



Communication behavior of the snow leopard (*Panthera uncia*): understanding marking-behavior patterns to optimize camera-trapping studies

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Abstract

Many carnivores rely on marking behavior for intraspecific communication with potential mates and competitors, using scent and visual markings to advertise their use of a territory and allow potential mates to assess their quality. However, obtaining data on communication behaviors of rare and elusive animals can be challenging. To better understand marking behavior of snow leopard (*Panthera uncia*), we combined camera-trapping, snow-tracking and transect counts of scrapes in the Altai Mountains, Mongolia, and measured frequencies of communication behaviors in both space and time. Next, we explored if this information could be used to improve the efficiency of snow leopard population monitoring through camera-trapping. Using the combination of all three methods, we detected seven communication behaviors. Most visits at marking sites began with sniffing (recorded at 56.4% visits) before progressing to other behaviors. Urine spraying (17.7% of visits) and scraping (16.8%) were exhibited at significantly more visits than other communication behaviors (flehmen, head/body rubbing, fecal deposition, claw marking). According to the snow-tracking data conducted in optimal habitats, scraping was the most frequent marking behavior with 12.8 scrapes/km, followed by urine marking with 10.5 marks/km. Along 32 transects, we recorded a mean of 8.0 cumulative scrapes/km, with highest marking rates recorded in gorges, which we recommend as prime habitats for deploying camera-traps. Finally, our results suggest that the number of scrapes observed at potential camera-trapping sites represents a good predictor of snow leopard visitation rate. Therefore, this parameter can be used when choosing camera-trapping locations to increase the efficiency of monitoring programs.

Significance statement

Camera-trapping is currently a preferred method for monitoring many elusive large carnivore species, including felids, as it often provides the most reliable population density estimates. However, gathering enough detections for robust estimates is difficult for species that occur at low densities and have large home ranges. Using marking locations can be an efficient approach to camera-trapping surveys, but it requires a good understanding of communication behavior. Snow leopard is a species of global conservation concern, but studies of marking behavior have been limited and only available from a small part of the species' distribution. We collected three different datasets that enabled us to fill several knowledge gaps, including some of the first records of marking rates in space and time. Our study also highlights the similarities of snow leopard marking with other solitary felids and provides useful recommendations for optimizing camera-trapping studies.

Keywords Intraspecific communication · Monitoring · Felids · Carnivores · Mongolia

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Introduction

Direct interactions and visual communication are infrequent in solitary apex predators, which typically have large home ranges and occur in low densities. As a result, many species rely on marking behavior, including scent marking and marking with visual cues (e.g. urine spraying, scraping, clawing or ground scratching), for indirect intraspecific communication with potential mates and competitors (Zub et al. 2003; Clapham et al. 2014; Allen et al. 2016; Cornhill and Kerley 2020). Marking is often concentrated in conspicuous areas that act as communication hubs for multiple individuals, allowing the local population to effectively communicate with each other (Clapham et al. 2013; Allen et al. 2015; Krofel et al. 2017; Melzheimer et al. 2020). Markings typically occur throughout an animal's territory, often being concentrated along travel routes and other areas that are more frequently visited (Zub et al. 2003; Krofel et al. 2017). When choosing scent-marking locations, carnivores often select microsites that better retain the smell and protect scent marks from precipitation, thus increasing scent-marking efficiency (Mohorović and Krofel 2020). Marking is effectively used to advertise the use of a territory, minimizing the need for conflict with potential competitors while allowing potential mates to assess their status and quality (Allen et al. 2015; Vogt et al. 2016; Cornhill and Kerley 2020). As such, marking behavior directly influences individual fitness, but there is variation in the forms of communication used even within families (e.g., Felidae; see review in Allen et al. 2016), requiring species-specific

studies. Understanding marking behavior is also important for the monitoring of carnivore populations, as marking sites are often targeted by camera-trapping surveys (Jackson et al. 2006; Fležar et al. 2023).

Snow leopards (*Panthera uncia*) are solitary apex predators and keystone species of conservation concern, who live at high elevations in low densities and use marking with scent and visual cues to communicate with conspecifics (Ahlborn and Jackson 1988; Wolf and Ale 2009; Li et al. 2013; Johansson et al. 2018). Snow leopards have been documented using seven of the communication behaviors common to felids (see review in Allen et al. 2016), including five producing communication behaviors (i.e. marking behaviors) and two investigating communication behaviors (Table 1). Snow leopards primarily seem to use scraping behavior (Ahlborn and Jackson 1988; Wolf and Ale 2009), with fecal deposition being less frequent, but often occurring at the scrape sites (Ahlborn and Jackson 1988). Urine spraying and head/body rubbing also seem to occur less frequently, with claw marking being the least frequent producing behavior reported (Ahlborn and Jackson 1988; Wolf and Ale 2009). Snow leopards also use sniffing (olfaction) and the flehmen response to investigate scent marks made by other individuals (Ahlborn and Jackson 1988). In captive conditions, males marked at higher frequencies than females (Rieger 1978), but it remains unknown whether the same is true for snow leopards living in the wild (Fox et al. 2024).

Snow leopards often mark at communal sites that are also used by other species in the carnivore community (Jackson et al. 2006; Li et al. 2013) and can influence the visitation and marking behavior of other species, such as the Pallas's cat (*Otocolobus manul*) (Allen et al. 2023). In the Himalayas, marking sites are often located in rugged terrain and rocky areas, especially at the base of cliffs, as well as on promontories, along rivers and other valleys, beneath trees, or among other prominent habitat features (Ahlborn and Jackson 1988; Fox et al. 1991, 2024; Sharma et al. 2006). Marking sites were also reported to be more often found in valley bottoms than along ridges or other areas (Ahlborn and Jackson 1988; Wolf and Ale 2009). Snow leopards also seem to choose microsites with substrate conducive to scraping, and northerly-oriented, mid-sized overhanging rocks and boulders on which to spray urine (Ahlborn and Jackson 1988; Jackson 1996; Sharma et al. 2006).

