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Scent Marking Mediates Spatial Interactions between Two Sympatric Mesocarnivores in Central Mongolia

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Scent marking is a fundamental component of carnivore communication and can mediate spatial interactions among sympatric species. In this study, we investigated olfactory marking behaviour and interspecific interactions between Pallas's cat (*Otocolobus manul*) and red fox (*Vulpes vulpes*) in the central Mongolian steppe. We aimed to assess whether Pallas's cat exhibits spatial or temporal responses to red fox scent marks. We analyzed data from a continuous camera-trapping survey conducted between August 2020 and August 2024 across 57 sites, totaling 32,722 trap-days.

Independent detection events involving olfactory behaviors were classified into scent-producing and scent-investigative categories. Spatial associations of the marking sites for both species were evaluated using contingency analyses, while temporal responses were assessed by comparing the time intervals between successive marking events. Pallas's cat and red fox were recorded in 267 and 798 independent detection events, respectively, with marking activity detected at 45 of the 57 camera-trap sites. Pallas's cat exhibited six types of olfactory behaviors, whereas red fox exhibited five, with olfactory investigation being the most frequent behavior in both species. Spatial analyses revealed a strong negative association between Pallas's cat and red fox marking sites, indicating marked spatial segregation consistent with avoidance by Pallas's cat. In contrast, no significant difference was detected in the temporal intervals between Pallas's cat markings following red fox activity and intervals between consecutive conspecific markings. These findings demonstrate that Pallas's cat responds to red fox presence primarily through spatial avoidance rather than temporal adjustment of marking behavior. This pattern suggests asymmetric interspecific interactions, potentially reflecting avoidance by Pallas's cat in response to red fox presence, highlighting the role of spatial mechanisms in structuring carnivore coexistence in open steppe ecosystems.

Keywords: Marking sites, Mesocarnivore guild, Olfactory communication, *Otocolobus manaul*, Spatial avoidance, *Vulpes vulpes*

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BACKGROUND

Territorial marking represents a key communicative strategy among mammals, enabling individuals to define ranges, attract mates, establish hierarchies, and signal their presence to conspecifics or potential competitors (Allen et al. 2015). Olfactory communication is central to this behavior, where chemical cues transmit signals from a sender to a receiver, prompting a behavioral or physiological response (Eisenberg and Kleiman 1972). Scent marking plays a crucial role in understanding interactions among different carnivore species that coexist in the same area, emphasizing its significance for conservation efforts amid ongoing biodiversity loss (Davies et al. 2007; Andermann et al. 2020; Krofel et al. 2025). Interactions between apex predators and species occupying lower trophic levels are among the most extensively studied (Allen et al. 2023), as understanding these relationships allows the identification of behavioral patterns and the

formulation of predictive ecological hypotheses (Salvatori et al. 2022; Augugliaro et al. 2021; Franchini et al. 2023). Mesopredators may perceive the presence of apex predators as either a risk factor (Cornhill AND Kerley 2020) or an indicator of food availability (Wikenros et al. 2017; Salvatori et al. 2022; Franchini et al. 2023). Apex predators can therefore exert strong influences on subordinate species, shaping their distribution through avoidance behaviors or reduced access to food resources (Leo et al. 2015; Haswell et al. 2018). A study conducted in the Altai Mountains (Allen et al. 2023) showed that Pallas's cat (*Otocolobus manul*) avoided areas scent-marked by snow leopard (*Panthera uncia*), suggesting that olfactory cues from dominant predators can strongly influence its spatial behavior. However, despite growing evidence that scent marking mediates interspecific interactions among carnivores, the role of marking sites in structuring relationships among mesocarnivores remains poorly understood. Although no study has examined scent-mark interactions between Pallas's cat and red fox (*Vulpes vulpes*), evidence from other carnivore guilds suggests that red fox may shape the behavior of smaller sympatric species. Red fox relies heavily on conspicuous scent marking to defend key resources (Monclús et al. 2009), shows substantial trophic overlap with subordinate carnivores such as stone martens in Mediterranean systems (Lanszki et al. 2007) and can reduce the use of shared feeding sites by smaller mesocarnivores through interference or competitive exclusion (Palomares and Caro 1999; Ritchie and Johnson 2009). While these studies do not address olfactory mechanisms directly, they collectively portray the red fox as a widespread and behaviorally flexible generalist capable of influencing the activity and space-use patterns of smaller carnivores. This broader evidence supports the plausibility that fox scent marks may also convey information pertinent to Pallas's cats, highlighting the need to examine olfactory-mediated interactions between the two species in the Central Asian steppe. Both species show partial overlap in diet and habitat use, as Pallas's cat primarily preys on small mammals such as pikas and voles, which are also opportunistically exploited by red fox (Ross 2009; Dell'Arte et al. 2007; Lanszki et al. 2007). Although direct predation of red fox on Pallas's cat has not been documented, red fox is a behaviorally flexible generalist and may exert competitive pressure through interference or exploitation of shared resources (Palomares and Caro 1999; Ritchie and Johnson 2009).The overall aim of this study was to investigate how olfactory communication mediates interspecific interactions between Pallas's cat and red fox, and to determine whether scent marking by a behaviorally dominant and generalist mesocarnivore influences the spatial and temporal behavior of a subordinate species within a shared steppe ecosystem in Central Mongolia. According to previous studies conducted in this region, these two species are among the most frequently detected carnivores (Augugliaro et al. 2020) and show a large overlapping activity pattern (Anile et al. 2021; Augugliaro et al. 2021). Accordingly, our specific objectives were to: (i) characterize olfactory behaviors in these two sympatric

carnivores; (ii) test whether Pallas's cat avoids or is attracted by the red fox scent marks; and (iii) assess whether Pallas's cat marking activity is temporally influenced by red fox presence. Considering the different positions of the two species within the predator hierarchy (Ross 2009; Ross et al. 2019), we hypothesized that they employ territorial marking in distinct ways, leading to variation in the type and distribution of markings used. Such differences may reflect species-specific strategies to minimize conflict and facilitate coexistence within shared habitats (Verschueren et al. 2023). We hypothesized that Pallas's cat would avoid red fox scent marks, consistent with evidence that body size asymmetry promotes avoidance and vigilance in smaller species (Leo et al. 2015; Haswell et al. 2018; Cornhill and Kerley 2020). Temporal segregation is likewise recognized as a coexistence mechanism among ecologically similar species (Lesmeister et al. 2015; Monterroso et al. 2015; Sunarto et al. 2015). In this context, Pallas's cat may avoid areas previously marked by red fox for more extended periods than those marked by conspecifics, which would result in comparatively longer intervals between successive markings in the former case.

