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Original Research Article

Seasonal variation in the density of the Persian leopard in the Hyrcanian forests of northern Iran

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ABSTRACT

Habitat compression increasingly confines Persian leopards (*Panthera pardus tulliana*) to the cores of protected areas, where refuge effects influence their spatial distribution and density. Understanding these patterns is crucial for effective habitat management, prey conservation, and mitigating intra- and interspecific competition. This study assessed Persian leopard density in Kiasar National Park and Dodangeh Wildlife Refuge across the cold and warm seasons, functioning as core habitats within the surrounding Hyrcanian–Alborz landscapes. Using camera traps and closed-population capture–recapture models over 12 months, we estimated seasonal leopard abundance and converted abundance estimates to density using a half mean maximum distance moved (HMMDM)-buffered effective sampling area. Camera traps recorded 18 individual Persian leopards (10 males and 8 females). HMMDM-based density estimates were 2.43 leopards/100 km^2 in the cold season and 3.36 leopards/100 km^2 in the warm season. Most individuals showed higher activity during the cold season. Our findings provide baseline information on Persian leopards in Kiasar National Park and Dodangeh Wildlife Refuge, highlighting these areas as relatively dense refuges for leopards in northern Iran. Individuals appear to concentrate in these areas, especially during the warm season, potentially due to habitat compression associated with livestock and human activities. To mitigate these pressures and their ecological consequences,

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expanding protected area boundaries, prioritizing prey-rich habitats, and maintaining continuous ranger patrols are essential, as they reduce habitat compression, lower intra- and interspecific competition, and enhance leopard survival.

1. Introduction

In the current Anthropocene era, global biodiversity is increasingly threatened by a suite of human-driven pressures (Seddon et al., 2016; Johnson et al., 2017; Finn et al., 2023). Rapid population growth and expanding development have intensified the conversion of natural ecosystems into agricultural and urban landscapes (van Vliet, 2019; Davison et al., 2021; Cafaro et al., 2022). This transformation, driven largely by the rising human demand for food and resources, has resulted in extensive habitat loss and fragmentation, fundamentally altering ecological processes and jeopardizing the persistence of countless species worldwide (Betts et al., 2017; Yuan et al., 2024; Olhnuud et al., 2025).

As a consequence, the habitats of many species, particularly large terrestrial mammals, have become increasingly reduced and isolated, turning protected areas into ecological islands that now serve as the last strongholds for native wildlife (Powers and Jetz, 2019; Kuipers et al., 2021; Chen et al., 2022; Li et al., 2024). However, these refuges are themselves under mounting stress from the pervasive effects of climate change, which continue to reshape habitat structure and resource availability (Trew and Maclean, 2021; Habibullah et al., 2022; Zhang et al., 2024). Together, these pressures have compressed wildlife populations into the inner cores of protected areas, where species are compelled to share the few remaining safe habitats (Fuller et al., 2021; Tucker et al., 2021; Williams et al., 2022).

In northern Iran, remnant populations of large native mammals, particularly endangered carnivores such as the Persian leopard (*Panthera pardus tulliana*), are increasingly constrained by anthropogenic pressures (Bleyhl et al., 2022; Farhadinia et al., 2022; Ghoddousi and Khorozyan, 2023). Among the most significant of these pressures are intensive livestock grazing and poaching, which further reduce habitat quality and availability while exacerbating resource competition and human–wildlife conflict (Soofi et al., 2018, 2019; Yusefi et al., 2022; Parchizadeh et al., 2024). With extensive home ranges and limited prey, Persian leopards are forced to share the few remaining suitable habitats with conspecifics, other native species, and, in many areas, domestic livestock (Soofi et al., 2018; Farhadinia et al., 2019; Rouse et al., 2021; Mohammadi et al., 2021). This overlap, combined with natural prey scarcity caused by poaching, intensifies both intra- and interspecific competition for food and habitat, ultimately leading to increased mortality and escalating human–wildlife conflicts (Farhadinia et al., 2018; Soofi et al., 2019; Ghoddousi et al., 2020; Yusefi et al., 2022; Parchizadeh et al., 2024).

Therefore, understanding the spatial occupancy and density of the Persian leopard within its natural and protected habitats is crucial for identifying core and high-use areas (Khorozyan et al., 2008; Rogan et al., 2019; Khosravi et al., 2024). Such knowledge provides essential guidance for habitat and prey management, expanding protected areas, and restoring ecological corridors to reconnect fragmented habitats (Mann et al., 2020; Askerov et al., 2022; Soofi et al., 2022). These actions are vital to reducing intra- and interspecific competition and mitigating human–wildlife conflicts, thereby enhancing the long-term persistence of the Persian leopard in northern Iran. However, only a few studies have been conducted in the southwestern and northeastern parts of the country (Ghoddousi et al., 2010; Hamidi et al., 2014; Farhadinia et al., 2019, 2021). The purpose of this study was to quantify seasonal variation in Persian leopard density within Kiasar National Park and Dodangeh Wildlife Refuge. Our results elucidate the seasonal density and population of Persian leopards in this ecological nexus, addressing pivotal gaps in understanding their range connectivity across northern Iran.

We hypothesized that Persian leopard density would be higher during the warm season than during the cold season because seasonal livestock grazing and associated human activities in surrounding habitats are expected to compress leopard distribution into the core protected areas. Consequently, leopards would become more concentrated within these protected refuges during the warm season. Therefore, the objectives of this study were to (1) estimate Persian leopard density during the warm and cold seasons in Kiasar National Park and Dodangeh Wildlife Refuge, and (2) evaluate whether seasonal density patterns are consistent with the habitat-compression and refuge-effect hypotheses.