Understanding marking behaviors and selection of marking sites often requires several methods for documenting marking behavior (e.g., camera trapping, snow tracking, transect counts), each of which provide insights on different aspects of this behavior. Given that snow leopards are among the most difficult large carnivores to study, the research focused on their marking behavior is very limited

Table 1 An ethogram of communication behaviors that we expected snow leopards could exhibit based on previous research. The first five are producing behaviors (i.e. marking behaviors) and the last two are investigating behaviors. See also Fig. 1 for examples of the most common communication behaviors

Behavior	Description
Claw Marking	The snow leopard scratches its claws on woody vegetation
Fecal Deposition	The snow leopard defecates, leaving scat at the marking site
Head/Body Rubbing	The snow leopard rubs its cheek, neck, or shoulder on an object at the marking site
Scraping	The snow leopard scrapes backwards with its hind feet to create a small depression and mound of material, and sometimes urinates and/or defecates on it
Urine Spraying	The snow leopard lifts its tail and sprays urine backwards onto a rock or other object, or squats and sprays urine on the ground or a scrape
Flehmen Response	The snow leopard lifts its head and curls back its neck, and curls back its lip to expose scent to its vomeronasal organ, usually in response to a scent mark
Sniffing (olfaction)	The snow leopard sniffs objects or scent marks left by other animals at the scent marking site

and for now almost exclusively restricted to the Himalayas, thus it is unclear whether these results are representative across the entire species range. Furthermore, we still lack data on individual marking frequencies. These knowledge gaps limit our ability to understand the behavioral ecology of snow leopards, which has implications for monitoring their populations. This is particularly relevant for camera-trapping surveys, which are nowadays the main method for estimating snow leopard abundance and camera-traps are often placed on marking sites (Jackson et al. 2006; Oberosler et al. 2022). However, it remains unknown to what degree the number of marking signs could predict snow leopard visitation rates in camera-trapping surveys.

To fill these knowledge gaps and provide more complete understanding of snow leopard communication behavior, we conducted the first study that combines camera-trapping, snow-tracking and transect counts of scrapes to measure the frequency of different communication behaviors by snow leopards in both space and time. We also tested how intrinsic (sex) and environmental variables (habitat type, weather conditions and moon phase) influence the marking frequency. Our study focused on the northern part of snow leopard distribution (Altai Mountains, Mongolia), where communication behavior remains poorly studied. We compared our results with previous research from the Himalayas and captivity, which allowed us to provide a more complete picture of snow leopard communication behavior across its range. Furthermore, we compared the results from snow leopard communication behaviors with results on detection rates from camera-trapping surveys conducted simultaneously in the same areas (Oberosler et al. 2022). This comparison allowed testing if the number of scrapes predicted the visitation rates, in order to provide guidelines for improving efficiency for future monitoring of snow leopards with the use of camera-trapping.

Materials and methods

Study area

We conducted most of our research in the Sutai mountain region (centered on 46°37' N, 93°35' E), an isolated massif in southwestern Mongolia that is part of the greater Altai Mountains (Fig. 2). The elevation of the mountain massif ranges between approximately 1800 m in valley bottoms, up to 4220 m at the mountain peaks. The region is characterized by a cold semi-arid climate, with strong winds, long cold winters and short summers, during which most precipitation falls. Desert-steppe vegetation is predominant with small patches of larch (*Larix sibirica*) forests on the northern slopes. Semi-nomadic herder families live across

the mountain range, moving seasonally to rotate grazing areas for their livestock. Density of snow leopards in Sutai was estimated at 1.31 individuals/100 km² (Oberosler et al. 2022). To increase the sample size for testing the relationship between the number of snow leopard signs (scrapes) and detection rates, we also used number of observed scrapes at the camera-trapping sites and snow leopard detection data collected in the Aj Bogd mountain massif (centered on 44°80' N, 95°19' E). This area is located approximately 240 km to the southeast of Sutai in the Altai-Gobi region and presents generally similar environmental, topographic, and climatic characteristics as Sutai, but lacking permanent ice cover. The massif elevation ranges from 1,600 to 3,800 m a.s.l.

Field methods

We used a combination of three methods (camera-trapping, snow-tracking and transect count of scrapes along linear topographic features) to collect data on occurrence and communication behaviors of snow leopards. We measured both spatial and temporal marking rates, as well as visitation rates at the monitored marking sites. First, we used camera-trapping to measure visitation rates of snow leopards (i.e. frequency of snow leopards visiting given marking site regardless of whether they marked the site or not during their visits). We used camera-trapping also to measure marking rates in time, which was done at the population level (any snow leopard marking given site) and at the individual level (frequency of particular individual marking the site; see below for methods used for individual-recognition). To estimate marking frequency in space, we used snow-tracking to measure individual marking rates along the path of a tracked snow leopard. In addition to estimating individual marking rates, we conducted transect counts along linear features (several types of ridges and valleys) to count the number of cumulative scrapes along the transect. These scrapes were often made in different times and possibly by several individuals. This measure provided us with information about relative distribution of scrapes in space and enabled us to compare relative marking frequency among different habitats. Because our study involved focal animals in the field, it was not possible to record data blind.

For camera-trapping in Sutai, we created a 4 × 4 km² grid and placed a camera trap in each grid on expected snow leopard marking sites or trails (see Oberosler et al. 2022 for further details). We monitored 61 sites with camera-traps from March 16 to June 29, 2019, covering approximately 850 km² from elevations of 2,115 to 3797 m. Among the 61 monitored sites, we determined that 43 were snow leopard marking sites (i.e., locations where marking by snow leopards was confirmed either by the presence of scrapes

at camera deployment or by communication behaviors recorded with camera-trapping during snow leopard visits to the sites) and 18 were treated as non-marking sites.

We used Reconyx HC500, HC600 and Hyperfire2 (Reconyx Inc., Holmen, WI, USA) camera traps, which take color images at day and monochromatic images at night, with a trigger time of 0.20 s. They were set to work in continuous mode, with no delay between consecutive triggers. We used a single camera trap at each sampling site, usually placed on rocks approx. 50 cm above the ground, and no baits or lures were used. The camera traps recorded the date, time, moon phase, and temperature for each photograph. After sampling completion, we extracted snow leopard images from the whole dataset and reviewed them independently by three different observers to identify individuals using the coat patterns along with any other potential distinctive characteristics and to determine sex by the presence/absence of scrotum (Jackson et al. 2006; Krofel et al. 2021; Oberosler et al. 2022). For each recorded snow leopard visit, we also recorded the visit duration, whether snow leopards exhibited any of the communication behaviors outlined in Table 1 and, if so, the duration of these behaviors. We also noted the weather (precipitating or not), temperature and whether snow was present on the ground or not for each photo during snow leopard visits. When several visits by the same individual were recorded at the same marking site, we recorded the interval between consecutive visits with marking (removing intervals that were less than 1 day apart) to estimate how often individual snow leopards return to the same locations to renew their markings.