MATERIALS AND METHODS

Study area

The study was conducted in central Mongolia, within the Bayan Onjuul district of Tuv Province (46.88 N, 105.89 E; WGS84 datum), a representative steppe ecosystem comprising grasslands, desert-steppe, rocky escarpments, sand dunes, and small lakes (Augugliaro et al. 2020). Elevation ranges from 1,200 to 1,715 m a.s.l. The continental climate features warm summers (mean +18.8°C in August) and extremely cold winters (mean -16.7°C in January), with an annual mean temperature close to 0°C. Precipitation occurs on ~140 days per year, totaling ~404.7 mm, mostly in July and August (NSOM, 2024). The vegetation is largely composed of species from the families Asteraceae, Poaceae, Fabaceae, Chenopodiaceae, and Compositae (Tserendulam et al. 2018), with *Ulmus pumila* and *Cotoneaster melanocarpa* commonly occurring in valley bottom and rocky escarpments. The local fauna encompasses carnivores such as Pallas's cat, grey wolf (*Canis lupus*), red fox, corsac fox (*Vulpes corsac*), beech marten (*Martes foina*), Asian badger (*Meles leucurus*), and steppe polecat (*Mustela eversmanii*) (Augugliaro et al., 2020). Ungulate species include the Mongolian gazelle (*Procapra gutturosa*), argali sheep (*Ovis ammon*), Siberian ibex (*Capra sibirica*), and wapiti (*Cervus canadensis*). Approximately 20 species of small mammals (*i.e.*, < 1 kg) are also present, including Mongolian silver vole (*Alticola semicanus*), Mongolian gerbil *(Meriones unguiculatus*), Daurian pika (*Ochotona dauurica*), and Tolai hare (*Lepus tolai*)

(Augugliaro et al. 2020). Among avian predators, steppe eagle (*Aquila nipalensis*), golden eagle (*Aquila chrysaetos*), and upland buzzard (*Buteo hemilasius*) are frequently observed, while scavengers such as the black vulture (*Aegypius monachus*), Himalayan vulture (*Gyps himalayensis*), and bearded vulture (*Gypaetus barbatus*) exploit the large availability of livestock carcasses. The total human population is 646 inhabitants across the whole district. Pastoralism with 4.150,1 livestock in Tuv province (NSOM, 2024), including horses (*Equus ferus caballus*), cattle (*Bos taurus*), sheep (*Ovis aries*), and goats (*Capra aegagrus*), shepherd by dogs (*Canis lupus familiaris*) is widespread, causing overgrazing (Shimada et al., 2007). The area is unprotected; hunting Pallas's cat is legal and regulated by law (Mongolian Law on Hunting 2000).

Sampling design

Camera-trapping surveys were conducted uninterruptedly from August 24, 2020, to August 31, 2024. A total of 57 cameras were deployed (Fig. 1), and SD cards were replaced approximately every 3 months. The number of cameras operating simultaneously varied over time, as the survey started with a limited number of units and progressively increased, while camera malfunction, battery depletion, theft, and relocation further contributed to temporal variation in sampling effort. This variability is accounted for by using trap-days as a standardized measure of effort. An approximate spacing of ~1 km between sites was maintained (Anile and Devillard 2018; Augugliaro et al. 2021). Each camera site was georeferenced with GPS and labelled with a unique alphanumeric code. The placement of camera traps was based on the habitat use of Pallas's cat (Moqanaki et al. 2022, Chapter 2-3). Cameras were positioned at marking sites and latrines, prey colonies (especially pika and vole burrows), within rock cavities or under shelters, oriented towards natural passages, between rocky areas that provide hunting opportunities, shelter, and animal dens (*e.g.*, marmot burrows) used as refugees. Most units were installed at ~25 cm height (range 10–40 cm) and 0.5–2 m from expected paths (Augugliaro et al. 2021; Moqanaki et al. 2022). Vegetation was cleared from the field of view and tilt adjusted to optimize PIR detection (Rovero and Zimmermann 2016). Three camera models were used: Browning, Cuddeback, and Uivision IR Plus. Due to malfunctioning and stolen cameras, the proportions of these models changed over the four-year sampling, but approximately 70% were Browning, 15% Cuddeback, and 15% Uivision IR Plus across the sampling period. The triggering speeds varied from 0.3 to 0.5 seconds, with a recovery time of less than 0.5 seconds. This setup ensured reliable capture of fast-moving individuals and consecutive behaviors (Moqanaki et al. 2022; Rovero and Kays 2021). All cameras operated 24h/day, programmed in photo mode, and a 5-minute delay between sequences. Camera deployment was not random but part of a long-term monitoring effort, with locations adjusted over time to maximize

detection of medium-sized carnivores. Cameras were placed at ecologically relevant features (e.g., rocky outcrops, burrows, and pathways) commonly used by multiple species. For this study, we retained only camera-trap sites and sampling periods in which both Pallas's cat and red fox were recorded, ensuring analyses were conducted on a shared set of sites relevant to both species. For analytical purposes, each site within each sampling year was treated as an independent observational unit, allowing repeated observations of the same location across years to be retained while accounting for temporal variation in site use.

