a).

### 3.2. Lynx

GLMMs included 384 observations (433 total kills including 343 single, 34 double, 6 triple, and 1 quadruple kills) across 4 study areas (Table S3b). Prey type, terrain ruggedness, and habitat openness were all retained in the top three models (combined  $W_i=0.85$ ;



**Fig. 4.** The effect of terrain ruggedness on (a) snow leopard and (b) lynx handling time and habitat openness (c) on lynx handling time. Lines are population-averaged fitted values with associated 95% confidence intervals representing smaller (yellow), medium (orange), and larger (brown) sized prey (a), and wild (green) and domestic (purple) prey types (b-c). The dark black lines show the population-averaged fitted values in the boxplots (c). Circles are observed values for wild (green) and domestic (purple) prey types (a-c). The top models from the AIC<sub>c</sub> model sets (Table S4) were used to generate population-averaged fitted values; season was set to winter, cat type to male, and prey type to wild.



Table S4b) that showed substantial support (i.e.,  $\Delta AIC_c < 2$ ). Prey type, terrain ruggedness, and habitat openness were also retained in the model that showed moderate support (i.e.,  $\Delta AIC_c$  2–7; Table S4b). Lynx handling time decreased when lynx were at domestic compared to wild prey kill sites, decreased when in open versus closed habitats, and increased with edible prey biomass (Figs. 2b, 4b–c). On average, lynx spent an extra  $\sim 12$  h handling wild ( $\bar{x} = 32.2$ ; 95% CI = 21.24, 43.63) compared to domestic ( $\bar{x} = 19.8$ ; 95% CI = 14.2, 26.5) prey (estimated at the mean biomass of 34.3 kg). We found some support for an interaction between prey type and terrain ruggedness; the interaction term was retained in two of the three models with substantial support (combined  $W_i = 0.51$ ; Table S4b), although the 90% CIs overlapped 0. We also found some support for a non-interactive effect of terrain ruggedness on lynx handling time; terrain ruggedness was retained in the second-best model and the 95% CI did not overlap 0 (Table S4b). The marginal and conditional pseudo- $R^2$  values (lognormal) for the top model were 0.19 and 0.19, respectively.

Domestic prey handling time increased as terrain became more rugged, while wild prey handling time remained relatively constant, or slightly decreased, with terrain ruggedness (Fig. 4b). We found some evidence of an effect of season and lynx reproductive status on handling time; both terms were retained in all three top models, although the 90% CIs overlapped 0 (Table S4a–S5a). We found little evidence that distance of the kill site to the nearest road affected lynx handling time; distance to nearest road was retained in the third-best model, however, the 90% CIs overlapped 0 (Table S4b–S5b).

In addition, we detected differences in handling times between the subcategories of domestic prey. Prey type, terrain ruggedness, and habitat openness were also all retained in the top two models that included the more detailed categorization of prey type, i.e., wild, domestic, and semi-domestic prey (combined  $W_i = 0.74$ ; Table S6). However, there was no evidence of an interaction between prey type and terrain ruggedness, i.e., the interaction was not retained in the top models (Table S6). Lynx spent less time near the kill sites of both semi-domestic (reindeer) and domestic (sheep) prey than wild prey, but the difference was smaller for domestic compared to semi-domestic prey (Fig. S3).

Lynx generally made fewer visits to the kill sites of domestic ( $\bar{x} = 2.6$ ) compared to wild ( $\bar{x} = 3.1$ ) prey ( $t_{60.8} = 2.0$ ;  $p = 0.05$ ; Fig. 3d). Lynx spent  $\sim 60\%$  of the time the kill was active near the kill site, but there was no difference in the proportion of time spent between wild ( $\bar{x} = 0.61$ ) and domestic ( $\bar{x} = 0.60$ ) prey ( $t_{68.8} = 0.36$ ;  $p = 0.72$ ; Fig. S2b).