In Sutai, we also followed snow leopard tracks in freshly fallen snow to record the frequency of different marking behaviors for individual animals moving through the environment. We used a handheld GPS to record the course and length of the animal path, and noted the coordinates for each type of marking. Scrapes were easily recognizable by fresh pits excavated in the snow, while we checked for hair and smell of urine every time snow leopards approached vertical objects with the hind or front part of the body to confirm urine spraying or head/body rubbing, respectively (following Krofel et al. 2017). With this method we could not detect investigating behaviors (sniffing and flehmen), because these usually do not leave detectable signs. For each marking, we recorded whether it was placed on the sunny (i.e. facing southern directions: southeast, south or southwest) or shady side of valleys (i.e. facing northern directions: northeast, north or northwest). We also recorded the object that was marked (for urine spraying, head/body rubbing and claw marking), or next to which the mark was made (for scraping and fecal deposition), including rocks (<3 m high), cliffs (>3 m high), trees, ridge saddles and flat ground. For rocks and cliffs, we also noted whether the marked surface

was overhanging, vertical or sloping. Due to minimal snow conditions during the fieldwork, we were limited to following trails on three occasions totaling 2,665 m of tracking. Most of these data were recorded along the river valleys (86%), as usually there was not enough snow on the mountain slopes and ridges to continue tracking once the snow leopards left the valleys.

Lastly, in Sutai we used transect surveys to count and determine the spatial distribution of snow leopard scrape sites and individual scrapes in respect to habitat characteristics. We defined scrape site as an area containing one or more scrapes, typically up to 100 m² in size and often located next to some kind of vertical object, on a ridge or on saddle. When counting the number of individual scrapes per site, we only considered obviously distinct scrapes, thus it is possible that some of the older scrapes that were over-marked might have been missed. We sampled along 32 transect surveys (total length=49.3 km) distributed across habitats with linear features (i.e. valleys and ridges). On transects we marked each scrape site and number of scrapes per site, noting the type of habitat (gorges, narrow valleys, wide valleys, narrow ridges and wide ridges), the orientation of the nearest vertical object (N, NE, E, SE, S, SW, W, NW), the type of substrate (sand, grass, leaves, snow), elevation and distance to the closest human disturbance. We defined gorges as valleys with cliffs on both sides of the valley, narrow valleys had bottoms (riverbed)<30 m wide (and no cliffs or cliff on only one side of the valley), and wide valleys had bottoms>30 m wide. Narrow ridges had clear ridgeline with steep slopes on both sides, while wide ridges had rounded, not clearly defined ridgelines. For human disturbance we collected locations of human presence and activities in the region, including an extended coal mine complex, human settlements and gers (individual households) used by people during sampling. For a subsample of scrapes ($n=72$) we also measured the overall length and width of the scrape, the length of the scrape mound and scrape pit, and the depth of the scrape pit.

To increase the sample size for predicting the number of detected snow leopard visits at the camera-trap sites based on the number of scrapes observed at site, we added data obtained in 2022 from 58 camera-trapping sites deployed in the Aj Bogd mountains. In this area we sampled 58 sites with camera-traps from March 24 to June 13, 2022, covering approximately 1,000 km² from elevations of 1,666 to 3,484 m a.s.l. We used the same cameras and deployment approach as described above for Sutai, but other data on marking behavior are not available from this study site, beside number of scrapes at the camera-trapping sites.

Statistical analyses

We used program R version 4.2.1 (R Core Team 2022) for all statistical analyses. We used t-tests to analyze differences in means and chi-square and Fisher's exact test to analyze differences in proportions, and a simple linear regression to investigate the effect of temperature on visit duration (*stats* v4.2 package; R Core Team 2022). To test how well the number of scrapes and other covariates related to a potential camera-trapping site predict snow leopard visitation rates, we used data from snow leopard camera-trapping surveys and built generalized linear models (GLM) with a negative binomial distribution, using the *MASS* package (v7.3-60.2; Venables and Ripley 2002). We used this instead of the Poisson distribution because the GLMs with the Poisson distribution indicated overdispersion and zero-inflation (measured with the *DHARMA* package, v0.4.7; Hartig 2024), and was thus a bad fit to our data. We used the number of visits per 100 days as response variable, for which we divided the number of independent snow leopard records (i.e. snow leopard detections recorded within 60 min were classified as the same record to avoid pseudo-replication) by the total number of days of camera deployment, and then multiplied it by 100 (Online Resource Material 2, Table S8). This was done in order to standardize the data and account for the differences in deployment days among the camera-trapping sites. As covariates we included the number of scrapes observed at the site, the distance to the closest human disturbance, topographic features (i.e. elevation, slope, and aspect), and study area (binary, with Aj Bogd as reference category). We obtained elevation from a digital elevation model with a 30-m resolution (ASTER DEM, Source: <http://search.earthdata.nasa.gov/>). We used the DEM layer to calculate slope and aspect, using the *terra* package (v1.7-23; Hijmans et al. 2022). We reclassified the aspect layer into four different categories: north (from 315° to 44°), east (from 45° to 135°), south (from 136° to 225°), and west (from 226° to 315°). We built several models with our set of covariates, as well as a null model, in order to evaluate the potential gain of adding these covariates in explaining snow leopard visits. We compared AIC values (Akaike's Information Criteria; Anderson and Burnham 2002) and calculated the difference (Δ) in AIC (lower values indicate a better fit) of each model to a null model (Online Resource Material 1, Table S1). We considered the estimated coefficients from the model(s) with the better fit ($\Delta\text{AIC} \leq 2$, Anderson and Burnham 2002) to evaluate our hypotheses. If two models showed a $\Delta\text{AIC} \leq 2$, we selected the simplest model. Furthermore, we examined model fit visually with QQ plots and residual plots using the *DHARMA* package. We did not detect spatial autocorrelation in the raw data or in the model residuals (Online Resource Material 1, Table S2; Moran's I,

ape package, v5.8; Paradis and Schliep 2019). Prior to modelling, we tested for collinearity between covariates using the variance inflation factor (VIF) and we did not combine in the same model variables that had a factor value > 3 (Zuur et al. 2010). We rescaled all the continuous covariates by subtracting their mean and dividing by 2 standard deviations (Gelman 2008), to improve model convergence.