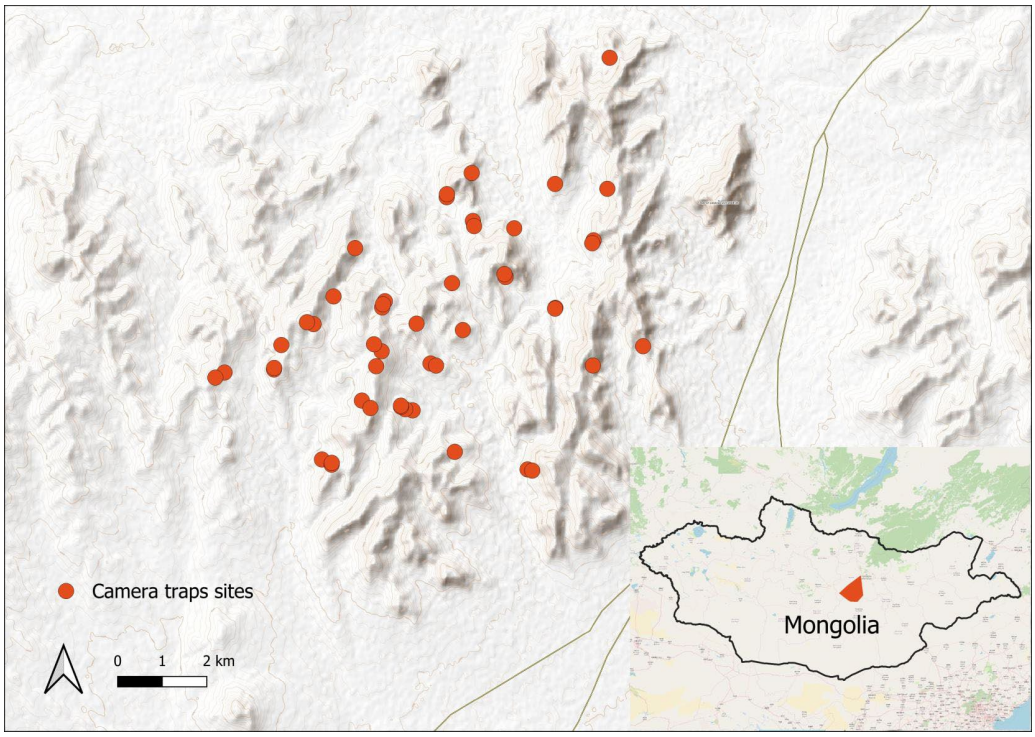

Fig. 1. Study area in Central Mongolia showing the location of camera-trap sites used to monitor Pallas's cat and red fox. The map includes the spatial distribution of sampling locations within the rocky steppe environment.

Data analysis

All the images were filtered for Independent Detection Events, defined as consecutive records of the same species at the same site separated by ≥ 15 minutes. A "sequence" was defined as a series of consecutive photographs triggered by a single detection event, typically consisting of multiple images captured within a short time interval (*i.e.*, before the programmed delay between triggers). The number of photographs per sequence varies depending on the duration of the animal's presence in front of the camera. Behavioral categories were assigned based on visual inspection of body posture, movement, and interaction with the substrate across consecutive images within each sequence, allowing reliable identification of scent-producing and scent-investigative behaviours

even in photo mode. Species-specific datasets for Pallas's cat and the red fox were compiled to record all olfactory events. Following Allen et al. (2023), photographs were screened for six behavioral categories: 1) claw-marking, in which the animal scratches the substrate (trees, rocks, or soil), leaving both visual traces and chemical cues from interdigital glands; 2) fecal deposition, the placement of feces in strategic and often conspicuous locations to serve as territorial marks or indicators of presence; 3) head/body rubbing, the rubbing of the head or body against surfaces or objects to transfer secretions from cutaneous glands as chemical signals; 4) urine spraying, the directional release of urine, typically onto vertical surfaces, functioning as a persistent olfactory cue for territorial delimitation or reproductive status; 5) the flehmen response, characterized by lifting the upper lip and inhaling to transfer chemical stimuli to the vomeronasal organ for enhanced chemosensory assessment; and 6) olfactory investigation, defined as intensive sniffing of surfaces or previous markings to acquire chemical information left by conspecifics or other species. Claw-marking, fecal deposition, head/body rubbing, and urine spraying were classified as scent-producing behaviors, whereas flehmen and olfactory investigation were classified as scent-investigative behaviors (Allen et al. 2016 2023; Macdonald 1979; Mellen 1993). Marking frequency was calculated for each camera-trap site as the number of marking events divided by the number of days that the camera was operational and expressed as marking events per 100 trap-days. This standardization accounts for unequal sampling effort across camera sites and ensures comparability among sampling units (Rovero and Zimmermann 2016; Rovero and Kays 2021). Marking data were converted into binary presence/absence per site to construct 2 × 2 contingency tables. This approach was adopted to evaluate co-use of marking location across sampling periods as discrete communication points, rather than variation in marking intensity, which may be influenced by short-term behavioral dynamics and detection stochasticity. The contingency analysis was designed to evaluate co-occurrence at marking sites, representing focal points of olfactory communication, rather than to infer habitat-level spatial overlap. A Pearson's chi-squared test of independence was then conducted to assess whether the spatial distribution of marking events by Pallas's cat and red fox deviated from that expected under the null hypothesis of independence. To determine whether deviations indicated attraction or avoidance, observed and expected values were directly compared, and standardized residuals were calculated. The contingency analysis was based on site-year observations, where each site in each sampling year represented an independent sampling unit. Effect sizes were quantified both through odds ratios with 95% confidence intervals, to evaluate the direction of the association, and through the Phi coefficient was calculated as $\Phi = \sqrt{(\chi^2/N)}$, where N corresponds to the total number of site-year observations included in the contingency table. (equivalent to Cramer's V in 2 × 2 tables), to assess the strength of the association (Allen et al. 2023). Temporal partitioning of marking events was assessed by comparing two types of intervals

at the same camera-trap site: (i) the interval between a red fox marking event and the subsequent Pallas's cat marking event, and (ii) the interval between two consecutive Pallas's cat marking events. To avoid potential confounding effects from other carnivore species, only sequences in which no other carnivore was recorded between the two focal events were retained. Intervals in which another carnivore species occurred between the focal events were excluded from the analysis. Mean time intervals between events were then compared using Welch's two-sample *t*-tests (Allen et al. 2023). Although interval data may deviate from normality, Welch's *t*-test was used due to its robustness to unequal variances and moderate departures from normality. This approach is appropriate for exploratory comparisons of mean differences, although interval data may exhibit skewed distributions. This analysis specifically examined whether Pallas's cat modified the timing of marking events following red fox activity and therefore focused on sequences in which Pallas's cat represented the responding species. A 2 × 6 contingency table was constructed to compare the frequency distribution of behavioral categories between Pallas's cat and red fox. Differences in behavioral allocation across categories were evaluated using a chi-square test. All tests were two-tailed with $\alpha = 0.05$, and results are presented with exact p-values and 95% confidence intervals. Analyses were performed in R (v.4.5.1; R Core Team 2023) within RStudio (Posit, v.2025.5.0.496), and data management and visualization were conducted using the tidyverse (Wickham et al. 2019) and ggplot2 (Wickham 2016) packages.