#### 4. Discussion

Our results suggest that preying on domestic ungulates altered the foraging behavior of two large felids, snow leopard and lynx. In general, both felids spent less time at domestic compared to wild prey, suggesting that domestic prey are utilized less than their biomass might otherwise indicate. Landscape characteristics also affected prey handling time for both species. For example, rugged terrain increased snow leopard handling time with larger prey (Figs. 2a, 4a), while for lynx, handling time increased with rugged terrain for domestic, but not wild, prey, and was greater in closed compared to open habitats (Figs. 2b, 4b–c). These results imply that access to escape terrain and refugia affects felid foraging behavior.

Decreased felid handling time with domestic prey may be the result of two different processes. First, research in other systems suggests that the potential for anthropogenic disturbance decreases felid handling time (Kerley et al., 2002; Smith et al., 2015; Smith et al., 2017). For example, cougars reportedly spend less time handling prey in higher density housing areas in California (Smith et al., 2015), and flee when humans are present, which reduces their overall foraging efficiency (Smith et al., 2017). Alternatively, the handling time of caracals (*Caracal caracal*) near Cape Town, South Africa increased during the day with proximity to urban areas (Leighton et al., 2021). Leighton et al. (2021) suggest that caracals remained near kill sites longer in urban areas when cover was available, likely hiding to mitigate the risk of human detection.

Similar to other large carnivores (Darimont et al., 2015), both snow leopard and lynx experience acute risk from humans. Although snow leopards are a protected species across their range, poaching is likely a major threat for most snow leopard populations (Li and Lu, 2014). The potential for anthropogenic disturbance at domestic prey kill sites is likely high in Mongolia, due to a combination of active herding and a history of retaliatory killings. Similarly, lynx depredation on sheep and reindeer is a source of conflict in Norway (Swenson and Andrén, 2005), resulting in both legal and illegal population control (Sunde et al., 1998; Andrén et al., 2006; Rauset et al., 2016). Poaching in Scandinavia accounts for almost 46% of adult lynx mortality, and together, legal and illegal hunting account for almost 75% of adult lynx mortality (Andrén et al., 2006). The link between handling time and landscape characteristics associated with refugia and escape terrain supports the idea that both felids are sensitive to anthropogenic disturbance.

An alternative explanation, however, is that felids spend less time handling domestic prey because they are easier to kill. Theory predicts that predator feeding times are shorter in more profitable environments (Cook and Cockrell, 1978). Thus, when prey are both abundant and easy to catch, predators may abandon their kills more quickly, i.e., utilizing the preferred, high-energy parts of the carcass, then leaving the rest behind to make a new kill. However, such a predation strategy necessitates knowing that your next target prey is equally as easy to catch. Snow leopard in the Tost region of Mongolia predominately prey on wild ungulates, which comprise  $\sim 75\%$  of their diet (Johansson et al., 2015), thus, their next kill is more likely to be wild than domestic. Thus, for snow leopard in our study area, decreased handling time with domestic prey is likely more closely linked to the risk of disturbance rather than an over-abundance of easy prey.

The situation with lynx in Norway is more complex. Lynx in the northern study systems only had access to semi-domestic reindeer and sheep. In Norway, free-ranging sheep lack most anti-predator defenses and represent vulnerable, easy prey (Odden et al., 2002; Odden et al., 2008). Semi-domesticated reindeer, on the other hand, display anti-predator behavior more similar to that of other wild ungulates (Baskin and Hjäältén, 2001; Rivrud et al., 2018), i.e., they are not as easily caught. However, both semi-domestic reindeer and sheep in Norway occur at much higher densities than wild prey (Melis et al., 2009; Mattisson et al., 2014), and encounter rates may therefore be higher (Odden et al., 2008). Furthermore, lynx are efficient hunters and kill rates are known to increase with increased

reindeer density (Mattisson et al., 2014). Thus, in northern Norway, decreased handling time with domestic prey could possibly be linked to a high density of domestic prey. In central and southern Norway, lynx have access to both wild and domestic prey i.e., roe deer, reindeer, and sheep (central), and roe deer and sheep (south). Similar to the Tost study system in Mongolia, lynx in the central and southern study areas in Norway prefer wild compared to domestic prey (Odden et al., 2013; Gervasi et al., 2014), implying that decreased domestic prey handling time in these areas is linked to the risk of human disturbance.

