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NOTE



Spatio-temporal occurrence and sensitivity to livestock husbandry of Pallas's cat in the Mongolian Altai

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Abstract

Biased research and conservation efforts result in some faunal groups (e.g., small felids) being understudied, and hence these groups are often declining without adequate knowledge to manage for threat reduction. The Pallas's cat (*Otocolobus manul*) occurs across central and western Asia with declining populations and the largest population is likely in Mongolia. A potential threat to this felid is livestock encroachment across its range, including within protected areas, yet we lack a clear understanding of the impact of livestock husbandry on this cat. We used motion-sensitive camera data from 216 sites in 4 study areas in western Mongolia to study the occurrence probability of Pallas's cat in relation to habitat characteristics and occurrence of livestock, and conducted a local assessment within a strictly protected area where we obtained the highest number of detections. We estimated a relatively low occupancy (0.33 ± 0.10), which is associated with sites with natural vegetation, steeper slopes, and greater prey abundance. Occupancy also increased with increasing livestock occurrence, particularly large herds of sheep and goats. Such co-occurrence was partially adjusted by diel activity segregation, presumably to limit direct encounters. Our results suggest that the preferred habitat by Pallas's cat in the study region coincides with areas encroached by livestock. The Pallas's cat's

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habitat is specialized and its dependence on areas that are increasingly used for grazing may eventually threaten the cat with habitat degradation, prey depletion, predation by dogs, and poisoning from pest control. Relevant conservation actions should regulate livestock encroachment within protected areas and improve grazing regimes. The Pallas's cat is an indicator species of mountainous and steppe ecosystems in central Asia; hence, further research towards the preservation of its populations would also benefit other key species across its range.

KEYWORDS

livestock husbandry, occupancy modelling, *Otocolobus manul*, Pallas's cat, regional assessment, small cat conservation, strictly protected area

Wildlife conservation has gained additional public attention because of the current extinction crisis (Pimm et al. 1995, Zhou et al. 2016). Research and conservation efforts are biased, with some faunal groups that are understudied and receive limited conservation funding (Lawler et al. 2006, Brodie 2009). Among mammals, the Felidae family is one of the most threatened taxa (Cardillo et al. 2004, Lamberski 2015), yet the majority of research and conservation effort has targeted the 7 species of large cats, while the 33 species of small cats have been largely overlooked (Brodie 2009). Less than 1% of conservation funding to all wild cats was devoted to small cats (Brodie 2009). Increased knowledge on the occurrence and vulnerability to changes of small cats is desirable. The use of motion-sensitive camera data from studies primarily focused on larger species or on the pool of medium to large mammals (Lama et al. 2019, Li et al. 2020, Greco and Rovero 2021) has potential to provide some of the missing data on small felids. We used data from a study on snow leopard (*Panthera uncia*) in western Mongolia to determine the spatio-temporal patterns of occurrence of the Pallas's cat (*Otocolobus manul*) and its sensitivity to environmental and anthropogenic factors, with a focus on the effects of grazing livestock.

The Pallas's cat, or manul, is a rare small felid with a vast but highly fragmented distribution in the steppes and mountainous areas of central and western Asia. Its dependence on cavities for shelter, vulnerability to aerial and terrestrial predators, and high dietary specialization underline its natural low density and patchy distribution (Ross et al. 2019b), making the species highly vulnerable (Ross et al. 2019b, Purvis et al. 2000). Although it was recently downlisted to least concern status by the International Union for Conservation of Nature (Moqanaki and Ross 2020), the species is declining (Chimed et al. 2021), with many populations that are small and isolated (Ross et al. 2020). While Mongolia is the stronghold of its distribution (Ross et al. 2020), only few inferential studies on their home range, spatial distribution, and density are available (Ross et al. 2019b, Anile et al. 2021, Chimed et al. 2021, Greenspan and Giordano 2021). Various factors threaten the Pallas's cat in Mongolia, including historical direct persecution for fur and medical uses (Barashkova and Smelansky 2011, Ross et al. 2020). Nonetheless, the greatest impact is thought to be caused by livestock overstocking, which causes habitat degradation due to heavy grazing (Ross et al. 2019b), an increase in predation by dogs (Farhadinia et al. 2016), and prey depletion due to eradication campaigns to reduce rodents (Delibes-Mateos et al. 2011, Ross et al. 2020). The number of domestic animals has exponentially increased in Mongolia in the last 20 years due to the worldwide demand for cashmere wool (National Statistical Office of Mongolia 2018). Livestock husbandry occurs throughout the country (Barashkova et al. 2007, Damdinsuren et al. 2008), and is permitted with few limitations even within protected areas according to the Mongolian Law on special protected areas (1994), with the exception of strictly protected areas (SPA). Despite the evidence that overstocking affects the Pallas's cat, quantitative knowledge on how livestock directly or indirectly affect Pallas's cat occurrence and activity pattern is scant.

We examined 4 areas across western Mongolia with different management regimes to estimate Pallas's cat occupancy (MacKenzie et al. 2002) in relation to habitat features, prey availability, and livestock grazing, and to investigate its diel activity pattern in relation to that of livestock. We hypothesized that 1) the cat's occupancy increases at sites that are steeper, have natural vegetation cover, and higher prey availability (Ross et al. 2012); 2) the cat's occupancy decreases at sites with higher livestock presence, or its diel activity pattern minimizes the overlap with that of domestic animals (Sévêque et al. 2020); and 3) large herds of goats and sheep have a greater effect on cat occupancy than the small herds of free-ranging, large-sized livestock (Augugliaro et al. 2020).