Results

Visitation to marking sites

At 43 marking sites monitored by camera-traps in Sutai, we documented 5.12 ± 0.56 (mean \pm SE) snow leopard visits per 100 trap nights ($n=4,014$ trap nights). We identified 23 individuals, including seven females, 11 males and five individuals of unknown sex. We could identify individuals and determine sex in 75.6% and 67.5% of the visits ($n=234$), respectively. Visitation varied significantly by sex (t-test, $df=84$, $p=0.001$), with males visiting the marking sites more than twice as often as females (males: 2.62 ± 0.35 ; females: 1.13 ± 0.27). The mean visit duration was 38.8 ± 8.7 s, and there was no evidence of variation by sex (t-test, $df=148$, $p=0.79$) with males averaging 46.1 ± 17.1 s and females 38.8 ± 12.1 s. Most visits were in dry weather (95.0%, $n=209$), without snow on the ground (76.8%, $n=169$). We did not find evidence that visit duration would be affected by snowing (t-test, $df=218$, $p=0.58$) or temperature (linear regression, $df=201$, $R^2=0.01$, $p=0.74$). Visits were relatively constant in occurrence across the moon phases (chi-square tests, $p>0.2$), with the most visits in the waning gibbous phase (16.8%, $n=37$) and least visits in the waning crescent phase (9.5%, $n=21$).

Communication behaviors recorded with camera-trapping

With camera traps deployed at the marking sites, we documented five of seven expected communication behaviors during 220 visits by snow leopards (Table 1; Fig. 1), with fecal deposition and claw marking not documented (although they were detected with snow-tracking, see below). The frequency of communication behaviors at individual marking sites was 3.09 per 100 trap nights for sniffing ($n=124$), 0.97 for urine spraying ($n=39$), 0.92 for scraping ($n=37$), 0.37 for head/body rubbing ($n=15$) and 0.35 for the flehmen response ($n=14$; Fig. 3) (Online Resource Material 2, Table S4). When considering individual identity of snow leopards and repeated visits with marking behaviors at the same marking location, the same individual renewed

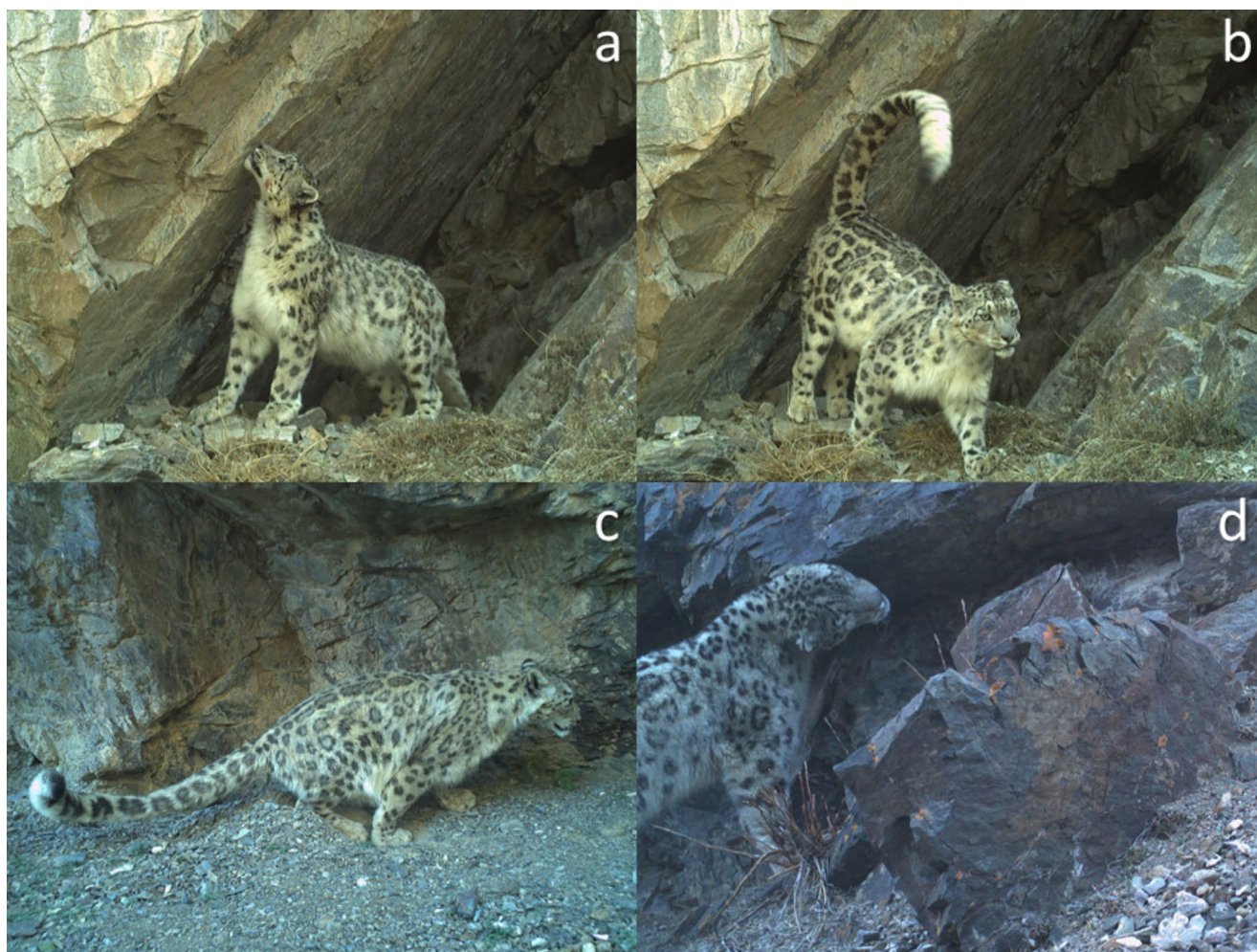


Fig. 1 Examples of the four most frequent communication behaviors by snow leopards detected by camera-traps at marking sites in Altai, Mongolia: **a**) sniffing, **b**) urine spraying, **c**) scraping, and **d**) head rubbing

the marking on average (\pm SD) at intervals of 15.82 ± 12.52 days ($n=24$).