For snow leopards, handling time increased as the terrain became more rugged with larger prey but stayed relatively constant across the terrain gradient with medium and smaller sized prey (Figs. 2a, 4a). This might represent a behavioral trade-off to mitigate risk at the cost of foraging. Smaller prey take less time to consume than larger prey, thus, handling time may remain steady, and lower, across all terrain types, i.e., the net risk in less rugged terrain while handling smaller prey might be relatively low, given the shorter consumption time required. However, larger prey take more time to consume simply because there is more biomass. This added time at the kill site may leave snow leopards more exposed to risk from both humans and competitors as the kill site matures, or the probability of kill-site detection by people and competitors increases, on the landscape. Thus, handling time for large prey may be comparatively greater in more rugged terrain, where the risk of disturbance is likely less.

Felids are cryptic and commonly use cover to hide. Lynx handling time was lower in open versus closed habitats (Fig. 4c), however, domestic livestock comprised the majority (98%) of lynx kills made in the open in our study (Fig. 4c). This likely reflected prey species habitat use; roe deer are commonly found in forest and agricultural land, while reindeer, and to a lesser extent sheep, are mostly found near or above tree line. This made it difficult to separate the effects of landscape characteristics versus prey type on lynx handling time. There was also some evidence that lynx handling time increased as the terrain became more rugged with domestic, but not wild, prey (Fig. 4b). This suggests rugged terrain in the open tundra may provide refugia from risk, but not necessarily from similar risks in closed habitats. Complex terrain may provide better refuge at lynx kill sites which are likely more detectable than resting sites, or when cover is unavailable. However, there was also some evidence that lynx handling time increased as the terrain became more rugged for both prey types (Table S4-S5) suggesting that rugged terrain provides better refuge in general.

Felids are also at risk of kleptoparasitism, or losing food biomass to scavengers (vertebrate, invertebrate and microbial), which can impact individual foraging patterns and have population- and ecosystem-level consequences (Elbroch et al., 2014a; Moleón et al., 2014; Balme et al., 2017; Teurlings et al., 2020). It is difficult to disentangle whether decreased handling time linked to certain landscape characteristics was due to potential risk associated with humans and dominant competitors, or because increased kill site detectability facilitated scavenging and food loss. Wolves are known to usurp kills from other large felids (Stahler et al., 2020), and are presumably capable of appropriating kills from snow leopard as well. Furthermore, wolves tend to hunt in more open areas, and are less adept at moving in steep, rugged terrain (Mallon et al., 2016). Rugged terrain is therefore likely a refuge for snow leopard from both wolves and humans. In Norway, wolverine regularly scavenge lynx-killed ungulates (Mattisson et al., 2011a), and are capable of influencing lynx behavior at kill sites (López-Bao et al., 2016). In general, larger carcasses are more likely to be detected by scavengers (Moleón et al., 2015), which means risk of kleptoparasitism is greater at the kill sites of larger prey. However, it is also plausible that detectability and accessibility are greater in open, flat terrain compared to covered habitat and complex, steep terrain (Mattisson et al., 2011a).

Although handling time was affected by similar factors for snow leopards and lynx in our study, the two felids exhibited distinct differences in kill-site behavior. For example, compared to lynx, snow leopards generally remained closer to their kill sites (Fig. S2), and made fewer kill-site visits (Fig. 3). Interestingly, snow leopards tended to leave and revisit domestic kills more often than wild kills, while lynx visited domestic kills less often than wild kills (Fig. 3). For snow leopard who show high kill-site fidelity, moving away from, and back to, domestic kill sites more often could be a behavioral response to mitigate risk in habitats that are usually open. However, almost all double kills (82%) by snow leopard were considered domestic (i.e., at least one of the kills was domestic), thus, domestic kill sites were slightly biased toward larger biomasses in the data set. When double kills were removed, the difference in the number of visits to wild and domestic prey kill sites disappeared. Compared to snow leopards, lynx commonly moved back and forth between distant day-beds and their kills (Fig. 3). Thus, decreased visits to domestic kill sites by lynx, combined with overall decreased handling time of domestic prey, suggests they likely abandoned their kills to mitigate anthropogenic risk.