STUDY AREA

The Mongolian Altai Mountains extend from the northwestern part of Mongolia to the south, stretching over 900 km, and ranging 500–4,500 m above sea level. The area is characterized by a semi-arid and cold continental climate, with long cold winters reaching temperature of -25°C in January and short summers with little precipitation averaging 45 mm in July and 20°C . The landscape is characterized by rocky, steep, and dry mountains, with high plateaus dominated by dry steppe vegetation, and valley bottoms covered by coniferous trees and sparse shrubs.

We conducted the study in 4 areas within the Altai Mountains range of Mongolia in 2015–2019 (Figure 1). The Siilkhem National Park, Part B (Siilkhem B; $49^{\circ}49'\text{N}$, $89^{\circ}44'\text{E}$; $1,400\text{ km}^2$) and the Tavan Bogd National Park (Tavan Bogd; $48^{\circ}3'\text{N}$, $88^{\circ}37'\text{E}$; $6,362\text{ km}^2$) are located at the northwestern corner of the country, bordering Russia and China. Tavan Bogd is the largest protected area in Mongolia, with the highest elevation in the country (4,374 m) at Khuiten Uul Mountain. To the south, approximately 45 km from the Chinese border, lies the Khork Serkh ($47^{\circ}93'\text{N}$, $90^{\circ}99'\text{E}$; 659 km^2), which is an SPA established in 1977, located between Bayan Olgii and Hovd provinces. The fourth area, Sutai massif ($46^{\circ}37'\text{N}$, $93^{\circ}35'\text{E}$; 850 km^2), is an inland, remote and isolated area that had no legal protection when surveyed, but it was granted Nature Reserve status in 2020. All 4 study areas fell within the range of potentially suitable habitat for the Pallas's cat (Barashkova et al. 2019, Ross et al. 2020, Greenspan and Giordano 2021; Figure 1).

Beside the Pallas's cat, the community of medium to large mammalian species in western Mongolia includes a variety of large and meso carnivores including snow leopards, wolves (*Canis lupus*), wolverines (*Gulo gulo*), foxes

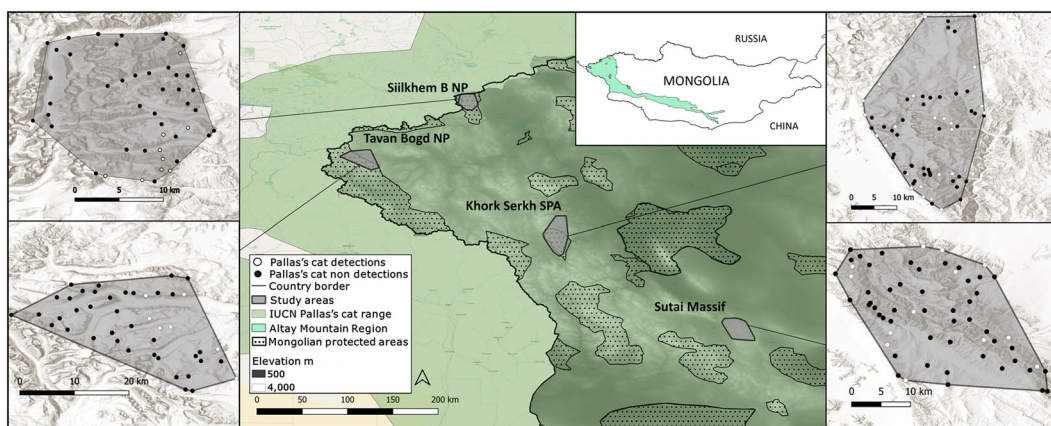


FIGURE 1 Western Mongolia with the 4 study areas: Siilkhem B National Park (sampled in 2015), Tavan Bogd National Park (2017), Khork Serkh Strictly Protected Area (2018), and Sutai Massif (2019). Pallas's cat distribution range is from the International Union for Conservation of Nature (IUCN) Red List website (Ross et al. 2020)



(*Vulpes vulpes*), lynxes (*Lynx lynx*), bears (*Ursus arctos*), and mustelids. Siberian ibexes (*Capra sibirica*), argali (*Ovis ammon*), and marmots (*Marmota marmota*) are the main wild herbivores. In the study area, human density is 1.5 person/km², with approximately 30% of the population being pastoral nomads or semi-nomads (Dagvadorj et al. 2009, World Bank 2018). Pastoralism is the primary form of livelihood in the country, with herder families moving seasonally to different grazing areas. In the province of Bayan Olgii alone, where the first 3 study areas are located, 2.2 million head of livestock were reported in 2018, 1.9 million of which were sheep and goats (National Statistics Office of Mongolia 2020). Except for the SPAs, traditional livestock husbandry is permitted in national parks only within limited use zones. Herd size can exceed 1,000 animals (Augugliaro et al. 2020), with large livestock (e.g., cows, yaks, horses) that are usually free-ranging in small clusters, while goats and sheep form large herds and are generally guarded by herders with dogs during the day and moved into corrals at night.