At least one communication behavior was exhibited at 69.5% of the visits ($n=220$). Urine spraying was never exhibited more than once per visit, while scraping, head/body rubbing, and the flehmen response each had one visit where the behavior was exhibited twice. The exception to this pattern was sniffing, which was exhibited once in 83.1%, twice in 13.7% and three times in 3.2% of visits including this behavior. Among visits with communication behavior ($n=153$), 78.4% began with sniffing before progressing to other behaviors and sniffing was exhibited at more visits (56.4%, $n=124$; chi-square test, $p<0.0001$; Fig. 3) than any other communication behaviors, and it was the only behavior exhibited at 29.1% of visits. Urine spraying (at 17.7% of visits, $n=39$) and scraping (16.8%, $n=37$) were exhibited at similar proportion of visits (Fig. 3) and more often (chi-square tests, $p \leq 0.001$) than head/body rubbing (6.8%, $n=15$) or the flehmen response (6.4%, $n=14$).

Males and females exhibited sniffing, scraping, head/body rubbing, and flehmen response at similar proportions of visits (chi-square and Fisher's exact tests, $p>0.45$; Fig. 3), but males urine sprayed at considerably more visits than females (male=24.8%, female=8.9%, Fisher's exact test, $p=0.03$) (Online Resource Material 2, Table S4).

We did not detect any significant effect of precipitation or snow cover on the frequency of communication behaviors during snow leopard visits (chi-square tests, $p>0.10$).

Communication behaviors recorded with snow tracking

During the three snow tracking sessions we recorded 72 marking events (Online Resource Material 2, Table S5). We documented five communication behaviors, including all producing behaviors and two that were not detected with camera-trapping (i.e., claw marking and defecation). However, limited snow availability during our fieldwork

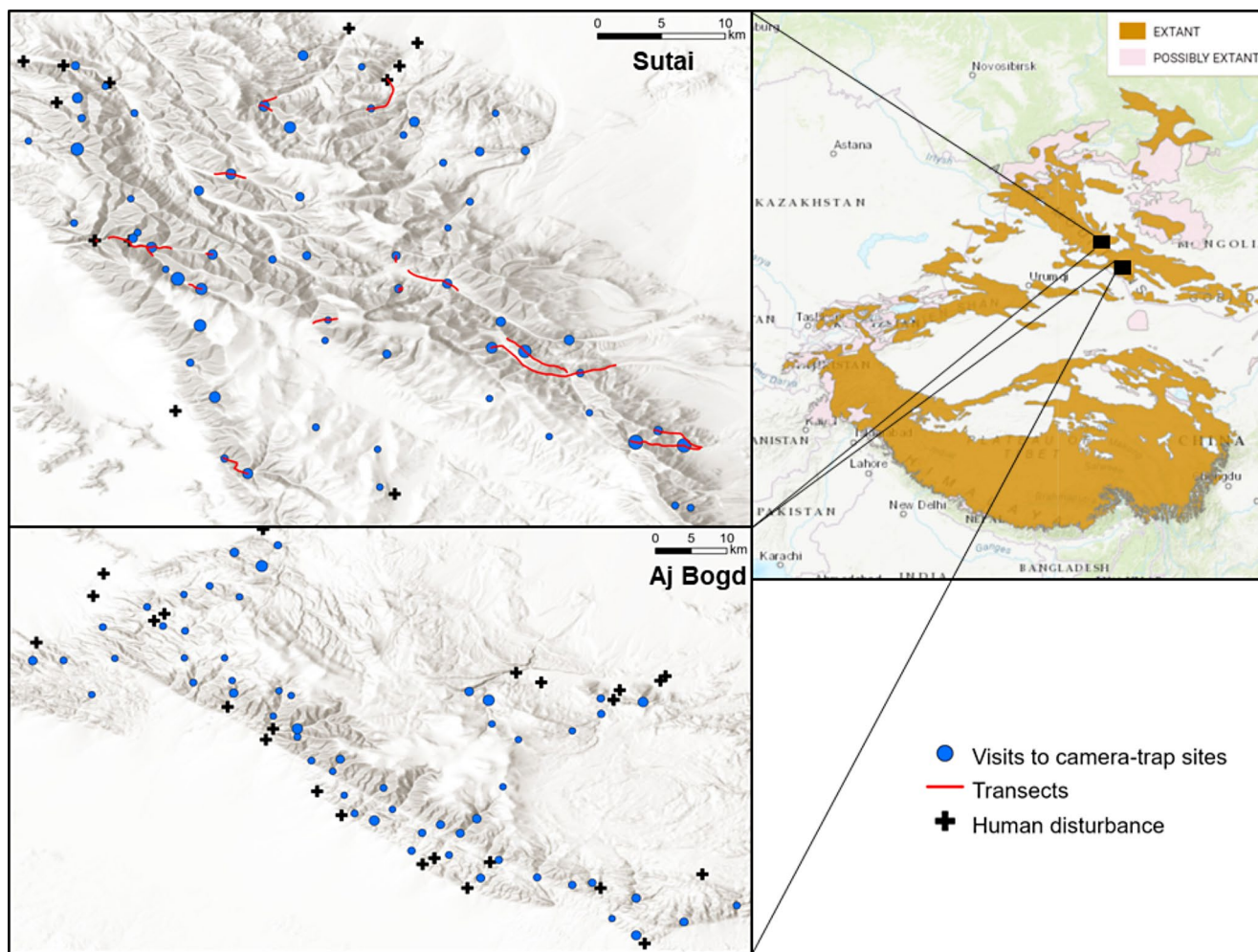


Fig. 2 Study areas with locations of camera-trapping sites (larger circles indicate more snow leopard visits per site; range is 0–14 snow leopard visits per site), transects with scrape counts (red lines) and locations of human disturbance sources (i.e. settlements, gers, and

mines) for Sutai (top left) and Aj Bogd (bottom left). The location of the study areas within the snow leopard global range (source: McCarthy et al. 2017) is shown in the map on the right



Fig. 3 Proportion of snow leopard visits ($n=220$) with different communication behaviors by all, male, female and unsexed individuals recorded with camera-traps at marking sites in Sutai, Mongolia in March–June 2019

precluded most statistical tests due to small sample sizes. Scraping was the most frequent communication behavior with 12.8 ± 4.0 (mean \pm SE) scrapes/km, followed by urine spraying with 10.5 ± 1.6 marks/km. Head and body rubbing was exhibited at 7.5 ± 1.4 marks/km, fecal deposition at 0.8 ± 0.5 mark/km, and claw marking at 0.4 mark/km.