Several other factors affected snow leopard and lynx handling time. For example, felid handling time increased with prey biomass in both systems (Figs. 2–3, Table S7), which is consistent with results from other large carnivores (e.g., Cristescu et al., 2014; Elbroch et al., 2014a; Tallian et al., 2021). We also found evidence that solitary female snow leopard handling time was less than male handling time, but no evidence that females with cubs had greater handling time. This is possibly because kills were consumed more quickly when a greater number of cats were present; snow leopard cubs stay with their mother for almost 2 years and can weigh over 30 kg at separation (Johansson et al., 2021). Previous studies show human-induced lynx mortality, and therefore risk, is negatively linked with distance to roads (Sunde et al., 1998; Basille et al., 2013), however, we did not find an effect of kill-site distance to roads on lynx handling time. This is possibly because a) road density was lower in the northern, compared to central and southern, study areas, and b) roads in the comparatively open northern tundra run along forested valley bottoms which lynx prefer, i.e., the differential effect of roads on lynx behavior between study areas may have masked each other's effects at this large spatial scale. Comparatively, established roads are virtually non-existent in the Tost Mountain region, and were not a factor affecting snow leopard behavior.

It is well-understood that large carnivore preference for domestic compared to wild prey varies between systems and the relative availability of prey types, employment of herding techniques, and the presence of individuals predisposed to killing domestic prey (Linnell et al., 1999; Khorozyan et al., 2015; Ghoddousi et al., 2016). Research suggests that felids avoid preying on domestic livestock when alternative prey are present at sufficient densities (Odden et al., 2008; Gervasi et al., 2014; Khorozyan et al., 2015), although abundant wild prey can imply a higher felid density and greater net predation on domestic livestock (Suryawanshi et al., 2017). However, wild prey depletion is a substantial threat to large carnivore populations worldwide (Ripple et al., 2014), and some

populations of large felids are already dependent on domestic (e.g., Kumbhøjkar et al., 2021) or semi-domestic (e.g., Mattisson et al., 2011b) prey. Shorter handling time suggests that domestic prey are utilized less than their biomass might otherwise indicate, i.e., they are utilized less effectively than wild prey. In the context of long-term conservation and management, this could a) be accompanied by an energetic or fitness cost of decreased felid foraging efficiency due to the risk of anthropogenic disturbance, or b) exacerbate conflict if reduced handling time associated with easy prey results in increased livestock depredation.

### CRedit authorship contribution statement

AT, GS, JM, and ÖJ conceived of the study; GS, JM, JO, and ÖJ collected and compiled the data; AT carried out statistical analysis and wrote the manuscript; JL, JM, and JO coordinated the long-term study in Norway; CM, GS, ÖJ, and PL coordinated the long-term study in Mongolia. All authors helped draft the manuscript and gave final approval for publication.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Data availability

Data are available on request.

### Acknowledgements

We would like to thank Amgаланбаатар Sukh, Richard Reading, Ganchimeg Wingard, the Ikh Nart Nature Reserve, Earthwatch Institute, and Denver Zoo for providing Argali lamb body masses, Gabriela Palomo-Munoz for providing the snow leopard silhouette, Intermap Technologies for providing the digital terrain models of the Tost Mountain Range, and the Stina Werner Foundation and the US Fulbright Global Scholars Program for financial support. The Norwegian part of the study was supported by the Research Council of Norway, the Norwegian Directorate for Nature Management, the Norwegian Institute for Nature Research, and Nature Protection Division of the County Governor's Office for several Norwegian counties, and would not have been possible without the help from a large number of local fieldworkers and students. The Mongolian part of the study would like to thank the David Shepherd Wildlife Foundation, Disney Conservation Fund, Whitley Fund for Nature, Acton Family Giving, Zoo Basel, Columbus Zoo & Aquarium, Bioparc de Doué-la-Fontaine, Zoo Dresden, Zoo Idaho, Kolmården Zoo, Korkeasaari Zoo, La Passarelle, Zoo New England, Tierpark Berlin, Tulsa Zoo, the Ministry for Environment and Green Development, Government of Mongolia, and the Mongolian Academy of Sciences for their support.

### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02650](https://doi.org/10.1016/j.gecco.2023.e02650).

### References

- Andrén, H., Linnell, J.D., Liberg, O., Andersen, R., Danell, A., Karlsson, J., Odden, J., Moa, P.F., Ahlqvist, P., Kvam, T., 2006. Survival rates and causes of mortality in Eurasian lynx (*Lynx lynx*) in multi-use landscapes. *Biol. Conserv.* 131, 23–32.
- Arnemo, J.M., A. Evans, and Å. Fahlman, 2011. Biomedical protocol for free-ranging brown bears, gray wolves, wolverines and lynx. Hedmark University College, Evenstad, Norway and Swedish University of Agricultural Sciences, Umeå, Sweden.
- Atwood, T.B., Madin, E.M., Harborne, A.R., Hammill, E., Luiz, O.J., Ollivier, Q.R., Roelfsema, C.M., Macreadie, P.I., Lovelock, C.E., 2018. Predators shape sedimentary organic carbon storage in a coral reef ecosystem. *Front. Ecol. Evol.* 6, 110.
- Atwood, T.C., Gese, E.M., Kunkel, K.E., 2009. Spatial partitioning of predation risk in a multiple predator–multiple prey system. *J. Wildl. Manag.* 73, 876–884.
- Balme, G.A., Miller, J.R., Pitman, R.T., Hunter, L.T., 2017. Caching reduces kleptoparasitism in a solitary, large felid. *J. Anim. Ecol.* 86, 634–644.
- Bartoń, K. 2023. MuMIn: Multi-Model Inference.
- Basille, M., Van Moorter, B., Herfindal, I., Martin, J., Linnell, J.D., Odden, J., Andersen, R., Gaillard, J.-M., 2013. Selecting habitat to survive: the impact of road density on survival in a large carnivore. *PLoS One* 8, e65493.
- Baskin, L.M., Hjaltnén, J., 2001. Fright and flight behavior of reindeer. *Alces: A J. Devoted Biol. Manag. Moose* 37, 435–445.
- Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2015. Package 'lme4': Linear mixed-effects models using Eigen and S4 classes. *J. Stat. Softw.* 67, 1–48.
- Brown, J.S., 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolut. Ecol. Res.* 1, 49–71.
- Bruskotter, J., Shelby, L., 2010. Human dimensions of large carnivore conservation and management: introduction to the special issue. *Hum. Dimens. Wildl.* 15, 311–314.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodal inference, a practical information theoretic approach, 2nd edition., Springer-Verlag., New York.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2010. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65, 23–35.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andren, H., et al., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* 346, 1517–1519.
- Cook, R., Cockrell, B., 1978. Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. *J. Anim. Ecol.* 529–547.