METHODS

Motion-sensitive cameras

For every study area, we collected motion-sensitive camera data in spring (Mar–Jun) from 2015 to 2019, sampling one study area per year with the exception of 2016 (Table S1, available in Supporting Information). We sampled 48–63 sites per study area (Table S1) with a criterion of ≥ 1.5 km between adjacent cameras. The regular design was constrained by topography and snow cover, and hence accessibility (Figure 1). Sampled sites covered 500–1,100 km² per study area at an elevation from 1,900 m to 3,500 m (Table S1). We placed motion-sensitive cameras on narrow valleys and ridges to maximize the chances to detect passing wildlife. Albeit aimed at primarily detecting snow leopards, such design and site selection proved efficient at detecting livestock and other wild mammals (Rovero et al. 2020) including the Pallas's cat. Pallas's cat and snow leopard occur at similar altitudinal ranges in the Altai Mountains (Snow Leopard Network 2014, Moqanaki et al. 2019), and display a comparable marking behavior (Allen et al. 2016). Such behavioral similarity, similar habitat preferences, and the relative homogeneity of the landscape, potentially allows the 2 species to use the same marking spots (Li et al. 2013). This further supports the effectiveness of site selection at detecting the Pallas's cat. We used heat-in-motion triggered cameras of different brands, and considered Reconyx (Holmen, WI, USA) as fast-triggered and other brands (Cuddeback, Green Bay, WI, USA; Browning, Birmingham, AL, USA; and UoVision, Shenzhen, China) as slow-triggered. We set cameras to work in continuous mode for 45–90 days (Table S1), with no delay between photographs; we used alkaline batteries, which outperform other types at cold temperatures. We placed motion-sensitive cameras on rock piles at approximately 50 cm from the ground. Upon retrieving cameras, we annotated images using the open-source software Wild.ID (Fegraus and MacCharty 2016).

Covariates

We used 8 environmental and anthropogenic covariates potentially associated to Pallas's cat occupancy (ψ) and detection probability (p). We selected covariates from a broader set of candidate variables (Table S2, available in Supporting Information) to avoid collinearity, based on Pearson's correlation coefficient ($r = 0.5$ as threshold). Hence, we used the motion-sensitive camera trigger speed (fast and slow) and sampling effort (camera days) as potentially affecting detectability. We derived the relative abundance index (RAI) of the pooled domestic species (i.e., livestock), with a 15-minute interval and normalized by the sampling effort, as an indicator of the intensity of livestock passage. We used site slope, site aspect, study area, and land cover (bare ground, managed ground, natural vegetation) as predictors of occupancy, and the occurrence probability of livestock modeled across sampling sites. We preferred this metric over the RAI of livestock as a predictor of Pallas's cat occupancy because we assumed it



more accurately measured the diffused presence of livestock across the landscape given it accounts for imperfect detection (MacKenzie et al. 2002, MacKenzie and Royle 2005).

We conducted a second analysis using only data from Khork Serkh SPA, where we obtained the highest number of detections of both Pallas's cat and livestock, which enabled us to conduct more detailed analysis of the target species. In addition, for Khork Serkh SPA we distinguished small-sized and large-sized livestock, and modeled their occupancy separately to determine the relative impact on Pallas's cat given their different herding and rearing management regimes (Augugliaro et al. 2020). The use of a greater number of motion-sensitive cameras in this area relative to other areas allowed us to also record small-sized species. Therefore, we recorded detections of voles (*Alticola* spp.) and pikas (*Ochotona* spp.) as preferred Pallas's cat prey (Ross et al. 2010b), and used independent photographs to compute their RAI, which we then used as a covariate of Pallas's cat occupancy.

To estimate livestock occupancy, we merged the number of domestic animals and human detections into a single category (i.e., livestock) and 2 categories (i.e., small and large livestock) for all study areas and the area sampled in 2018, respectively, and used single-season occupancy models. We modeled occupancy in relation to distance to the herders' tents or houses (i.e., ger) and elevation; we also fitted the distance to herders' houses to detectability, on the assumption that livestock herds would be more compact and hence more easily detected where closer to houses. Based on Akaike's Information Criterion (AIC) and model-averaging procedures described below, we derived occupancy estimates at motion-sensitive camera sites, and used them as a covariate of Pallas's cat occupancy models. We extracted all environmental variables using the geo-processing tools available in Quantum GIS (QGIS Development Team 2019), with the land cover extracted using the GLC2000 dataset (European Commission 2003) and altitudes extracted using a 30-m digital elevation model (Jarvis et al. 2008).