RESULTS

The sampling effort totaled 32,722 trap-days ($\bar{x} = 574.07 \pm 54.25$ SE). Pallas's cats and red fox were respectively recorded in 267 and 798 independent detection events. Of 57 camera-trap sites, 45 (78.95%) captured markings from at least one focal species. Markings were exclusive to Pallas's cat at five sites (8.77%), exclusive to red fox at 19 sites (33.33%), and shared by both species at 21 sites (36.84%). Mean visits per site, standardized by trap-days, were 0.76 ± 0.23 SE (SD = 1.71) for Pallas's cat and 2.24 ± 0.76 SE (SD = 5.71) for red fox. Visits represent independent detections at a camera site, whereas marking events refer specifically to scent-marking behaviors recorded during a visit. For the marking behavior, the mean marking frequency per site, expressed as marking events per 100 trap-days, was 0.20 ± 0.09 SE (SD = 0.67) for Pallas's cat and 0.52 ± 0.25 SE (SD = 1.86) for red fox (95% CI: 0.19–0.25 and 0.52–0.61, respectively). Pallas's cat exhibited all six recorded marking behaviors, for a total of 71 events: claw marking 1.41%, fecal deposition 7.04%, head/body rubbing 23.94%, urine spraying 7.04%, flehmen response 2.82%, and olfactory investigation 57.75%. Red fox exhibited five marking behaviors, totaling 183 events: claw

marking 2.73%, fecal deposition 1.64%, head/body rubbing 0.55%, urine spraying 3.83%, and olfactory investigation 91.26% (Fig. 2). The chi-squared test based on site-year presence/absence observations yielded $\chi^2 = 58.44$, $d.f. = 1$, $p < 0.001$, rejecting the null hypothesis of independence and indicating that the occurrence of marking events by Pallas's cat and red fox deviated from random expectation across sampling periods. While the chi-squared statistic itself shows only that the association is highly significant, the strength of this relationship was quantified using the Phi coefficient, which in 2 × 2 tables is equivalent to Cramer's V. The strength of this association was quantified using the Phi coefficient ($\Phi = 0.746$), calculated from the site-year contingency table (N = 105). Comparison between observed and expected frequencies further clarified the direction of this association: Pallas's cat markings were more frequent than expected in the absence of red foxes (+4.82 standardized residual) and less frequent than expected when both species co-occurred (-3.28 standardized residual). These results support the interpretation of strong spatial segregation consistent with avoidance of red foxes by Pallas's cats. A chi-square test based on a 2 × 6 contingency table revealed a significant difference in the distribution of behavioral categories between Pallas's cat and red fox ($\chi^2 = 57.93$, $d.f. = 5$, $p < 0.001$). The two-sample *t*-test returned $t = –1.69$, $d.f. = 20.48$, $p = 0.11$, failing to reject the null hypothesis and indicating no statistically significant difference in mean intervals between the time interval separating a red fox marking and a subsequent Pallas's cat marking, and the interval between two consecutive Pallas's cat markings. Variation over time within each category is illustrated in the boxplot (Fig. 3A), while the temporal sequence of marking events between Pallas's cat and red fox at a shared marking site is schematically represented (Fig. 3B).