2. Method and material

2.1. Study area

Our study was conducted in Kiasar National Park and Dodangeh Wildlife Refuge in northern Iran, encompassing ~290 km^2 along the northern Alborz Mountains (711–2880 m a.s.l.). This area, part of a global biodiversity hotspot, features a pronounced elevational gradient from humid lowland Hyrcanian forests to high-altitude alpine zones and adjoins Parvar and Bula Protected Areas, forming a continuous habitat for the Persian leopard (Darvishsefat, 2006; Marchese, 2015; Karami et al., 2016). This variation in elevation creates diverse habitats that support a rich assemblage of fauna, including the Brown bear (*Ursus arctos*), Caspian red deer (*Cervus elaphus maral*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and wild goat (*Capra aegagrus*) (Karami et al., 2016; Khorozyan et al., 2018; Farhadinia et al., 2022). The landscapes surrounding these core protected areas face pressures from human expansion, logging activities, and livestock grazing (Sagheb Talebi et al., 2014; Khorozyan et al., 2018; Soofi et al., 2018; Ghorbanalizadeh and Akhani, 2022). Over half of the local livestock owners follow traditional or nomadic lifestyles, relying on natural pastures that

influence the spatial distribution of both domestic and wild fauna in the region. Herds are seasonally moved between low-elevation winter ranges (October–March) and high-altitude summer pastures (April–September) in the southern portion of the study area (Fig. 1).

2.2. Data collection

To monitor wildlife in the study area, we deployed 23 camera traps arranged in a 5 × 5 km grid, covering nearly the entire site with one camera per cell (Sanei et al., 2020; Bleyhl et al., 2021; Petridou et al., 2023). One northeastern grid cell was excluded from the analysis because its proximity to settlements and roads substantially increased the risk of camera theft. Within each cell, camera locations were selected based on recent evidence of target species, including tracks, scat, and prior observations along forest paths, ridgelines, and large mammal trails, following guidelines by Szabó et al. (2024), to maximize detection probability. Cameras were installed during spring and summer (Salmanpour et al., 2023; Yildiz, Uzun, 2024) at 40–80 cm above the ground with lenses-oriented northward to minimize sunlight interference.

Over a period of approximately 12 months (late summer 2022 to mid-fall 2023), most cameras were relocated once within their respective grid cells after 120–150 days, with an average shift of ~2.4 km per grid. Relocation was intended to increase spatial coverage and reduce microsite-specific detection bias within each sampling unit (Kolowski et al., 2021). We separated the data into warm and cold seasons to compare the leopard density and abundance. We defined the warm season as May–October, corresponding to the period when livestock are generally grazing in summer pastures. The cold season was defined as November–April, when most livestock return to their winter grazing areas. Cameras recorded 30-second video clips with 1-second intervals to improve species identification and reduce double-counting, based on recommendations from Reyes et al. (2017), who reported higher accuracy with video compared to still images. Across the study period, we accumulated 3461 trap-nights with 1808 in the warm season across 22 operational stations and 1653 in the cold season across 25. These totals reflect the rotation of 23 physical camera units among relocated sampling sites.

Individual leopards were identified using their unique rosette patterns, which are stable over time and allow reliable discrimination among individuals of large felids such as the Persian leopard. Identification was based on detailed visual comparison of flank, shoulder, and hindquarter rosette configurations obtained from video frames, following standard photo-identification protocols for spotted