Occupancy modeling

We used single-season occupancy models (MacKenzie et al. 2002) to study the spatial patterns of the Pallas's cat in relation to covariates. Occupancy (ψ) is defined as the proportion of sites a species is expected to occur while accounting for imperfect detection, expressed in probability scale. Given the limitations of estimating true occupancy from point detectors within a continuous habitat, we interpreted occupancy as the proportion of area occupied (Neilson et al. 2018). For the multiple-area analysis, we summarized detection and non-detection data in a 2-dimensional array Y_{ij} of 216 sites \times 131 sampling occasions, using a resolution of 1 day. Its elements y_{ij} , denoted if the cat was detected ($y = 1$) or undetected ($y = 0$) at site i during sampling occasion j . We used NA to denote that a site was not sampled during a specific occasion. We ran models using the package unmarked (Fiske and Chandler 2011) in the R environment (R Core Team 2019). We standardized continuous covariates to have mean of zero and unit variance, built models with various combinations of covariates, and included the null model (i.e., no covariates). We ranked models according to the principle of parsimony, using the AIC and considered as equally best-supported those with $\Delta AIC < 2$ (Burnham and Anderson 2002). In the case of multiple best models, we used a model-averaging method through the package AICmodavg (Mazerolle 2019) to estimate the relative importance of the parameters and predicted occupancy and detection probabilities from the averaged models. We used the same procedure for the analysis on Khork Serkh SPA data but without using study area, and including the RAI of prey and the occupancy of both large- and small-sized livestock as covariates. For this study area we also mapped the occupancy values estimated at the scale of motion-sensitive camera sites and derived from the averaged models.

Analysis of diel activity pattern

To investigate activity patterns of livestock and Pallas's cat, we used a kernel density estimation function implemented in the R package overlap (Meredith and Ridout 2014), which allowed us to compute activity distribution



curves for the 2 groups and carry out a pairwise comparison. Hence, we considered all the domestic species as a single category (i.e., livestock) and used the time converted in radians of each independent event (>30 min) of cats and livestock to create temporal density curves (Zimmermann et al. 2016). Specifically, to determine whether the cat shifted diel activity depending on the intensity of site use by livestock, we built 2 density curves for the Pallas's cat: 1 for its detections at sites where livestock were also detected (i.e., RAI of livestock > 0) and 1 for detections at sites where livestock were not detected (RAI = 0). This resulted in 111 sites with and 105 sites without livestock occurrences, corresponding to 63 and 44 detections of Pallas's cat in the 2 subsets, respectively. Thus, to simultaneously compare Pallas's cat and livestock activities and test if the cat's diel activity shifts across the 2 scenarios, we plotted each of the cat's density curves with the one of livestock activity across the whole area. We then tested for significant differences between the 2 pairs of curves with a Wald test (Zimmermann et al. 2016). By using the R package *activity* (Rowcliffe et al. 2014), we computed overlap coefficient (Δ) between the 2 sets of curves, and specifically used Δ_4 for the scenario with livestock and Δ_1 for the one without livestock, in relation to the number of cat's detections (Meredith and Ridout 2014). We then computed 1,000 bootstraps iterations on the overlap values to estimate 95% confidence intervals (Ridout and Linkie 2009). The coefficient assesses the degree of overlap from 1 (complete overlap) to 0 (no overlap). Finally, we used the Welch 2-sample *t*-test to assess if the 2 generated distributions of Δ values were significantly different.

RESULTS

We obtained 1,298 images of Pallas's cats, corresponding to 107 detection events at 52 sites of the 216 sampled, between 2,223 m and 3,300 m in elevation, through 13,890 camera days across all study areas, with an average of 62 camera days per sampling unit (Table 1, S1). We detected 7 domestic species (Table S3, available in Supporting Information) at 111 sites, with an overall mean estimated occurrence probability of 0.51 (Siilkhem B $\psi = 0.55$, Tavan Bogd $\psi = 0.41$, Khork Serkh SPA $\psi = 0.57$, Sutai Massif $\psi = 0.52$). The highest numbers of raw detections (538) and occupancy (0.57) of livestock were recorded at Khork Serkh SPA. Livestock occupancy (as a whole category and considering small- and large-sized livestock separately) increased at lower elevations and in proximity to the herders' camps across the 4 study areas and in the focal area (Table 2; Table S4, available in Supporting Information).

For both the overall and the focal area assessment, multiple Pallas's cat occupancy models were best-supported (Table 3). Pallas's cat average estimated occupancy was 0.33 ± 0.10 (SE), and was lower in Tavan Bogd compared to other study areas (Figure 2A). Estimated detection probability was low ($p = 0.02 \pm 0.003$) and increased where cameras had faster ($p = 0.03 \pm 0.003$) than slower trigger speeds ($p = 0.01 \pm 0.004$). Occupancy was higher in areas with sparse and natural vegetation ($\psi = 0.73 \pm 0.11$) than with bare and managed ground (Table 4; Figure 2B) and it increased significantly with livestock occupancy (Table 4; Figure 2C). In Khork Serkh, the occurrence probability of

TABLE 1 Number of independent events per day and naïve occupancy of domestic species (i.e., livestock, dogs, and humans) and Pallas's cat, and the number of sites where the cat was detected. Data were collected using cameras in the 4 study areas in western Mongolia, 2015–2019

Study area	Protection level	Livestock		Pallas's cat		Number of successful sites
		Events	Naïve ψ	Events	Naïve ψ	
Siilkhem B	National park	316	0.44	11	0.19	9
Tavan Bogd	National park	138	0.29	10	0.16	7
Khork Serkh	Strictly protected	538	0.60	62	0.37	23
Sutai Massif	Unprotected	244	0.62	24	0.21	13