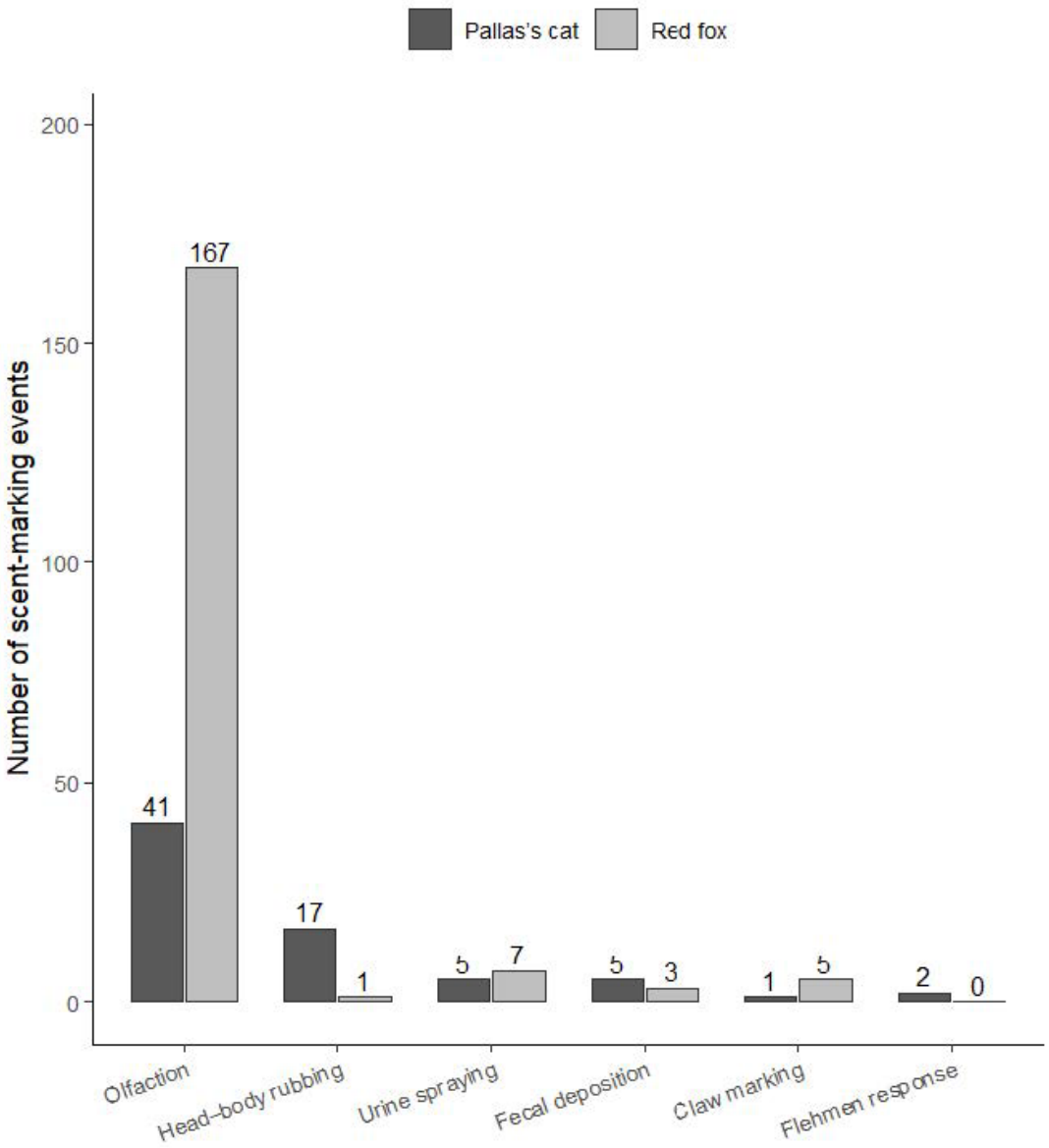

Fig. 2. Frequency of observed behavioural categories for Pallas's cat and red fox at camera-trap sites. Behavioural categories include scent-producing and scent-investigative actions recorded from camera-trap sequences. Values represent the total number of events observed for each category.

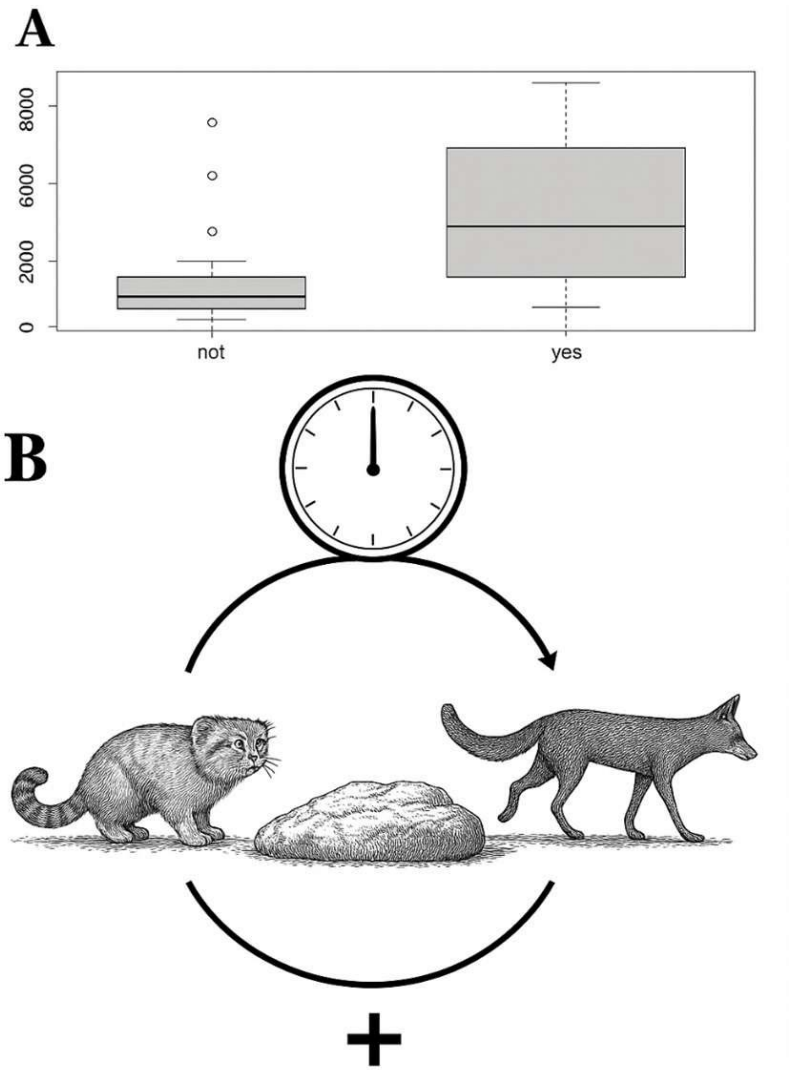

Fig. 3. Temporal patterns of marking behavior at shared camera-trap sites. (A) Distribution of time intervals (hours) between consecutive marking events for each category, shown as boxplots. Sample sizes were n = 14 for intervals between a red fox marking event and the subsequent Pallas's cat marking event, and n = 24 for intervals between two consecutive Pallas's cat marking events. (B) Conceptual diagram illustrating the temporal sequence and reciprocal use of marking sites by Pallas's cat and red fox.

DISCUSSION

This study offers new insights into the scent-marking behavior of Pallas's cats and red foxes in the Mongolian mountain steppe. It enhances our understanding of how olfactory cues influence the interactions between these two sympatric carnivores. Given the wide distribution and significant ecological overlap of both species across the Mongolian-Manchurian Grassland Ecoregion, our findings are relevant beyond the immediate study area and may provide useful information for similar steppe ecosystems (Augugliaro et al. 2020). Both species displayed a wide range of marking behaviors, with olfactory signals being the most common. This predominance is not surprising, as