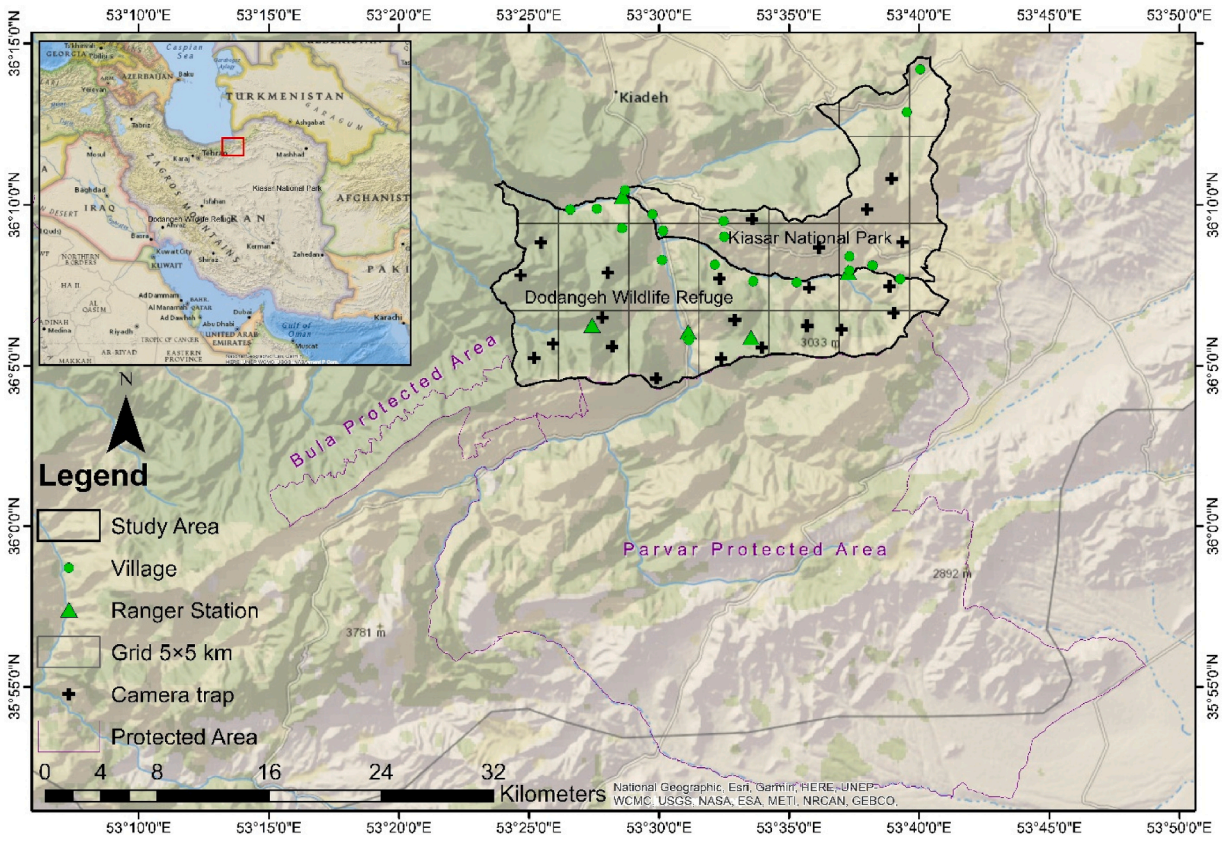


Fig. 1. Map of the study area in Kiasar National Park and Dodangeh Wildlife Refuge, northern Iran. Camera-trap locations are shown with plus symbols, ranger stations with green triangles, and surrounding villages with green circles. The purple boundary indicates the protected areas. The inset map shows the regional location of the study area within Iran, highlighted by a red box.

carnivores (Wattegedera et al., 2022). Because single cameras were deployed at each station, individual identification relied on images of a single visible flank. Therefore, detections with obscured flank patterns or insufficient image quality were excluded from individual identification analyses. Only records with sufficient image quality and clear lateral views were used to minimize misidentification. This approach enabled confident assignment of detections to known individuals and avoided double-counting across camera stations (Fig. 2).

2.3. Statistical analyses

Leopard abundance (N) was estimated separately for warm and cold seasons using closed population capture–recapture models. Comparable capture–recapture approaches have been widely used to estimate Persian leopard abundance and density in Iran (e.g., Hamidi et al., 2014; Farhadinia et al., 2019, 2021). Competing detection models were compared using Akaike's Information Criterion (AIC), and the best-supported model for each season was retained for inference. To estimate leopard density (D; individuals per 100 km^2), abundance estimates were divided by an effective sampling area derived from mean maximum distance moved (MMDM) calculations, with a half mean maximum distance moved (HMMDM) buffer applied around camera locations. Density standard errors were scaled directly from abundance standard errors using the effective sampling area as a fixed constant; thus, uncertainty in the effective area was not propagated. Spatially explicit capture–recapture (SECR) models implemented in the R package secr (Efford, 2022) were used to estimate the spatial scale parameter (σ), representing the extent of leopard movements during the sampling period, and to ensure that buffer distances used for density estimation were sufficient to minimize edge effects.

Capture histories were pooled into 5-day sampling occasions to minimize sparsity in detection histories and increase recapture