TABLE 2 Parameter estimates from model-averaging of the best-supported models for the occupancy (ψ) and detection (p) probability of livestock in western Mongolia, 2015–2019. For the assessment across the 4 study areas, we considered all livestock, humans, and dogs as a single category, while for the focal area assessment, we considered small- and large-sized livestock separately. Parameters include elevation and distance to herders' tents or houses (i.e., ger)

Parameter	Estimates	SE	Z	P
Four areas, western Mongolia—livestock				
ψ distance to closest ger	−1.11	0.50	2.21	0.03
ψ elevation	−0.38	0.31	1.23	0.21
p distance to closest ger	−0.62	0.18	3.41	<0.01
Focal area, Khork Serkh—small-sized livestock				
ψ distance to closest ger	−1.92	0.64	−2.99	<0.01
ψ elevation	−0.84	0.35	−2.36	0.02
p distance to closest ger	−0.63	0.24	−2.66	<0.01
Focal area, Khork Serkh—large-sized livestock				
ψ distance to closest ger	−0.57	0.49	1.16	0.25
ψ elevation	−0.38	0.31	1.25	0.22
p distance to closest ger	−0.45	0.23	1.96	0.04

the Pallas's cat increased significantly with increasing occupancy of sheep and goats ($\beta = 1.25 \pm 0.47$, $P < 0.01$; Figure 3; Table 4) and the occupancy of large livestock was not retained in the best models, showing a positive but non-significant effect. Similar to the model for all areas, the cat's occupancy increased in habitat with natural vegetation ($\psi = 0.70 \pm 0.12$, $P = 0.01$). Moreover, occupancy tended to increase with increasing steepness of the terrain ($\beta = 0.79 \pm 0.42$, $P = 0.05$), and higher relative abundance of rodents ($\beta = 0.67 \pm 0.41$, $P = 0.09$; Table 4; Figure 3).

Overall, Pallas's cat displayed a cathemeral behavior with multiple peaks of activity through the 24 hours (Figure 4), with detections during 1400–1700 that were less frequent. Across the 4 areas, the overlap between Pallas's cat and livestock curves was lower at sites where livestock was also detected ($\Delta = 0.28$, 95% CI = 0.25–0.31) than at sites where livestock was not detected ($\Delta = 0.45$, 95% CI = 0.41–0.49; Figure 4). The difference in activity pattern was significant in the former case ($W = 20.44$, $P < 0.001$) and non-significant in the latter ($W = 2.26$, $P = 0.13$). The t -test for differences in activity overlaps between the 2 scenarios had a significant outcome ($P < 0.001$).

DISCUSSION

Motion-sensitive camera detections of Pallas's cat from snow leopard surveys in the Mongolian Altai Mountains enabled us to evaluate the spatio-temporal patterns and responses of this little-known felid to a suite of covariates, with a particular focus on the sensitivity to grazing livestock. Previous information on Pallas's cat occupancy was limited to local ecological knowledge (Chimed et al. 2021). We are aware of the limitations of our sampling that primarily targeted the snow leopard (Rovero et al. 2020), and we acknowledge that occupancy may simply reflect the proportion of area used by the Pallas's cat (Efford and Dawson 2012, Neilson et al. 2018). Yet, being a metric that accounts for imperfect detection, its usefulness to assess habitat associations has been revealed by many studies (Niedballa et al. 2015, Gompper et al. 2016, Moll et al. 2016, Greco et al. 2021).



TABLE 3 Summary of the single-species single-season occupancy (ψ) and detection (p) models of the Pallas's cat across the 4 study areas and for the focal area (i.e., Khork Serkh Strictly Protected Area), in western Mongolia, 2015–2019. We ranked models using Akaike's Information Criterion (AIC), and considered models with $\Delta\text{AIC} < 2.00$ equally best-supported. Only the 10 top models and the null models are shown. We also provide number of parameters (K) and Akaike weights (w_i). Focal area models included a relative abundance index (RAI) of domestic livestock, dogs, and humans (domestics), and of prey species