- Cristescu, B., Stenhouse, G.B., Boyce, M.S., 2014. Grizzly bear ungulate consumption and the relevance of prey size to caching and meat sharing. *Anim. Behav.* 92, 133–142.
- Darimont, C.T., Fox, C.H., Bryan, H.M., Reimchen, T.E., 2015. The unique ecology of human predators. *Science* 349, 858–860.
- Elbroch, L., Lendrum, P., Allen, M., Wittmer, H., 2014a. Nowhere to hide: pumas, black bears, and competition refuges. *Behav. Ecol.* 00, 1–8.
- Elbroch, L.M., Allen, M.L., Lowrey, B.H., Wittmer, H.U., 2014b. The difference between killing and eating: Ecological shortcomings of puma energetic models. *Ecosphere* 5, 1–16.
- Gervasi, V., Nilsen, E.B., Odden, J., Bouyer, Y., Linnell, J., 2014. The spatio-temporal distribution of wild and domestic ungulates modulates lynx kill rates in a multi-use landscape. *J. Zool.* 292, 175–183.
- Ghoddousi, A., Soofi, M., Kh. Hamidi, A., Lumetsberger, T., Egli, L., Khorozyan, I., Kiabi, B.H., Waltert, M., 2016. Assessing the role of livestock in big cat prey choice using spatiotemporal availability patterns. *PLoS One* 11, e0153439.
- Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M., Nilsen, E.B., 2012. Habitat heterogeneity and mammalian predator-prey interactions. *Mammal. Rev.* 42, 55–77.
- Hijmans, R.J., et al., and 2023. raster: Geographic Data Analysis and Modeling.
- Hilborn, A., Pettorelli, N., Caro, T., Kelly, M.J., Laurenson, M.K., Durant, S.M., 2018. Cheetahs modify their prey handling behavior depending on risks from top predators. *Behav. Ecol. Sociobiol.* 72, 1–10.
- Johansen, B., P.A., Aarrestad, D.I., Øien, 2009. Vegetasjonkart for Norge basert på satellittdata. Delprosjekt 1: Klasseinndeling og beskrivelse av utskilte vegetasjonstyper. NORUT/NINA/NTNU.
- Johansson, Ö., McCarthy, T., Samelius, G., Andrén, H., Tumursukh, L., Mishra, C., 2015. Snow leopard predation in a livestock dominated landscape in Mongolia. *Biol. Conserv.* 184, 251–258.
- Johansson, Ö., Ausilio, G., Low, M., Lkhagvajav, P., Weckworth, B., Sharma, K., 2021. The timing of breeding and independence for snow leopard females and their cubs. *Mamm. Biol.* 101, 173–180.
- Kaczensky, P., 1999. Large carnivore depredation on livestock in Europe. *Ursus* 59–71.
- Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B., Hornocker, M.G., 2002. Effects of roads and human disturbance on Amur tigers. *Conserv. Biol.* 16, 97–108.
- Khorozyan, I., Ghoddousi, A., Soofi, M., Waltert, M., 2015. Big cats kill more livestock when wild prey reaches a minimum threshold. *Biol. Conserv.* 192, 268–275.
- Kohl, M.T., Ruth, T.K., Metz, M.C., Stahler, D.R., Smith, D.W., White, P., MacNulty, D.R., 2019. Do prey select for vacant hunting domains to minimize a multi-predator threat. *Ecol. Lett.* 22, 1724–1733.
- Krofel, M., Kos, I., Jerina, K., 2012. The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behav. Ecol. Sociobiol.* 66, 1297–1304.
- Kumbhojkar, S., Yosef, R., Kosicki, J.Z., Kwiatkowska, P.K., Tryjanowski, P., 2021. Dependence of the leopard *Panthera pardus fusca* in Jaipur, India, on domestic animals. *Oryx* 55, 692–698.
- Kusler, A., Elbroch, L.M., Quigley, H., Grigione, M., 2017. Bed site selection by a subordinate predator: an example with the cougar (*Puma concolor*) in the Greater Yellowstone Ecosystem. *PeerJ* 5, e4010.
- Leighton, G.R., Bishop, J.M., Merondun, J., Winterton, D.J., O’Riain, M.J., Serieys, L.E., 2021. Hiding in plain sight: risk mitigation by a cryptic carnivore foraging at the urban edge. *Anim. Conserv.*
- Li, J., Lu, Z., 2014. Snow leopard poaching and trade in China 2000–2013. *Biol. Conserv.* 176, 207–211.
- Linnell, J.D., Odden, J., Smith, M.E., Aanes, R., Swenson, J.E., 1999. Large carnivores that kill livestock: do "problem individuals" really exist. *Wildl. Soc. Bull.* 698–705.
- Linnell, J.D., Odden, J., Mertens, A., 2012. Mitigation methods for conflicts associated with carnivore depredation on livestock. *Carniv. Ecol. Conserv.: a Handb. Technol.* 314–332.
- López-Bao, J.V., Mattiison, J., Persson, J., Aronsson, M., Andrén, H., 2016. Tracking neighbours promotes the coexistence of large carnivores. *Sci. Rep.* 6, 1–9.