Scrapes ($n=26$) were found equally (50.0% of each) at the sunny and shady side of valleys, while urine sprays ($n=28$) were slightly more often in the sunny side (61.5%) than shady side (38.5%), and body/head rubbing ($n=17$) was equally (50.0% of each) in the sunny and shady side of valleys. Scrapes were more often along cliffs (77.2%) than other landscape features (Fisher’s exact test, $p < 0.001$), while urine sprays were equally on cliffs (50.0%) and rocks (41.7%), and head/body rubbings were more often on cliffs (66.7%) than rocks (33.3%). Marking on cliffs and rocks ($n=69$) was most frequent on overhanging surfaces (compared to vertical or sloping surfaces) for all of the three most

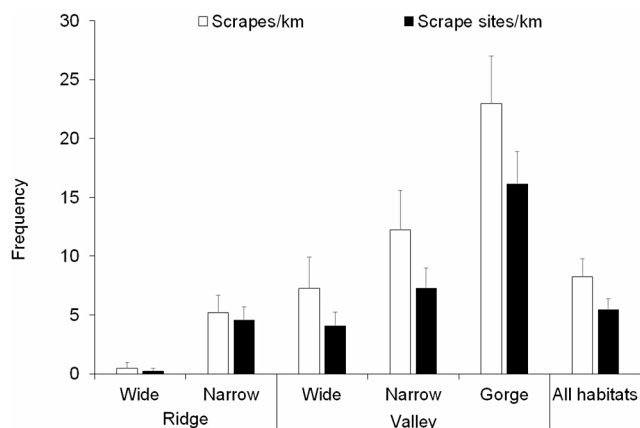


Fig. 4 Frequency (\pm SE) of scrapes and scrape sites made by snow leopards on 32 transects sampled along different types of ridges and valleys in Sutai, Mongolia (total transect length=49.7 km; $n_{\text{scrapes}} = 335$, $n_{\text{scrape sites}} = 217$)

frequent behaviors: scrapes (75.0%), urine sprays (57.1%), and head/body rubbing (75.0%).

Scrapes recorded along transects

We collected data along 32 transects totaling 49.7 km (mean length \pm SD: 1.55 ± 0.29 km) and in total documented 335 individual scrapes at 217 scrape sites with a mean of 1.51 ± 0.06 scrapes per scrape site (range: 1–8 scrapes per scrape site) (Online Resource Material 2, Table S6). Note that observed values do not refer to the individual marking rates, but to the total number of cumulative scrapes, which were often made in different times and possibly by several individuals.

The mean \pm SE frequency for all transects was 8.0 ± 1.5 scrapes/km and 5.3 ± 0.9 scrape sites/km. We recorded higher frequency of scrapes in the valleys (10.9 ± 2.2 scrapes/km) than on the ridges (3.8 ± 1.2 scrapes/km; t-test, $df=30$, $t=2.54$, $p=0.02$). Among different types of valleys, gorges had the highest frequency of scrapes (20.6 ± 4.0 scrapes/km), followed by narrow valleys (12.2 ± 3.4 scrapes/km; comparison with gorges: t-test, $df=7$, $t=1.32$, $p=0.23$) and wide valleys (7.2 ± 2.7 ; comparison with gorges: t-test, $df=11$, $t=2.30$, $p=0.04$). Among ridges, narrow ridges had considerably more scrapes/km (5.2 ± 1.5) compared to wide ridges (0.5 ± 0.5), although the significance was marginal (t-test, $df=11$, $t=1.80$, $p=0.06$). The same patterns also held for scrape sites/km (Fig. 4).

We measured dimensions of 72 scrapes (Online Resource Material 2, Table S7), which averaged (\pm SD) 35.3 ± 0.7 cm in total length, with the scrape pit averaging 25.0 ± 0.6 cm and the scrape mound averaging 10.4 ± 0.4 cm. The average width of scrapes was 24.4 ± 0.4 cm, while the scrape pit averaged 4.6 ± 0.2 cm in depth, and the scrape mound

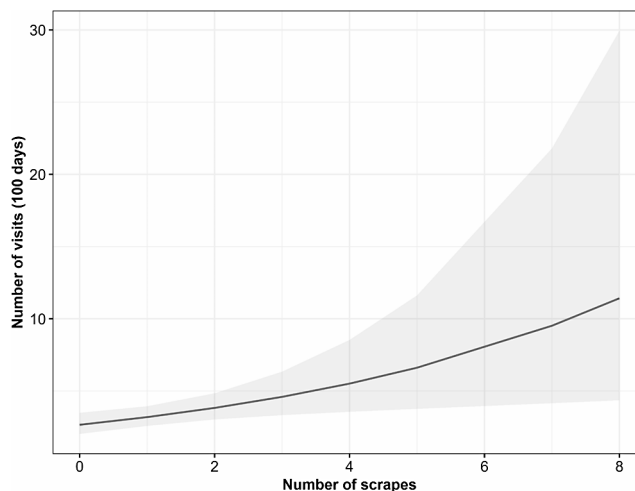


Fig. 5 Number of snow leopard visits in respect to the number of scrapes observed at a camera-trapping location predicted by the top-ranked model. The shaded grey area shows the 95% confidence intervals

averaged 7.8 ± 0.3 cm in height. At the scrape sites, we found scat at 14.7% of sites (maximum=2 scats), urine marking at 4.6% of sites, and hair at 1.8% of sites. Scrape sites were more often made in the sand/gravel (86.6%) than any other substrate (chi-square tests, $p<0.0001$), and they were more often located on the sunny side of valleys (60.9%) than the shady side of valleys or in the middle of the riverbed (chi-square tests, $p<0.0001$). There was also evidence that scrape sites were more often next to high cliffs (44.6%) than other objects (chi-square tests, $p<0.01$), but were also frequently found at ridge saddles (27.7%) or next to rocks (21.6%). There was strong evidence that scrape sites faced south significantly more often than any other direction (47.5%, chi-square tests, $p<0.0001$).