Models	K	AIC	ΔAIC	w_i
Across the 4 areas—western Mongolia				
p (trigger speed) $\sim \psi$ (habitat cover + study area)	8	1,145.84	0.00	0.59
p (trigger speed) $\sim \psi$ (occupancy domestics + habitat cover)	6	1,147.33	1.50	0.28
p (trigger speed) $\sim \psi$ (habitat cover)	5	1,149.45	3.61	0.10
p (trigger speed) $\sim \psi$ (aspect + study area + habitat cover)	9	1,159.93	6.09	0.03
p (trigger speed) $\sim \psi$ (aspect + habitat cover)	8	1,167.31	21.48	0.00
p (trigger speed) $\sim \psi$ (aspect + study area + habitat cover)	11	1,167.83	21.99	0.00
p (trigger speed) $\sim \psi$ (slope + study area)	7	1,170.19	24.36	0.00
p (trigger speed) $\sim \psi$ (slope + habitat cover)	6	1,170.27	24.43	0.00
p (trigger speed) $\sim \psi$ (aspect + occupancy domestics + slope + habitat cover)	10	1,171.01	25.17	0.00
p (trigger speed) $\sim \psi$ (slope + occupancy domestics + study area)	8	1,171.54	25.70	0.00
p (1) $\sim \psi$ (1)	2	1,180.76	34.63	0.00
Focal area—Khork Serkh Strictly Protected Area				
p (trigger speed + RAI domestics) $\sim \psi$ (occupancy small livestock + RAI prey + slope + habitat cover)	9	581.12	0.00	0.43
p (trigger speed + RAI domestics) $\sim \psi$ (occupancy small livestock + slope + habitat cover)	8	582.74	1.62	0.19
p (trigger speed + RAI domestics) $\sim \psi$ (slope \times occupancy small livestock + habitat cover)	9	583.98	2.86	0.10
p (trigger speed + RAI domestics) $\sim \psi$ (occupancy small livestock + habitat cover)	7	584.70	3.58	0.07
p (trigger speed + RAI domestics) $\sim \psi$ (occupancy large livestock + habitat cover + slope)	8	586.05	4.93	0.04
p (trigger speed + RAI domestics) $\sim \psi$ (occupancy small livestock + slope)	6	586.20	5.08	0.03
p (trigger speed + RAI domestics) $\sim \psi$ (slope \times occupancy small livestock)	7	586.97	5.85	0.02
p (trigger speed + RAI domestics) $\sim \psi$ (occupancy small livestock + RAI prey + slope)	7	587.05	5.93	0.02
p (trigger speed + RAI domestics) $\sim \psi$ (occupancy large livestock + habitat)	7	588.60	7.48	0.01
p (trigger speed + RAI domestics) $\sim \psi$ (RAI prey + habitat cover + slope)	8	588.68	7.56	0.00
p (1) $\sim \psi$ (1)	2	647.60	66.48	0.00

Moreover, our inference is related to the gradient of protected areas encroached by livestock (2 national parks, 1 SPA, 1 area that was not protected at the time of sampling), and not to the wider steppe ecosystem in western Mongolia. The moderate occupancy and very low detectability we estimated are broadly consistent with the presumed low density of this species (Ross et al. 2012, Anile et al. 2021), while the proportion of sites used on sites sampled is comparable with that of Chimed et al. (2021). The significantly lower occupancy in Tavan Bogd may

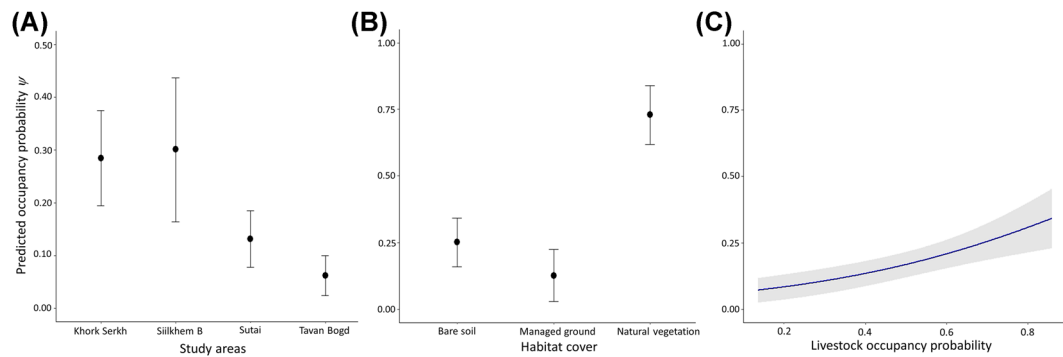


FIGURE 2 Estimated occupancy probability (ψ) of the Pallas's cat in western Mongolia, spring 2015–2019, in relation to A) the study areas, B) the 3 main habitat land cover types, and C) the occupancy of domestic animals (SE in grey). Values are in probability scale and are derived from averaging the best-supported models

TABLE 4 Parameter estimates from model-averaging of the best-supported models of Pallas's cat occupancy (ψ) and detection (p) probability across 4 study areas and a focal area in western Mongolia, 2015–2019

Parameter	Estimates	SE	Z	P
Across the 4 areas—western Mongolia				
ψ habitat cover–natural vegetation	2.11	0.49	4.30	<0.01
ψ habitat cover–managed ground	–0.88	0.83	1.06	0.29
ψ occupancy of domestic animals	0.44	0.22	1.96	0.04
ψ study area–Tavan Bogd NP	–1.78	0.68	2.63	<0.01
ψ study area–Siilkhem B NP	0.07	0.72	0.11	0.92
ψ study area–Sutai Massif	–0.96	0.55	1.75	0.08
p trigger speed – slow	–0.77	0.36	2.17	0.03
Focal area—Khork Serkh Strictly Protected Area				
ψ abundance of small-sized livestock	1.25	0.47	2.62	<0.01
ψ habitat cover–natural vegetation	2.52	1.00	2.52	0.01
ψ habitat cover–managed ground	1.42	1.41	1.01	0.31
ψ slope	0.79	0.42	1.88	0.05
ψ relative abundance of prey species	0.67	0.41	1.66	0.09
p trigger speed–slow	–1.68	0.57	2.96	<0.01
p RAI domestics ^a	–0.15	0.13	1.14	0.26

^aRelative abundance index of domestic livestock, dogs, and humans.