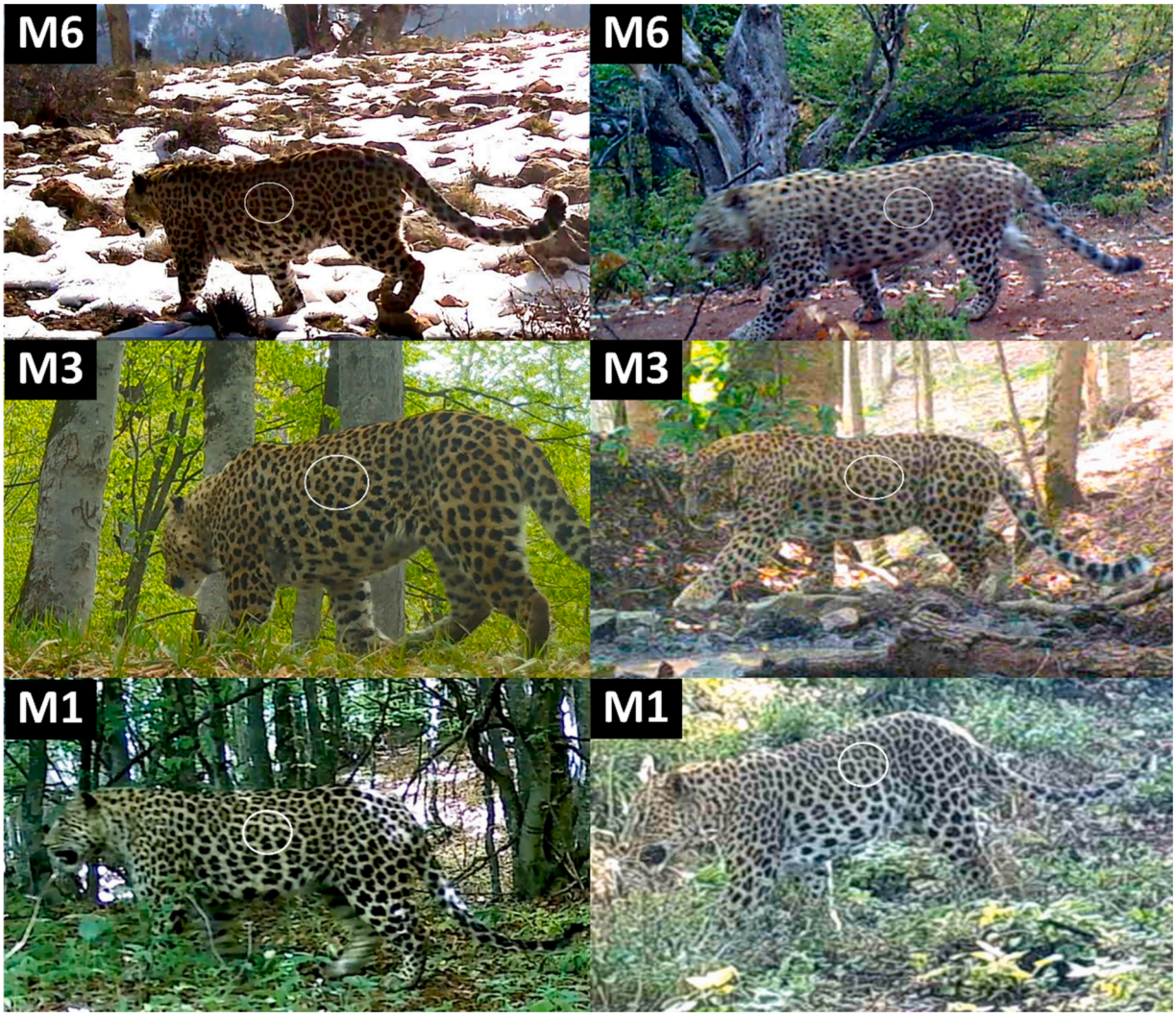


Fig. 2. Representative camera-trap images illustrating individual identification of Persian leopards based on unique rosette patterns. Shown are individuals M1, M3, and M6, each exhibiting distinct and stable flank rosette configurations used for individual recognition in this study.

frequencies while maintaining a sufficient number of sampling occasions for closed-population analyses. Similar multi-day sampling occasions have been used in camera-trap studies of large felids (Karanth and Nichols, 1998). Candidate models representing constant capture probability (M0) and capture heterogeneity (Mh) were compared using AIC and Bayesian Information Criterion (BIC). Models selected for inference were required to meet a predefined precision criterion (CV $\leq$ 0.15).

MMDM was calculated using the secr::MMDM () function in the R package secr based on individuals detected at more than one camera station. To estimate leopard density, an effective sampling area (ESA) was calculated by applying a HMMDM buffer around the camera-trap array. MMDM was estimated using the secr package, and density was calculated as:

$$D = \frac{\hat{N}}{ESA} \times 100$$

where N is estimated abundance and ESA is the HMMDM-buffered effective sampling area (km^2). Density was expressed as the number of leopards per 100 km^2. To evaluate the robustness of density estimates derived from the HMMDM approach, we additionally fitted SECR models using the R package *secr* (Efford, 2022). Half-normal (HN) and hazard half-normal (HHN) detection functions were fitted separately for the cold and warm seasons and compared using AIC. When competing models received comparable support (ΔAIC $<$ 2), density and abundance estimates were model-averaged using AIC weights following Burnham and Anderson (2002). The SECR integration mask was constructed with a grid spacing of 150 m and a 15-km buffer beyond the outer boundary of the camera-trap array. Buffer adequacy was evaluated using sensitivity analyses with alternative buffer widths of 15, 20, and 25 km, as well as the suggest.buffer() function implemented in the *secr* package (Efford, 2022). Model outputs included density (individuals per 100 km^2), abundance, and the spatial scale parameter (σ). Because cameras were relocated during the sampling period, MMDM-based inter--detection distances for individuals detected before and after relocation may incorporate camera displacement, potentially inflating the effective sampling area and leading to conservative (lower) density estimates. Therefore, SECR-derived estimates are presented alongside the HMMDM-based estimates as a complementary analysis.

3. Results

During the study, wildlife cameras documented 115 images, including 69 detections during the cold season and 46 during the warm season, representing 18 individual leopards (10 males and 8 females). Males comprised 55.6% of identified individuals, whereas females accounted for 44.4%. Detection frequencies varied between 1 and 25 in the cold season and between 1 and 12 in the warm season. The individual with the highest activity was Male number two (M-2) with 25 detections in the cold and 12 in the warm season. Some individuals, such as F-2, F-3, F-6 and M-10, were recorded only once in total. In general, majority of individuals demonstrated higher detection frequencies during the cold season (Fig. 3).