olfaction is the most prevalent and evolutionarily established form of communication among carnivores (Root-Gutteridge et al. 2025). The Flehmen response was recorded exclusively in Pallas's cat because it is a behavior widely observed among felids (Allen et al. 2015; Hart and Leedy 1987) but negligible in canids such as the red fox (Kleiman and Eisenberg 1973; Ortiz-Leal et al. 2020). The additional contingency analysis suggests that Pallas's cat and red fox differ in the relative allocation of behavioral categories at shared sites. This indicates that the two species may rely differently on specific olfactory communication behaviors, potentially reflecting distinct strategies in the use of marking locations. The high spatial segregation observed between Pallas's cat and red fox across site-year observations can be interpreted as an adaptive avoidance strategy by the former. This pattern is consistent with reduced marking occurrence during sampling periods in which red fox activity was recorded. Comparable responses have been documented in the Altai Mountains, where Pallas's cats reduced their use of olfactory communication when snow leopards had visited marking sites recently (Allen et al. 2023). Although the red fox and snow leopard differ markedly in their position within the predator hierarchy, these findings collectively suggest that olfactory cues from behaviorally influential or potentially threatening carnivores can influence the species' marking behavior, possibly as a means of minimizing the likelihood of antagonistic encounters. Such avoidance may represent a mechanism of niche partitioning that facilitates coexistence in the structurally open habitats of the Mongolian mountain-steppe, where opportunities for concealment and refugia are limited. The two-sample *t*-test showed no evidence of temporal adjustment in marking behavior. Specifically, the time interval between a red fox marking event and a subsequent Pallas's cat marking did not differ from the interval between two consecutive Pallas's cat markings. This result suggests that Pallas's cats neither delayed nor advanced their marking activity in response to red fox presence. Taken together, the two analyses indicate a consistent pattern: Pallas's cat avoids red foxes mainly through spatial segregation, as supported by the highly significant chi-squared test, whereas no evidence was found for a temporal adjustment in marking behavior. However, this analysis focused only on the response of Pallas's cat to red fox and did not evaluate the reciprocal response of red fox to Pallas's cat, nor did it differentiate between scent-producing and scent-investigative behaviors, which may influence the interpretation of temporal patterns. In addition, camera placement was not random and may influence detection probabilities. Although cameras were positioned at landscape features used by multiple species and analyses were restricted to shared sites, results should be interpreted as reflecting interaction patterns at selected marking sites rather than general co-occurrence across the landscape. Furthermore, the use of presence/absence data simplifies variation in marking frequency and temporal dynamics across the study period. While this approach reduces complexity and avoids overrepresentation of highly active sites, it may mask differences in marking intensity and temporal variation. Furthermore, the

relatively small sample size and the potential non-normal distribution of interval data may limit the statistical power of the temporal analysis. Although alternative approaches such as non-parametric tests or time-to-event modelling could be applied, our analysis was intended as an exploratory comparison of mean intervals. From a behavioral ecology perspective, this pattern likely reflects the relative costs and benefits of temporal adjustments in an open steppe environment, where avoiding specific sites may be a more effective and less costly strategy to reduce competitive interactions than altering activity schedules (Greco et al. 2021). Our findings align with Augugliaro et al. (2021), who showed that both red fox and Pallas's cat exhibit cathemeral activity patterns with wide temporal overlap, suggesting that competition between the two species is unlikely to be mediated by temporal factors. Comparable patterns have also been observed in the Qinghai, Tibet Plateau, where Wang et al. (2022) found that Pallas's cat and red fox exhibit substantial spatial overlap, consistent with our findings. From a cost-benefit perspective, the lower scent-marking activity exhibited by Pallas's cat in the presence of red fox likely reflects an adaptive trade-off, whereby the risk of antagonistic encounters exceeds the benefits of increased territorial advertisement (Clermont et al. 2025). Given the widespread distribution of red fox across the Mongolian steppe, such avoidance strategies may not be restricted to Pallas's cat alone but could extend to other mesocarnivores within the same community. Evidence from other carnivore systems supports this interpretation: subordinate species have been shown to adjust their scent-marking or spatial behavior in response to the olfactory cues of dominant competitors, indicating that dominant carnivores can impose community-wide behavioral constraints (Allen et al. 2017). These parallels suggest that, in steppe systems where large carnivores such as wolves are generally alone, occurring at low density (Salvatori et al. 2022), ecologically dominant generalists such as the red fox can mainly influence the behavior of smaller mesocarnivores. Within a broader theoretical context, the landscape of fear framework (Gaynor et al. 2019) highlights how perceived risk can shape carnivore behavior across space and time, providing a useful conceptual lens for interpreting patterns of spatial avoidance observed in this study. Consistent with this view, studies from other ecosystems report context-dependent coexistence mechanisms, in which mesocarnivores adjust niche use in response to ecological conditions and interspecific interactions (Haswell et al. 2020; Vilella et al. 2020; Wu et al. 2025).

Several methodological limitations should be considered when interpreting our results. The conversion of marking data into presence/absence per site does not account for variation in marking frequency or temporal dynamics and treats all sites equally regardless of intensity of use. Additionally, the conversion of marking data into binary presence/absence at the site-year level simplifies variation in marking frequency and temporal dynamics within sampling periods. Although repeated observations of the same sites across years were retained as independent site-

year units, this approach does not account for variation in marking intensity within each sampling period. Consequently, our findings should be interpreted as reflecting patterns of co-use and segregation across site-year observations rather than intensity-dependent interactions or fine-scale temporal dynamics.

Future studies integrating repeated-measures frameworks, such as generalized linear mixed models, may help disentangle intensity-dependent responses, although their application in this system may be constrained by low marking frequencies and high variability.

CONCLUSIONS

In conclusion, this study presents the most comprehensive assessment to date of scent-marking behavior in Pallas's cat and red fox, including their interactions at shared marking sites. Relying on the largest and most continuous systematic fine-scale camera-trap dataset currently available for

Pallas's cat, derived from a systematic four-year survey, our results offer a robust and reliable contribution to understanding interspecific scent-marking dynamics between these two sympatric carnivores. Our findings, supported by non-random segregation across site-year observations and the absence of temporal adjustment, suggest an asymmetric avoidance in which a behaviorally flexible and generalist canid constrains the marking behavior of a more specialized felid. In ecosystems where large apex predators occur rarely, such dynamics indicate that, here, the behaviorally influential mesocarnivore, the red fox, may exert top-down behavioral pressure on co-occurring species, influencing their space use and potentially shaping the broader carnivore community. These results have important ecological and conservation implications. First, they underscore the role of generalist carnivores as key structuring agents within steppe carnivore assemblages, particularly in landscapes where apex predators are rare or declining. Second, the spatial sensitivity exhibited by Pallas's cat underscores its vulnerability to anthropogenic pressures that alter habitat structure, such as overgrazing, livestock expansion, and human-mediated resource subsidies, which should be taken into account to preserve this species.