indicate that this area is suboptimal for this felid, likely because it is generally higher in elevation and has more extensive glacial and snow cover relative to the other areas (Ganyushkin et al. 2018). The Pallas's cat appears to prefer areas that are steep, with natural vegetation and higher occurrence of prey, matching the high habitat and dietary specialization known for this species (Ross et al. 2019a, Chimed et al. 2021, Greenspan and Giordano 2021). The importance of areas with vegetation emerged clearly from both analyses (i.e., the entire region and the focal area of Khork Serkh SPA), while a weak preference for steep areas only emerged from the focal area. For this area

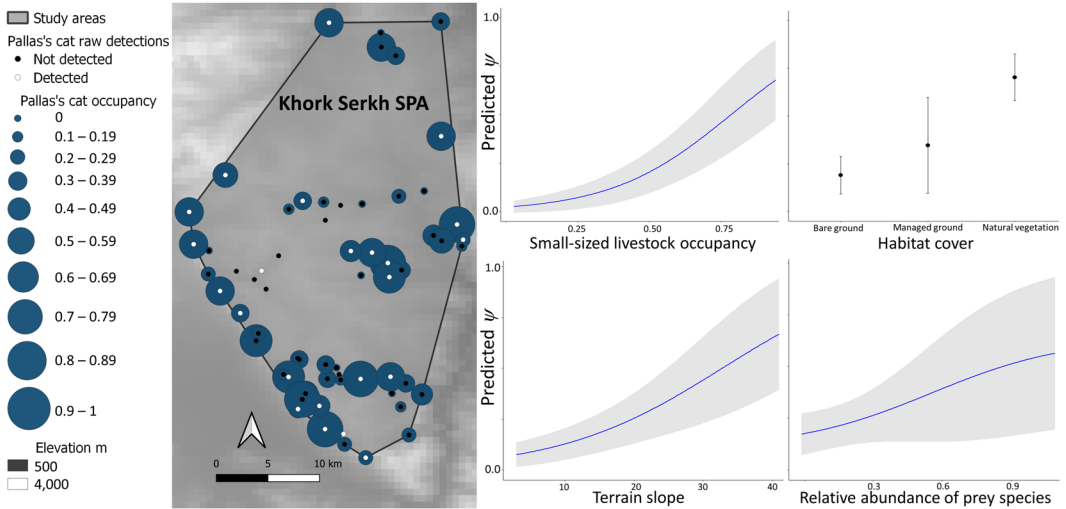


FIGURE 3 Occupancy probability distribution of the Pallas's cat in Khork Serkh Strictly Protected Area (2018), western Mongolia. Circles indicate occupancy probability, with larger ones representing higher values. We modeled occupancy as a function of the occupancy of small-sized domestic animals (i.e., sheep and goats), habitat land cover type, slope, and relative abundance of prey species

we could also consider prey availability in the model, and this variable too resulted to be weakly associated to Pallas's cat's occupancy. The weak association may have been affected by natural fluctuations in the abundance of prey (Andreassen et al. 2021, Otgonbayar and Suuri 2021) or our placement of motion-sensitive cameras to target snow leopard may have biased low the detection of small animals. Similar to the effect of land cover, the positive association with the occupancy of livestock was revealed in both assessments, and it was relatively more attributable to small-sized livestock in the focal area. Pallas's cat was significantly more detectable in all study areas when using fast-trigger motion-sensitive cameras, as reported for other elusive felids and small mammals (Wellington et al. 2014, Greco and Rovero 2021).

The positive association of the Pallas's cat with vegetated and prey-rich habitat where also grazing livestock occur is partially in contrast to our hypothesis. Such spatial association may be due to the higher abundance of prey species near camps due to fertilization promoting vegetation growth (Bülow-Olsen 1980, Ross 2009) or areas with natural vegetation that are associated with a greater presence of pikas and other small rodents (Ross 2009). The presence of livestock could also trigger a form of mesopredator release, with herding dogs and livestock that might disperse larger carnivores (Ross 2009, Anile et al. 2021). The convergence in habitat preferences between domestic species and Pallas's cat suggests that the preferred habitat by the cat in the study region coincides with areas encroached by livestock. The spatial association is especially pronounced with sheep and goats that are managed as large herds and represent the majority of livestock, being therefore of potential greater impact on the vegetated areas (Augugliaro et al. 2020). Thus, the Pallas's cat is able to populate the preferred habitat despite its use by livestock; however, in line with our hypothesis, a coping mechanism is the shift in the diel activity pattern of the felid at grazing sites in the direction of minimizing temporal activity overlap with livestock, which are usually reared in corrals at night in the study region, particularly for small-sized livestock (Augugliaro et al. 2020). In view of these results, we suggest that the convergence between Pallas's cat preferred habitat and grazing areas of livestock may represent a serious, impending threat to the felid, as suggested by its shift in diel activity pattern to limit direct encounters. Temporal niche partitioning in response to anthropogenic disturbance is known from a range of other study systems where wild species co-occur with humans and livestock, with animals minimizing risk by shifting the temporal, rather than the spatial niche (Poudel et al. 2015, Oberosler et al. 2017, Gaynor et al. 2018).