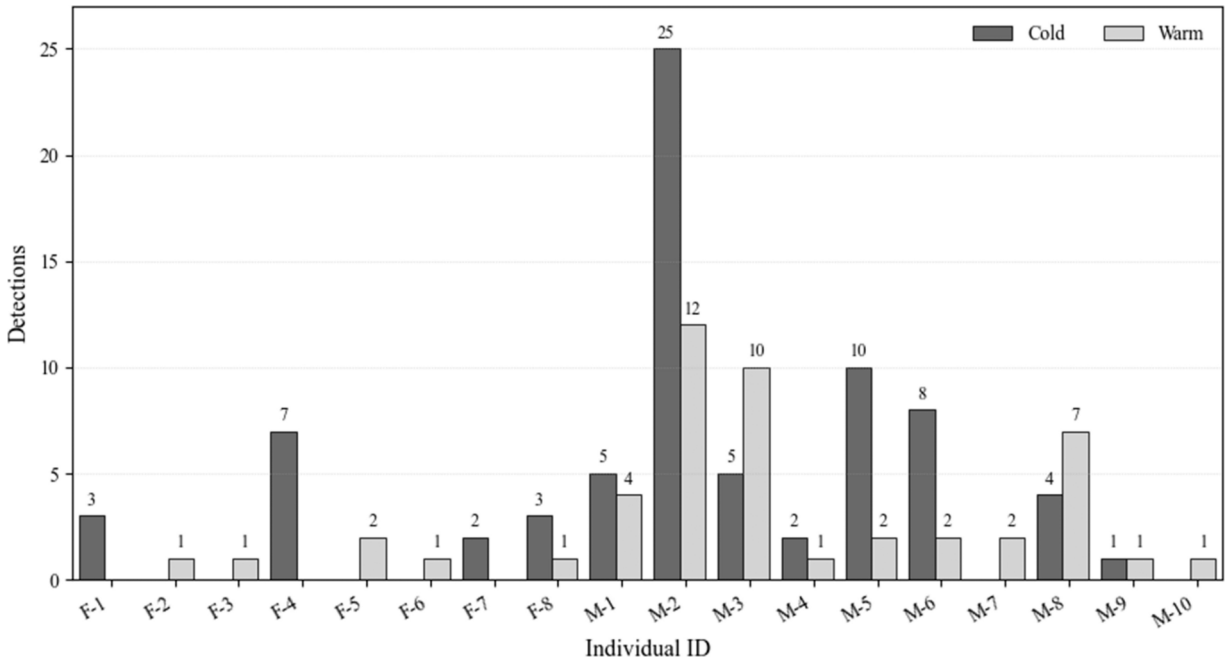


Fig. 3. Number of detections recorded for each individual Leopard during cold and warm seasons. Dark gray bars show cold season, and light gray bars show the warm season. M-X represent male leopards and F-X represent female leopards.

3.1. Population size and density

The MMDM was 6.75 km during the cold season and 6.74 km during the warm season. The effective sampling area was defined using a buffer equal to HMMDM, resulting in buffer widths of 3.37 km for the cold season and warm season. Applying these buffers yielded an effective sampling area of 508.64 km^2 for both seasons.

In the cold season (13 pooled occasions), M0, assuming constant capture probability, was strongly supported and had the lowest information-criterion values (AIC = 140.89; BIC = 141.86). In the warm season (9 pooled occasions), several heterogeneity models achieved lower AIC values (e.g., Mh Darroch; AIC = 89.69), but these models were associated with low precision, as indicated by large standard errors and high coefficients of variation. To avoid over-parameterized models under limited recapture information, model selection for the warm season was restricted to candidates meeting a predefined precision criterion (CV $\leq$ 0.15), resulting in M0 being selected as the most reliable model for inference. Goodness-of-fit was assessed using the deviance-based test in closedp.t() (R package Rcapture; Baillargeon and Rivest, 2007), where degrees of freedom (*df*) scales with the number of pooled occasions ($2^t - 1 - 2$) rather than sample size, explaining the large df despite few detected individuals. This assessment indicated no evidence of lack of fit (cold season: $\chi^2 = 112.89$, $(df) = 8189$, $P > 0.99$; warm season: $\chi^2 = 75.50$, $(df) = 509$, $P > 0.99$). In the cold season, 12 unique individuals were detected, including 10 recorded at multiple camera stations and 11 detected on two or more pooled sampling occasions; corresponding values for the warm season were 15, 5, and 7 individuals, respectively. Estimated capture probabilities under the selected M0 models were 0.236 and 0.208 for the cold and warm seasons, respectively. During the cold season, the abundance of Persian leopards was $\hat{N} = 12.37 \pm 0.66$ SE (95% CI: 11.07–13.67; CV = 0.05). Using the HMMDM-buffered effective sampling area of 508.64 km^2, this corresponds to a density of 2.43 leopards per 100 km^2. In the warm season, the estimated abundance was $\hat{N} = 17.1 \pm 1.89$ SE (95% CI: 13.40–20.8; CV = 0.11), generating a density of 3.36 leopards per 100 km^2 within the same effective area (508.64 km^2). Based on HMMDM approach, leopard density was approximately 38% higher during the warm season than the cold season (Table 1).

SECR analyses provided an additional assessment of leopard density using model-based estimation of animal activity centers and detection processes. Half-normal (HN) and hazard half-normal (HHN) detection functions received similar support in both seasons ($\Delta AIC < 0.1$), and density estimates were therefore model-averaged using AIC weights. Model-averaged SECR density estimates were 1.09 ± 0.41 leopards per 100 km^2 (95% CI: 0.29–1.88) during the cold season and 1.13 ± 0.37 leopards per 100 km^2 (95% CI: 0.41–1.86) during the warm season (Table 2). Corresponding estimates of the movement scale parameter (σ) were 5.40 km (95% CI: 3.96–7.35 km) and 6.69 km (95% CI: 5.08–8.79 km) for the cold and warm seasons, respectively.

Model-averaged SECR estimates of the baseline detection probability (g_0) were 0.015 (SE = 0.003) in the cold season and 0.013 (SE = 0.004) in the warm season. Buffer sensitivity analyses indicated that cold-season density estimates were stable across alternative state-space definitions, whereas warm-season estimates were more sensitive to buffer width, likely reflecting the limited number of spatial recaptures during the warm season.

4. Discussion

Our findings revealed that 55.6% of the individually identified leopards were males and 44.4% were females, closely matching the sex ratios reported by Hamidi et al. (2014) in Golestan National Park (58.8% males vs. 41.2% females) and by Farhadinia et al. (2019) in northeastern Iran (approximately 53.5% males vs. 46.5% females). In contrast, our results differed from those reported for the arid landscapes of Yazd Province, where females constituted a higher proportion of detections (58% females vs. 42% males; Farhadinia et al., 2021). The higher proportion of female detections reported from the arid landscapes of Yazd Province may reflect differences in resource distribution and habitat use. In water-limited environments, permanent water sources often represent critical focal points for wildlife activity, potentially increasing the detectability of females if they concentrate their movements around these resources, particularly when accompanied by dependent cubs (Farhadinia et al., 2019; 2021). In contrast, the forested landscapes of the Hyrcanian region provide more widely distributed water and cover resources, which may contribute to the male-biased detection patterns observed in our study. When considering the total number of detections rather than individuals, males accounted for 94 of 115 photographic records (81.7%), whereas females accounted for 21 of 115 (18.3%). This male-biased pattern is similar to that reported in northeastern Iran (≈80% males; Farhadinia et al., 2019) but differing from Yazd, where detections were more balanced (≈54% males and 46% females; Farhadinia et al., 2021). The pronounced male bias in photographic detections likely reflects differences in movement behaviour and space use between the sexes. Male leopards generally occupy larger home ranges and travel longer distances than females, increasing their probability of encountering camera stations and consequently their detectability in camera-trap surveys (Martins and Harris, 2013; Ray-Brambach et al., 2018; Kumbhojkar et al., 2020).