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REFERENCES

Allen ML, Wittmer HU, Houghtaling P, Smith J, Elbroch LM, Wilmers CC. 2015. The role of scent marking in mate selection by female pumas (*Puma concolor*). PLoS ONE **10:**e0139087. doi:10.1371/journal.pone.0139087.

Allen ML, Gunther MS, Wilmers CC, Elbroch LM. 2016. Scent marking in Sunda clouded leopards (*Neofelis diardi*): Novel observations close a key gap in understanding felid communication behaviours. Sci Rep **6:**35433. doi:10.1038/srep35433.

Allen ML, Gunther MS, Wilmers CC. 2017. The scent of your enemy is my friend? The acquisition of large carnivore scent by a smaller carnivore. J Ethol **35:**13–19. doi:10.1007/s10164-016-0492-6

Allen ML, Rovero F, Oberosler V, Augugliaro C, Krofel M. 2023. Effects of snow leopards (*Panthera uncia*) on olfactory communication of Pallas's cats (*Otocolobus manul*) in the Altai Mountains, Mongolia. Behaviour **160:**807–815. doi:10.1163/1568539X-bja10229

Andermann T, Faurby S, Turvey ST, Antonelli A, Silvestro D. 2020. The past and future human impact on mammalian diversity. Sci Adv **6:**eabb2313. doi:10.1126/sciadv.abb2313.

Anile S, Augugliaro C, Munkhtsog B, Dartora F, Vendramin A et al. 2021. Density and activity patterns of Pallas's cats, *Otocolobus manul*, in central Mongolia. Wildl Res **48:**264. doi:10.1071/WR20061

Anile S, Devillard S. 2018. Camera-trapping provides insights into adult sex ratio variability in felids. Mammal Rev **48:**168–179. doi:10.1111/mam.12120.

Augugliaro C, Anile S, Munkhtsog B, Janchivlamdan C, Batzorig E et al. 2021. Activity overlap between mesocarnivores and prey in the Central Mongolian steppe. Ethol Ecol Evol **34:**514–530. doi:10.1080/03949370.2021.1975312.

Augugliaro C, Worsøe Havmøller R, Monti I, Worsøe Havmøller L, Janchivlamdan C et al. 2020. Non-volant mammal inventory of western Mongolian-Manchurian Grassland Ecoregion: a biogeographic crossroad worth preserving. Check List **16:**287–301. doi:10.15560/16.2.287.

Clermont J, Dulude-de Broin F, Poulin M-P, Berteaux D. 2025. Territoriality modulates the effect of conspecific encounters on the foraging behaviours of a mammalian predator. Ecol Evol **15:**e71058. doi:10.1002/ece3.71058.

Cornhill KL, Kerley GIH. 2020. Cheetah communication at scent-marking sites can be inhibited or delayed by predators. Behav Ecol Sociobiol **74:**21. doi:10.1007/s00265-020-2802-9.

Davies TJ, Meiri S, Barraclough TG, Gittleman JL. 2007. Species co-existence and character divergence across carnivores. Ecol Lett **10:**146–152. doi:10.1111/j.1461-0248.2006.01005.x.

Dell'Arte GL, Laaksonen T, Norrdahl K, Korpimäki E. 2007. Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. Acta Oecol **31:**276–281. doi:10.1016/j.actao.2006.12.007.

Eisenberg JF, Kleiman DG. 1972. Olfactory communication in mammals. Annu Rev Ecol Syst **3:**1–21. oi:10.1146/annurev.es.03.110172.000245.

Franchini M, Atzeni L, Lovari S, Nasanbat B, Ravchig S et al. 2023. Spatio-temporal behaviour of predators and prey in an arid environment of Central Asia. Curr Zool **69:**670–681. doi:10.1093/cz/zoac093

Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS. 2019. Landscapes of fear: spatial

patterns of risk perception and response. Trends Ecol Evol **34:**355–368. doi:10.1016/j.tree.2019.01.004.

Greco I, Oberosler V, Monti IE, Augugliaro C, Barashkova A, Rovero F. 2021. Spatio-temporal occurrence and sensitivity to livestock husbandry of Pallas's cat in the Mongolian Altai. J Wildl Manag **85:**e22150. doi:10.1002/jwmg.22150.

Hart BL, Leedy MG. 1987. Stimulus and hormonal determinants of flehmen behavior in cats. Horm Behav **21:**44–52. doi:10.1016/0018-06X(87)90029-8.

Haswell PM, Jones KA, Kusak J, Hayward MW. 2018. Fear, foraging and olfaction: how mesopredators avoid costly interactions with apex predators. Oecologia **187:**573–583. doi:10.1007/s00442-018-4133-3

Haswell PM, Kusak J, Jones KA. 2020. Fear of the dark? A mesopredator mitigates large carnivore risk through nocturnality, but humans moderate the interaction. Behav Ecol Sociobiol **74:**144. doi:10.1007/s00265-020-02831-2.

Krofel M, Oliveira T, Rovero F, Groff C, Augugliaro C et al. 2025. Communication behavior of the snow leopard (*Panthera uncia*): understanding marking-behavior patterns to optimize camera-trapping studies. Behav Ecol Sociobiol **79:**32. doi:10.1007/s00265-025-03574-8.

Kleiman DG, Eisenberg JF. 1973. Comparisons of canid and felid social systems from an evolutionary perspective. Anim Behav **21:**637–659. doi:10.1016/S0003-3472(73)80088-0.

Lanszki J, Körmendi S, Hancz C, Biro Z. 2007. Comparison of red fox (*Vulpes vulpes*) and pine marten (*Martes martes*) food habits in a deciduous forest in Hungary. Wildl Biol **13:**258–271. doi:10.2981/0909-6396(2007)13[258:CORFVV]2.0.CO;2

Leo V, Reading R, Letnic M. 2015. Interference competition: odours of an apex predator and conspecifics influence resource acquisition by red foxes. Oecologia **179:**1033–1040. doi:10.1007/s00442-015-3423-2.

Lesmeister DB, Nielsen CK, Schauber EM, Hellgren EC. 2015. Spatial and temporal structure of a mesocarnivore guild in midwestern North America. Wildl Monogr **191:**1–61. doi:10.1002/wmon.1015

Macdonald DW. 1979. Some observations and field experiments on scent marking in the red fox, *Vulpes vulpes* L. J Zool **187:**427–436.