Number of scrapes and snow leopard visitation rates at the camera-trapping sites

Camera-trapping sites with at least one scrape had 2.1-times more snow leopard visits (3.69 ± 3.32 visits per 100 trapping days) compared with sites without scrapes (1.75 ± 2.73) (Online Resource Material 2, Table S8). The best model explaining the number of snow leopard visits included only the number of scrapes at the camera-trapping sites while all other models had $\Delta\text{AIC}>2$ and therefore were not evaluated further (Online Resource Material 1, Table S1). The model predicted a steady increase in the expected number of snow leopard detections with an increasing number of scrapes observed at the camera-trapping site (Fig. 5; Online Resource Material 1, Table S3).

Discussion

We used a combination of three different methods to study communication behaviors in snow leopards. This allowed us to detect a broad range of communication behaviors and provided some of the first insights into marking behavior of snow leopards in the wild. Furthermore, we established that the number of marking signs (i.e. scrapes) observed in the field highly correlates with the snow leopard visitation rates. Therefore, the number of scrapes at potential camera-trapping site can be used as a useful predictor of snow leopard photo-captures to guide the selection of sites used for camera-trapping surveys. This approach should increase the efficiency of snow leopard monitoring programs and improve density estimates in capture-recapture analyses.

Each of the methods used had its own benefits and drawbacks. Camera traps allow visual documentation of communication behaviors, including the sequence of behaviors performed, the duration of each behavior and marking rates in time, including return intervals for individual animals. A drawback of camera traps is that they only monitor a point location, not allowing to detect local shifts in marking sites outside of the camera viewpoint and not documenting anything if placed poorly. Snow tracking provides nuanced understanding of in-situ behaviors and individual marking rates in respect to the distance travelled. However, this method is season-dependent and limited by snow availability, with unpredictable or low snow cover in many parts of the snow leopard range. Snow tracking also requires considerable effort and makes it difficult to detect animals' investigating communication behaviors (e.g. sniffing), although these could possibly be interpreted from the positioning of tracks. Transects with sign surveys provide understanding of abundance and spatial distribution of marking sites across the landscape, but are limited to only certain communication behaviors (mainly scraping) and provide little information on the number, identity or sex of the individuals that left the signs. The benefit of using all three methods simultaneously is that it provides a more holistic understanding of the full spectrum of snow leopard behaviors and minimizes the drawbacks inherent in each method. Using these multiple methods, we were able to document all seven communication behaviors previously described for snow leopards in the wild, although no single method detected all behaviors. For example, we did not document claw marking with camera traps, which was due to low number of camera-trapping sites set at trees. On the other hand, we could not detect investigative behaviors (sniffing and the flehmen response) with snow tracking and transects, although sniffing was the most frequent behavior exhibited with our camera trap monitoring.

Similar to other felids (e.g., Allen et al. 2014, 2016; Vogt et al. 2014), the most frequent communication behaviors of snow leopard were those connected with obtaining information (investigation), especially sniffing, which was usually the first behavior exhibited at visits to marking sites we monitored with camera traps. In this way, snow leopards likely obtained information about previous scent marks left by themselves, other snow leopards and possibly other species. This information was possibly used for decision-making about leaving a new marking or not. Among producing communication behaviors, both snow-tracking and camera-trapping suggest that scraping and urine-spraying are the most frequently used marking behaviors and occur at similar rates, while defecating, head/body rubbing and clawing are used less frequently. Previous research in the Himalayas suggested that scraping and defecating are the most frequent communication behaviors of snow leopards (Ahlborn and Jackson 1988; Sharma et al. 2006; Wolf and Ale 2009). This difference might be connected to the different methodologies applied, as previous studies relied primarily on sign surveys, which make behaviors that leave less conspicuous signs (i.e., urine spraying and head/body rubbing) difficult to detect and possibly underrepresented when sampling. Sign surveys are also unable to detect investigating behaviors.

We provide some of the first estimates of individual marking rates for snow leopards based on snow-tracking and camera-trapping, so there is little previous data available for comparison. The marking rates we documented through snow tracking (12.8 scrapes and 10.5 urine sprays per km) are much higher than the average of 0.3 scrapes and 0.1 scats per km reported for snow leopards by Schaller (1977) based on four marking events. Our estimates are also higher than most records of marking rates published for other large felids walking along linear structures (reviewed in Krofel et al. 2017), comparable only to the marking frequency of Eurasian lynx (*Lynx lynx*) walking along human routes (11.2 urine sprays per km). Our high rates are probably related with the fact that we followed most of the tracks along gorges and narrow valleys, where marking rates appear to be highest (according to the transects data from various habitats). It should also be kept in mind that our sample size from snow-tracking was relatively small (72 marking events) due to low availability of snow and results should be therefore treated with caution, as they might have limited representability.

We obtained larger sample sizes to study marking rates at marking sites monitored with camera-trapping, but also for these estimates there are few data available for comparison from elsewhere. The visitation rates at the marking sites, duration of visits and marking rates we observed for snow leopards appeared to be very similar to values reported for

Eurasian lynx and pumas (*Puma concolor*) in the same season (i.e. late mating season and the following months; Vogt et al. 2014; Allen et al. 2016), probably reflecting the persistence of the felid scent mark, which typically remains detectable to humans for a few weeks (Mohorović and Krofel 2020). Since our dataset was limited to late winter and spring period, it would be valuable to conduct further studies also in the other seasons.

Marking rates could be affected by several extrinsic and intrinsic factors. The former includes the presence of other snow leopards and breeding season, as visitation rates at monitored sites seem to decline in spring and summer (Ahlborn and Jackson 1988). For precipitation, snow cover and moon phase we did not detect significant effects on marking rates. However, we did observe some differences in marking rates between sexes, namely higher urine-spraying rates in males compared to females, while scraping and other communication behaviors were exhibited at similar rates in both sexes. This partly supports previous research from captivity, where similar higher urine-spraying rates were observed in males (Rieger 1978). However, the captive study also reported higher scraping rates in males compared to females, which was not the case in our data from the wild. At the moment it is difficult to determine whether the difference could be connected with captive conditions, seasonal differences or small number of individuals included in the captive study (one male and one female; Rieger 1978). We also observed higher visitation rates to the marking sites by males, which is in line with previous research on other felids, where visits and marking rates are typically higher in males (Smith et al. 1989; Bothma and le Riche 1995; Vogt et al. 2014; Krofel et al. 2017). It should be noted, however, that our sampling period partly overlapped with denning period in females, when their movements are restricted and that there might be additional factors that influence marking rates in snow leopards, which we did not test in this study (e.g. inter-specific interactions; Allen et al. 2023).