Moreover, 60% of all detections in our study occurred during the cold season, a pattern opposite to that reported by Farhadinia

Table 1
Seasonal abundance and density estimate of Persian leopards in the Hyrcanian Forest based on closed-population capture–recapture models. Abundance (N) and density (D) estimates are accompanied by standard errors (SE) and 95% confidence intervals (CI). CV = coefficient of variation.

Season	$\hat{p}$ (M0)	$\geq$ 2 stations	$\geq$ 2 pooled occasions	Abundance	SE(N)	LCL 95% (N)	UCL 95% (N)	CV(N)	Density (/100 km^2)
Cold	0.236	10	11	12.37	0.66	11.07	13.67	0.05	2.43
Warm	0.208	5	7	17.1	1.89	13.40	20.8	0.11	3.36

Table 2
Model-averaged SECR estimates for Persian leopards in Kiasar National Park and Dodangeh Wildlife Refuge.

Season	D (per 100 km^2)	SE	95% CI	N (mask)	SE	95% CI (N)	σ (m)
Cold	1.09	0.41	0.29–1.88	23.1	7.2	9.1–37.1	5365
Warm[a]	1.13	0.37	0.41–1.86	24.1	6.1	12.1–36.0	6693

[a] Cold-season density estimates were stable across 15–25 km buffers, whereas warm-season estimates declined from 1.13 to 0.79 leopards/100 km^2 as buffer width increased, indicating greater sensitivity to state-space definition.

et al. (2021), who found only about 27% of detections in winter and 73% in summer. This contrast likely reflects ecological differences between humid montane habitats and arid desert systems, where water availability strongly influences leopard detectability, particularly for females that depend more on reliable water sources during the dry season (Farhadinia et al., 2019).

Capture–recapture estimates indicated that leopard density was higher in the warm season (3.36 ± 0.37 SE individuals per 100 km^2) than in the cold season (2.43 ± 0.13 SE). By comparison, SECR-based density estimates were broadly comparable between seasons once parameter uncertainty was taken into account (Table 2), likely reflecting the smaller warm-season sample available for spatial modeling. The density estimates are higher than, those reported from the arid mountains of Yazd Province (1.0–1.6 individuals/100 km^2; Farhadinia et al., 2021) and Bamu National Park in southern Iran (1.87 individuals/100 km^2; Ghoddousi et al., 2010). Relative to Golestan National Park (2.6 individuals/100 km^2; Hamidi et al., 2014) cold season density was slightly lower, whereas warm season density was higher. Both seasonal estimates remained lower than densities reported from northeastern Iran (3.1–8.9 individuals/100 km^2; Farhadinia et al., 2019). Regional variation in density likely reflects differences in prey availability, habitat productivity, and human disturbance, as well as intraspecific and interspecific competition, highlighting the importance of both ecological interactions and anthropogenic pressures in shaping leopard population dynamics (Balme et al., 2019; Pokheral and Wegge, 2019; Rouse et al., 2021; Soofi et al., 2022; Vinks et al., 2022). The comparatively higher densities reported from northeastern Iran may reflect favorable prey conditions and the conservation benefits of well-protected mountain habitats, both of which are known to influence leopard population density (Taghdisi et al., 2013; Farhadinia et al., 2014; Farhadinia et al., 2019). In contrast, leopard populations in the Hyrcanian forests are increasingly exposed to anthropogenic pressures, including livestock grazing, poaching, habitat fragmentation, and human disturbance, which may reduce habitat suitability and limit the number of individuals that can be supported within the landscape.

In a broader biogeographic context, leopard densities vary substantially across their global range, from 0.64 individuals/100 km^2 in the Western Cape (Hinde et al., 2023) to 11.8 ± 2.6 individuals/100 km^2 in South Africa (Balme et al., 2019), with African estimates ranging from 0.7 to 12.2 leopards/100 km^2 (mean = 2.9 ± 2.7; Loveridge et al., 2022). These values further illustrate the remarkable ecological flexibility of leopards and the strong influence of local environmental conditions and anthropogenic pressures on population density (Balme et al., 2019; Rouse et al., 2021; Soofi et al., 2022).

The HMMDM results indicate that leopard density was approximately 38% higher in the warm season than in the cold season. The SECR analysis, however, did not provide clear evidence of seasonal variation in leopard density. The warm-season SECR estimate was sensitive to the definition of the integration mask, whereas the cold-season estimates were relatively stable across buffer widths. Therefore, the seasonal difference suggested by the HMMDM analysis should be interpreted with caution, as it was not clearly supported by the SECR analysis. Despite seasonal differences in leopard density, MMDM values were nearly identical between seasons (6.75 km and 6.74 km), indicating that movement scales remained broadly consistent throughout the year. The similarity in MMDM values suggests that seasonal variation in density was not associated with substantial changes in movement extent and may instead reflect changes in the spatial distribution of individuals within the study area.