Mellen JD. 1993. A comparative analysis of scent-marking, social and reproductive behavior in 20 species of small cats (*Felis*). Am Zool **33:**151–166. doi:10.1093/icb/33.2.151.

Monclús R, Saavedra I, de Miguel J. 2009. Red foxes (*Vulpes vulpes*) use rabbit (*Oryctolagus cuniculus*) scent marks as territorial marking sites. J Ethol **27:**153–156. doi:10.1007/s10164-008-0109-0.

Mongolian Law on Hunting. 2000. Compendium of environmental law and practice in Mongolia.

Ministry of Environment and Tourism of Mongolia, Ulaanbaatar.

Monterroso P, Alves PC, Ferreras P. 2015. Ecological interactions and species coexistence in Iberian mesocarnivore communities: extended summary and main results. Galemys **27:**47–57. doi:10.7325/Galemys.2015.A6.

Moqanaki E, Barashkova A, Ross S, Augugliaro C, Smelansky I et al. 2022. Manul signs and sampling locations. *In*: Moqanaki E, Samelius G (eds) Monitoring the manul: guidelines for practitioners. The Pallas's Cat International Conservation Alliance (PICA). Available at: https://www.researchgate.net/publication/366192764_Manul_signs_and_sampling_locations.

Moqanaki E, Barashkova A, Augugliaro C, Smelansky I, Samelius G. 2022. Camera trapping. *In*: Moqanaki E, Samelius G (eds) Monitoring the manul: guidelines for practitioners. The Pallas's Cat International Conservation Alliance (PICA). Available at: https://www.researchgate.net/publication/366192592_Camera_trapping.

NSOM. 2024. National Statistics Office of Mongolia. NSOM, Ulaanbaatar, Mongolia. Available at: https://www.nso.mn/en.

Ortiz-Leal I, Torres MV, Pastor LM. 2020. The vomeronasal organ of wild canids: the fox (*Vulpes vulpes*) as a model. J Anat **237:**319–335. doi:10.1111/joa.13254.

Palomares F, Caro TM. 1999. Interspecific killing among mammalian carnivores. Am Nat **153:**492–508. doi:10.1086/303189.

Ritchie EG, Johnson CN. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecol Lett 12:982–998. doi:10.1111/j.1461-0248.2009.01347.x.

Root-Gutteridge H, Buesching CD, Sin YW, Jordan NR. 2025. Common scents? A review of potentially shared chemical signals in the order Carnivora. Chem. Senses **50:**bjaf019. doi:10.1093/chemse/bjaf019.

Ross S. 2009. Providing an ecological basis for the conservation of the Pallas's cat (*Otocolobus manul*). PhD dissertation, University of Bristol, Bristol, United Kingdom.

Ross S, Moqanaki EM, Barashkova A, Dhendup T, Smelansky I et al. 2019. Past, present and future threats and conservation needs of Pallas's cats. Cat News, Special Issue **13:**46–51.

Rovero F, Kays R. 2021. Camera trapping for conservation. *In*: Wich SA, Piel AK (eds) Conservation technology. Oxford University Press, Oxford, United Kingdom, pp. 79–101. doi:10.1093/oso/9780198850243.003.0005.

Rovero F, Zimmermann F. 2016. Camera trapping for wildlife research. Pelagic Publishing, Exeter, United Kingdom.

Salvatori M, Oberosler V, Augugliaro C, Krofel M, Rovero F. 2022. Effects of free-ranging livestock on occurrence and interspecific interactions of a mammalian community. Ecol Appl **32:**e2644. doi:10.1002/eap.2644.

Shimada S, Sekiyama A, Yokohama M, Aosier B, Tamaki K. 2007. Developing the prediction method of soil moisture and vegetation cover ratio in Mongolian grassland using remote sensing images. J Arid Land Stud **17:**77–80.

Sunarto S, Kelly MJ, Parakkasi K, Hutajulu MB. 2015. Cat coexistence in central Sumatra: ecological characteristics, spatial and temporal overlap, and implications for management. J Zool **296:**104–115. doi:10.1111/jzo.12218.

Tserendulam T-O, Bayarsaikhan U, Oyuntsetseg B, Wesche K. 2018. The vascular plant flora of Hustai National Park, Mongolia: composition, life forms, ecological groups and geographical elements. Feddes Repert **129:**137–160. doi:10.1002/fedr.201700006.

Verschueren S, Fabiano EC, Nghipunya EN, Cristescu B, Marker L. 2023. Social organization of a solitary carnivore, the leopard, inferred from behavioural interactions at marking sites. Anim Behav **200:**115–124. doi:10.1016/j.anbehav.2023.03.019.

Vilella M, Ferrandiz-Rovira M, Sayol F. 2020. Coexistence of predators in time: effects of season and prey availability on species activity within a Mediterranean carnivore guild. Ecol Evol **10:**11408–11422. doi:10.1002/ece3.6778.

Wang D, Sai Q, Wang Z, Zhao H, Lian X. 2022. Spatiotemporal overlap among sympatric Pallas's cat (*Otocolobus manul*), Tibetan fox (*Vulpes ferrilata*) and red fox (*Vulpes vulpes*) in the source region of the Yangtze River. Biodivers Sci **30:**21365. doi:10.17520/biods.2021365.

Wikenros C, Jarnemo A, Frisén M, Kuijper DPJ, Schmidt K. 2017. Mesopredator behavioral response to olfactory signals of an apex predator. J Ethol **35:**161–168. doi:10.1007/s10164-016-0504-6.

Wickham H. 2016. ggplot2: elegant graphics for data analysis. Springer, New York, USA. doi:10.1007/978-3-319-24277-4.

Wickham H, Averick M, Bryan J, Chang W, McGowan LD et al. 2019. Welcome to the tidyverse. Journal of Open Source Software **4:**1686. doi:10.21105/joss.01686.

Wu F, Hua Y, Dou H, Zhang Y, Dong X, Zhu D, Gao H. 2025. Temporal, spatial and prey niche partitioning reveals coexistence mechanism of mesocarnivores in Guangdong Province, South China. Ecol Evol **15:**e71797. doi:10.1002/ece3.71797.