- Mabille, G., Stien, A., Tveraa, T., Mysterud, A., Brøseth, H., Linnell, J.D., 2015. Sheep farming and large carnivores: what are the factors influencing claimed losses. *Ecosphere* 6, 1–17.
- Mallon, D., Harris, R.B., Wegge, P., 2016. Snow leopard prey and diet. *Snow Leopards*. Elsevier, pp. 43–55.
- Mattiison, J., Andrén, H., Persson, J., Segerström, P., 2011a. Influence of intraguild interactions on resource use by wolverines and Eurasian lynx. *J. Mammal.* 92, 1321–1330.
- Mattiison, J., Odden, J., Nilsen, E.B., Linnell, J.D., Persson, J., Andrén, H., 2011b. Factors affecting Eurasian lynx kill rates on semi-domestic reindeer in northern Scandinavia: can ecological research contribute to the development of a fair compensation system. *Biol. Conserv.* 144, 3009–3017.
- Mattiison, J., Odden, J., Linnell, J., 2014. A catch-22 conflict: access to semi-domestic reindeer modulates Eurasian lynx depredation on domestic sheep. *Biol. Conserv.* 179, 116–122.
- Melis, C., Jedrzejewska, B., Apollonio, M., Barton, K.A., Jedrzejewski, W., Linnell, J.D.C., Kojola, I., Kusak, J., Adamic, M., Ciuti, S., Delehan, I., Dykyy, I., Krapinec, K., Mattioli, L., Sagaydak, A., Samchuk, N., Schmidt, K., Shkvyrya, M., Sidorovich, V.E., Zawadzka, B., Zhyla, S., 2009. Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe. *Glob. Ecol. Biogeogr.* 18, 724–734.
- Merrill, E., Sand, H., Zimmermann, B., McPhee, H., Webb, N., Hebblewhite, M., Wabakken, P., Frair, J.L., 2010. Building a mechanistic understanding of predation with GPS-based movement data. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 2279–2288.
- Mijidodorj, T.N., Alexander, J.S., Samelius, G., Badola, R., Rawat, G., Dutta, S., 2018. Corrigendum to: livestock depredation by large carnivores in the South Gobi, Mongolia. *Wildl. Res.* 45, 381–381.
- Moleón, M., Sánchez-Zapata, J.A., Selva, N., Donazar, J.A., Owen-Smith, N., 2014. Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages. *Biol. Rev.* 89, 1042–1054.
- Moleón, M., Sánchez-Zapata, J.A., Sebastián-González, E., Owen-Smith, N., 2015. Carcass size shapes the structure and functioning of an African scavenging assemblage. *Oikos* 124, 1391–1403.
- Muff, S., Nilsen, E.B., O’Hara, R.B., Nater, C.R., 2021. Rewriting results sections in the language of evidence. *Trends Ecol. Evol.*
- Mukherjee, S., Heithaus, M.R., 2013. Dangerous prey and daring predators: a review. *Biol. Rev.* 88, 550–563.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142.
- Odden, J., Linnell, J.D., Moa, P.F., Herfindal, I., Kvam, T., Andersen, R., 2002. Lynx depredation on domestic sheep in Norway. *J. Wildl. Manag.* 98–105.
- Odden, J., Herfindal, I., Linnell, J.D., Andersen, R., 2008. Vulnerability of domestic sheep to lynx depredation in relation to roe deer density. *J. Wildl. Manag.* 72, 276–282.
- Odden, J., Nilsen, E.B., Linnell, J.D., 2013. Density of wild prey modulates lynx kill rates on free-ranging domestic sheep. *PLoS One* 8, e79261.
- Rauset, G.R., Mattiison, J., Andren, H., Chapron, G., Persson, J., 2013. When species’ ranges meet: assessing differences in habitat selection between sympatric large carnivores. *Oecologia* 172, 701–711.
- Rauset, G.R., Andren, H., Swenson, J.E., Samelius, G., Segerstrom, P., Zedrosser, A., Persson, J., 2016. National Parks in Northern Sweden as refuges for illegal killing of large carnivores. *Conserv. Lett.* 9, 334–341.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D., Wirsing, A.J., 2014. Status and ecological effects of the world’s largest carnivores. *Science* 343.
- Rivrud, I.M., Sivertsen, T.R., Mysterud, A., Åhman, B., Støen, O.G., Skarin, A., 2018. Reindeer green-wave surfing constrained by predators. *Ecosphere* 9, e02210.
- Sheehy, D.P., D., Damiran, 2012. Assessment of Mongolian rangeland condition and trend. Final report for the World Bank and the Netherlands-Mongolia Trust Fund for Environmental Reform (NEMO):0–47.
- Smith, J., Wang, Y., Wilmers, C.C., 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proc. R. Soc. B-Biol. Sci.* 282.

- Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., Wilmers, C.C., 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. *Proc. R. Soc. B: Biol. Sci.* 284, 20170433.
- Stahler, D.R., Wilmers, C.C., Tallian, A., Anton, C.B., Metz, M.C., Ruth, T.K., Smith, D.W., Gunther, K.A., MacNulty, D.R., 2020. Competition and coexistence among Yellowstone's meat eaters. In: Smith, D.W., Stahler, D.R., MacNulty, D.R. (Eds.), *Yellowstone Wolves: Science and Discovery in the World's First National Park*. University of Chicago Press, Chicago, IL, pp. 223–241.
- Sunde, P., Overskaug, K., Kvam, T., 1998. Culling of lynxes *Lynx lynx* related to livestock predation in a heterogeneous landscape. *Wildl. Biol.* 4, 169–175.
- Suryawanshi, K.R., Redpath, S.M., Bhatnagar, Y.V., Ramakrishnan, U., Chaturvedi, V., Smout, S.C., Mishra, C., 2017. Impact of wild prey availability on livestock predation by snow leopards. *R. Soc. Open Sci.* 4, 170026.
- Swenson, J., Andrén, H., 2005. A tale of two countries: large carnivore depredation and compensation schemes in Sweden and Norway. *Conserv. Biol. Ser. Camb.* 9, 323.
- Tallian, A., Ordiz, M.C., Metz, B., Zimmermann, C., Wikenros, D.W., Smith, D.R., Stahler, W.P., Swenson, J.E., Sand, H., Kindberg, J., 2021. Of wolves and bears: seasonal drivers of interference and exploitation competition between apex predators. *Ecol. Monogr.*, e1498.
- Tallian, A., Ordiz, A., Metz, M.C., Zimmermann, B., Wikenros, C., Smith, D.W., Stahler, D.R., Wabakken, P., Swenson, J.E., Sand, H., 2022. Of wolves and bears: seasonal drivers of interference and exploitation competition between apex predators. *Ecol. Monogr.* 92, e1498.
- Teurlings, I.J., Odden, J., Linnell, J.D., Melis, C., 2020. Caching behavior of large prey by Eurasian lynx: quantifying the anti-scavenging benefits. *Diversity* 12, 350.
- van der Meer, E., Moyo, M., Rasmussen, G.S., Fritz, H., 2011. An empirical and experimental test of risk and costs of kleptoparasitism for African wild dogs (*Lycaon pictus*) inside and outside a protected area. *Behav. Ecol.* 22, 985–992.
- Walton, Z., Mattisson, J., Linnell, J.D., Stien, A., Odden, J., 2017. The cost of migratory prey: seasonal changes in semi-domestic reindeer distribution influences breeding success of Eurasian lynx in northern Norway. *Oikos* 126, 642–650.