Based on our density estimates and comparisons with other regions, Kiasar National Park and Dodangeh Wildlife Refuge appear to support relatively higher leopard densities. We hypothesize that this pattern may reflect a refuge effect, arising from habitat compression along the periphery due to poaching and livestock grazing pressures (Soofi et al., 2018; Khorozyan et al., 2018; Tizrouyan et al., 2026; Salmanpour et al., 2026b). Previous studies have shown that leopards preferentially select areas offering safety and abundant prey (Loveridge et al., 2022; Balme et al., 2019), and tend to utilize the interior of protected areas where human disturbance is minimal (Mohammadi et al., 2021). In our study area, intensive ranger patrols and support from community rangers likely enhanced both security and prey availability, thereby increasing relative leopard densities compared to surrounding regions. Furthermore, the proximity of Bula and Parvar Protected Areas provides a contiguous habitat network for leopards and their natural prey (Darvishsefat et al., 2006; Salmanpour et al., 2026a). Adjacent habitats also function as active corridors for leopards, as documented by Ardani et al. (2023), further supporting high leopard presence in the study area.

We hypothesize that this pattern is likely influenced by livestock presence during the warm season, as portions of the study area, its margins, and surrounding habitats are used for summer grazing (Khorozyan et al., 2018; Tizrouyan et al., 2026). Previous studies have demonstrated that livestock grazing and associated human disturbances negatively affect leopard presence (Soofi et al., 2018; Loveridge et al., 2022; Balme et al., 2019). Consequently, one possible explanation is that habitat compression may be more pronounced during the warm season, potentially enhancing the refuge effect within the study area, whereas the return of livestock to low-elevation pastures in the cold season may alleviate habitat compression. Seasonal differences in leopard movement scales are consistent with transhumance grazing patterns in the Hyrcanian-Alborz region (Farhadinia et al., 2019; Soofi et al., 2019; Mohammadi et al., 2021).

5. Conclusion

Our study provides valuable camera-trap records and baseline information on Persian leopards in this understudied region. It highlights the potential importance of Kiasar National Park and Dodangeh Wildlife Refuge as relatively important habitats that may provide refuge for Persian leopards, particularly during the warm season, as suggested by the HMMDM analysis but not clearly supported by the SECR analysis. Livestock presence may contribute to habitat compression and greater leopard concentration during this period, although this explanation was not directly tested in our study. To mitigate potential seasonal pressures, we recommend expanding the boundaries of protected areas, prioritizing prey-rich habitats, and maintaining continuous ranger patrols. These measures may help reduce habitat compression and alleviate intraspecific and interspecific competition, ultimately supporting leopard survival and population persistence in the Hyrcanian-Alborz region.

6. Limitations

Our study was conducted over a single year, which may not capture interannual variations in leopard density. Additionally, while our data cover the boundaries of Kiasar National Park and Dodangeh Wildlife Refuge, habitats outside these protected areas remain largely unstudied. It is likely that local density in some parts of the study area may be higher or lower than the overall mean, and therefore, our results should be interpreted with these limitations in mind. A limitation of the HMMDM approach is that most cameras were relocated once within their grid cells during the study period. Consequently, MMDM-based movement distances may partly reflect camera relocation rather than animal movement, potentially inflating the effective sampling area and producing conservative density estimates. This limitation further supports the inclusion of the complementary SECR analysis.

Future research should focus on adjacent habitats, identifying potential source areas with high leopard densities, and mapping connective corridors between them. Such studies are crucial for effective habitat restoration and conservation planning to ensure long-term persistence and connectivity of leopard populations across the landscape. The HMMDM-derived effective sampling area (508.64 km^2) extended beyond the protected area (~290 km^2). Therefore, these density estimates represent the effective sampling area rather than the protected area alone. We complemented this approach with SECR analyses, which estimate density from the spatial detection process within a defined habitat mask.

A key limitation of this study is that we did not directly quantify seasonal livestock pressure, distinguish core from edge habitat use, or examine the spatial relationship between leopard detections and grazing or human activity. Therefore, habitat compression remains a plausible but untested explanation for the observed seasonal pattern. Future spatially explicit studies integrating these factors will be needed to evaluate this hypothesis.

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CRediT authorship contribution statement

Mehdi Tizrouyan: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – original draft, Writing – review & editing, Visualization. **Ali Lotfi:** Conceptualization, Formal analysis, Methodology, Resources, Software, Writing – review & editing. **Farid Salmanpour:** Conceptualization, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Writing – original draft, Writing – review & editing. **Kaveh Ateni Mofrad:** Data curation, Writing – review & editing. **Panteha Ardani:** Data curation, Formal analysis, Methodology, Resources, Software, Writing – original draft, Writing – review & editing. **Eshagh Sadati:** Data curation, Writing – review & editing. **Omid Hedayatpour:** Data curation, Writing – review & editing. **Mohsen Yasari:** Data curation, Writing – review & editing. **Amirhosein Gohardehi:** Data curation, Writing – review & editing. **Mohammad Abbaszadeh:** Data curation, Writing – review & editing. **Alireza Ebrahimi:** Data curation, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

References

Ardani, P., Rezaei, H.R., Kaboli, M., 2023. Individual identification of Panthera pardus saxicolor using non-invasive sampling and molecular techniques in Iran: a case study in Parvar Protected Area. Mammal. Study 48 (1), 59–68.