More data are available for comparison from previous snow leopard studies for number of scrapes found along transects. These data reflect both individual marking rates, as well as the cumulative markings over time, which may be connected with the habitat selection and population density in given area. The average number of cumulative scrapes (8 scrapes/km) we documented along our transects fit within the range values reported from the Himalayas, including 0.01–11.3 scrapes/km in India (Fox et al. 1991; Sharma et al. 2006) and 28 scrapes/km in Nepal (Ahlborn and Jackson 1988). This corresponds to the data on estimated snow leopard densities, as our study area with estimated of 1.31 individuals/100 km² falls within the medium range reported for this species globally (Oberosler et al. 2022). However, it should be noted that the number of scrapes is not the best

predictor of snow leopard densities, since several other factors influence marking rates, as observed also in this study.

We observed that the marking rate (number of scrapes/km) varied by habitat, with higher rates in the valleys compared to ridges and the highest rates in gorges (23 scrapes/km). This supports results from previous studies that found selection for rivers and valleys (Ahlborn and Jackson 1988; Wolf and Ale 2009). Concentration of scrapes in the valleys may reflect regular use of these habitats by snow leopards for easier and faster travel. Furthermore, valleys could increase the efficiency of communication with marking, as these linear features channelize animal movement and thus increase the probability of a signal being received by a conspecific, similar to what was suggested for marking along the linear human infrastructure by other felids (Krofel et al. 2017; Rafiq et al. 2020). This could be especially relevant for gorges, where movement is most restricted. Besides, abundant vertical and overhanging structures in the gorges provide numerous suitable sites for marking, thus it is not surprising that we observed the highest marking rates in this habitat.

Besides differences in general habitat types, snow leopards appeared to select marking sites also in respect to microhabitat features. We observed a tendency for the snow leopards to scrape and urine-spray on the sunny side of valleys and at rock surfaces facing south. This seems in contradiction with observations from the Himalayas, where snow leopards mostly used northern aspects (Ahlborn and Jackson 1988; Sharma et al. 2006) and is more similar to marking by Eurasian lynx from milder climates (Allen et al. 2017). Scraping and urine spraying was most frequent along or on the cliffs, especially on overhanging surfaces, which supports the findings of previous studies on snow leopards (Ahlborn and Jackson 1988; Sharma et al. 2006) and other felids (Smith et al. 1989; Allen et al. 2017). It is also in accordance with experimental research on persistence of felid odor on various surfaces, which confirmed prolonged durability of scent marks deposited on overhanging rocks (Mohorović and Krofel 2020).

The measurements and shape of scrapes, as well as the frequency of fecal deposition on scrapes that we observed in Altai correspond well with data reported from the Himalayas (Schaller 1977; Ahlborn and Jackson 1988). Thus, overall the documented communication behaviors of snow leopards and their use of specific microhabitats in the Altai Mountains was mostly similar to reports from the Himalayas (Schaller 1977; Ahlborn and Jackson 1988; Fox et al. 1991, 2024; Sharma et al. 2006; Wolf and Ale 2009), with the exception of the preferred aspect of marked surface. This suggests that marking patterns by snow leopards may be largely consistent across their range, at least for most of the parameters studied so far at multiple regions.

Our study also highlights the similarities of snow leopard communication behaviors with other solitary felids (e.g., Smith et al. 1989; Bothma and le Riche 1995; Vogt et al. 2014; Allen et al. 2015, 2016, 2017; Krofel et al. 2017; Rafiq et al. 2020). However, some differences emerged that might warrant further research. Most notably, female snow leopards exhibited scraping behavior as often males, which contrasts with other felid species with scraping behavior, where males scrape more often, such as pumas (Allen et al. 2015) and Sunda clouded leopards (*Neofelis diardi*) (Allen et al. 2016). However, differences between studies may also reflect seasonal variation and the timing of when the studies were performed.

Results on marking behaviors from our study provide important information for optimizing snow leopard monitoring programs, which primarily rely on camera-trapping and often target marking sites (Jackson et al. 2006; Oberosler et al. 2022). An advantage of using marking sites for camera-trapping is the higher detection rate, which generally results in larger sample sizes and consequently more robust density estimates (Fležar et al. 2023). Our data provide clear evidence that the number of snow leopard scrapes observed on the ground at a potential camera-trapping site is not only indicating high frequency of marking behavior, but it is also a good predictor of the future number of visits at the site. Therefore, we recommend that field personnel should pay close attention to the number of scrapes in the landscape and use this indicator for choosing optimal camera-trapping sites. This can significantly increase the number of detections and therefore improve the efficiency of snow leopard surveys and provide more robust density or abundance estimates. Based on the results of spatial distribution of markings, we also recommend focusing the search for potential camera-trapping sites to gorges and narrow valleys, which are the habitats that in our study yielded the highest number of marks and snow leopard visits. Besides, they are often more accessible than high ridges. Using this information can further improve efficiency of snow leopard monitoring, which is often challenging due to remote habitats selected by the species.

Additional advantage of using marking sites for camera-trapping beside increasing the sample sizes include the fact that snow leopards often stop at a marking site to investigate previous marks and/or produce their own marks (in our case an average visit at marking site lasted 37 s). This usually results in large number of clear images that ease individual identification and determination of sex. It also often provides multiple views from both sides of each individual, which helps with individual identification, especially in surveys with a single-camera setup (Jackson et al. 2006; Oberosler et al. 2022; Fležar et al. 2023). However, researchers need to be aware that using marking sites for camera-trapping surveys can also introduce certain biases, for example if location type (marking vs. non-marking sites) and sex are

not taken into account when estimating population densities with spatial capture-recapture (Fležar et al. 2023).

We encourage future studies of communication behavior of snow leopards and other felids to further understand the use and function of their communication behaviors, including potential variation across their distribution range. As demonstrated in this study, such results can also provide important insights relevant for the monitoring and conservation of threatened species.

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Data availability Data generated or analysed during this study are included in this published article and its supplementary information files, except of the sensitive records (i.e. exact coordinates of the marking sites).

Declarations

Ethical approval This study only used non-invasive research methods and therefore no approval of the Ethics Committee was required. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed and the work conforms to the legal requirements of the country in which it was carried out.

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Conflict of interest The authors declare that they have no conflict of interest.

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