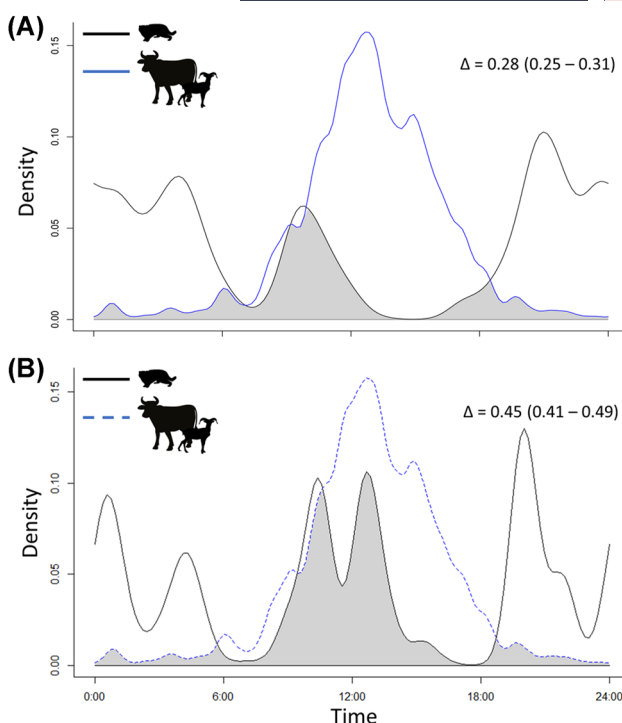


FIGURE 4 Temporal overlap in activity between the Pallas's cat and livestock in western Mongolia, 2015–2019. The figure displays the diel activity pattern of the felid A) at sites where livestock were detected (111 sites, 63 cat's detections) and B) at sites where livestock were not detected (105 sites, 44 cat's detections). Both Pallas's cat activity curves were plotted against the diel activity pattern of livestock across the whole area, to point out the felid's variation in activity pattern. The coefficient (Δ) assessed the degree of overlap between the diel activity curves of the 2 taxa (1 = complete overlap, 0 = no overlap)

When considering that livestock numbers have markedly increased across Mongolia over the last decades (Berger et al. 2013, Pfeiffer et al. 2018), and that we also recorded diffused livestock presence into protected areas (this study, Augugliaro et al. 2020, Salvatori et al. 2021), our findings are of conservation concern for a number of reasons. First, the Pallas's cat is specialized in its habitat choice, and only uses a small fraction of area available within the steppe ecosystem (10–30%; Ross et al. 2019a); it is dependent on areas that are protected but also increasingly used for grazing, which may eventually threaten the cat from habitat degradation affecting the abundance of small rodents, hence progressively reducing prey availability (Cao et al. 2016, Schieltz and Rubenstein 2016). Second, the proximity of preferred areas to herders' houses and camps implies higher chances of Pallas's cat predation by dogs, considered one of the most important causes of human-related deaths of these cats (Ross 2009; Barashkova 2012, 2017), and poisoning, directly as a predator control method or as consequence of poisoning of Pallas's cat's primary prey for pest or disease control (Tseveenmyadag and Nyambayar 2002). This latter threat is particularly critical for Mongolia (Winters 2006). The detrimental effects of such practices and overharvesting are also currently threatening marmot (*Marmota* spp.) species (Zahler et al. 2004, Clayton 2016), on whose cavities Pallas's cats are dependent on for denning and resting sites (Ross et al. 2010a). These concerns are augmented when considering that hunting of Pallas's cats is still permitted in Mongolia (Murdoch et al. 2007, Barclay et al. 2019) where Pallas's cats were traded until recently on local markets (Wingard et al. 2018), poaching of this species within protected areas has been documented as frequently occurring (Murdoch et al. 2007), and Pallas's cats are occasionally shot when mistaken for marmots (Ross et al. 2019b). Field observations from our sampling reported



Pallas's cat skins found in several nomads' tents across 3 out of 4 areas (F. Rovero, University of Florence, and C. Augugliaro, University of Lausanne, personal observation).

Habitat degradation resulting from livestock grazing has detrimental effects on large mammals (Ripple et al. 2014, 2015; Soofi et al. 2018), while a general trend of total abundance declining with grazing is also documented for small mammals (Schultz and Rubenstein 2016). But studies on the specific effects on small carnivores are few and with contrasting outcomes (Blaum et al. 2007a, 2007b, 2009; Bösing et al. 2014; Williams et al. 2018). For example, a study in South Africa reported that stocking rate of livestock was inversely related to local abundance of small- and medium-sized predators, including felids (Blaum et al. 2009). While our data on the Pallas's cat do not provide for inference on population trends, the consistency in the results across study areas with different protection regimes and between the regional and the focal area indicates that the causalities we suggest to explain the spatio-temporal responses of Pallas's cat to livestock are founded.

MANAGEMENT IMPLICATION

We suggest that the most relevant conservation actions for Pallas's cat should include regulations of livestock encroachment within protected areas by improving enforcement efficacy. Additionally, in consideration of the cat's association with natural vegetation and prey abundance, we suggest improving protection for this habitat and banning the eradication campaigns of rodents through poisoning. We further believe that a review of its legal status in Mongolia based on updated and quantitative evidence should be carried out. Because our knowledge of Pallas's cat ecology, behavior, distribution, and population status is scarce, further research on their populations is required for the conservation of the species and to benefit other key species across its range.

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ETHICS STATEMENT

For our research, no animals were handled and permission to conduct the study was granted by the Ministry of Environment and Tourism of Mongolia (protocol number 10/1674).

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SUPPORTING INFORMATION

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