Askerov, E., Trepet, S.A., Eskina, T.G., Bibina, K.V., Narkevich, A.I., Pkhitikov, A.B., Zazanashvili, N., Akhmadova, K., 2022. Estimation of the population densities of species prey or competitor to the Leopard (Panthera pardus) in Hyrcan National Park, Azerbaijan. Biol. Bull. 49 (7), 953–960.
Baillargeon, S., Rivest, L.-P., 2007. Rcapture: loglinear models for capture-recapture in R. J. Stat. Softw. 19 (5), 1–31. https://doi.org/10.18637/jss.v019.i05.
Balme, G., Rogan, M., Thomas, L., Pitman, R., Mann, G., Whittington-Jones, G., Midlane, N., Broodryk, M., Broodryk, K., Campbell, M., Alkema, M., 2019. Big cats at large: Density, structure, and spatio-temporal patterns of a leopard population free of anthropogenic mortality. Popul. Ecol. 61 (3), 256–267.
Betts, M.G., Wolf, C., Ripple, W.J., Phalan, B., Millers, K.A., Duarte, A., Butchart, S.H., Levi, T., 2017. Global forest loss disproportionately erodes biodiversity in intact landscapes. Nature 547 (7664), 441–444.
Bleyhl, B., Gerngross, P., Askerov, E., Farhadinia, M.S., Ghoddousi, A., Heidelberg, A., Khorozyan, I., Manvelyan, K., Mengüllüoglu, D., Ostrowski, S., Rosen, T., 2022. Mapping the distribution and habitat of Persian leopard across its historical range. Cat. N. 15, 9–18.
Bleyhl, B., Ghoddousi, A., Askerov, E., Bocedi, G., Breitenmoser, U., Manvelyan, K., Palmer, S.C., Soofi, M., Weinberg, P., Zazanashvili, N., Shmunk, V., 2021. Reducing persecution is more effective for restoring large carnivores than restoring their prey. Ecol. Appl. 31 (5), e02338.
Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer-Verlag, New York.
Cafaro, P., Hansson, P., Götmark, F., 2022. Overpopulation is a major cause of biodiversity loss and smaller human populations are necessary to preserve what is left. Biol. Conserv. 272, 109646.
Chen, C., Brodie, J.F., Kays, R., Davies, T.J., Liu, R., Fisher, J.T., Ahumada, J., McShea, W., Sheil, D., Agwanda, B., Andrianarisoa, M.H., 2022. Global camera trap synthesis highlights the importance of protected areas in maintaining mammal diversity. Conserv. Lett. 15 (2), e12865.
Darvishsefat, A.A., 2006. Atlas of protected areas of Iran.
Davison, C.W., Rahbek, C., Morueta-Holme, N., 2021. Land-use change and biodiversity: challenges for assembling evidence on the greatest threat to nature. Glob. Change Biol. 27 (21), 5414–5429.
Efford, M. (2022, August). *Secr 4.5-spatially explicit capture–recapture in R*.
Farhadinia, M.S., Alinezhad, H., Hadipour, E., Memarian, I., Ostrowski, S., Hobeali, K., Dadashi-Jourdehi, A., Johnson, P.J., Macdonald, D.W., Hunter, L.T., 2018. Intraspecific killing among leopards (Panthera pardus) in Iran (Mammalia: Felidae). Zool. Middle East. 64 (3), 189–194.
Farhadinia, M.S., Behnoud, P., Hobeali, K., Mousavi, S.J., Hosseini-Zavarei, F., Gholikhani, N., Akbari, H., Braczkowski, A., Eslami, M., Moghadas, P., Macdonald, D. W., 2021. Estimating the density of a small population of leopards (Panthera pardus) in central Iran using multi-session photographic-sampling data. Mamm. Biol. 101 (3), 363–371.
Farhadinia, M.S., McClintock, B.T., Johnson, P.J., Behnoud, P., Hobeali, K., Moghadas, P., Hunter, L.T., Macdonald, D.W., 2019. A paradox of local abundance amidst regional rarity: the value of montane refugia for Persian leopard conservation. Sci. Rep. 9 (1), 14622.
Farhadinia, M.S., Moqanaki, E.M., Hosseini-Zavarei, F., 2014. Predator–prey relationships in a middle Asian Montane steppe: Persian leopard versus urial wild sheep in Northeastern Iran. Eur. j. wildl. res. 60 (2), 341–349.
Farhadinia, M.S., Soofi, M., Rosen, T., Moghadas, P., Hobeali, K., Behnoud, P., Amanov, A., Dieterich, T., Hojamuradov, H., Hudaikuliev, N., Karryeva, S., Kaczensky, P., Mengliev, S., Muhashov, A., Nurmuhambetov, Z., Pestov, M., Potaeva, A., Terentyev, V., Salmanpour, F., Tizrouyan, H., Alinezhad, H., Jafari, B., Ommatmohammadi, M., Rabie, K., Veyisov, A., Linnell, J., 2022. Status of Persian leopards innorthern Iran and central Asia. Cat. N. 3–9.
Finn, C., Grattarola, F., Pincheira-Donoso, D., 2023. More losers than winners: investigating Anthropocene defaunation through the diversity of population trends. Biol. Rev. 98 (5), 1732–1748.
Fuller, A., Mitchell, D., Maloney, S.K., Hetem, R.S., Fonsêca, V.F., Meyer, L.C., Van de Ven, T.M., Snelling, E.P., 2021. How dryland mammals will respond to climate change: the effects of body size, heat load and a lack of food and water. J. Exp. Biol. 224 (_1), jeb238113.
Ghoddousi, A., Bleyhl, B., Sichau, C., Ashayeri, D., Moghadas, P., Sepahvand, P., Kh Hamidi, A., Soofi, M., Kuemmerle, T., 2020. Mapping connectivity and conflict risk to identify safe corridors for the Persian leopard. Landsc. Ecol. 35 (8), 1809–1825.
Ghoddousi, A., Hamidi, A.K., Ghadirian, T., Ashayeri, D., Khorozyan, I., 2010. The status of the endangered Persian leopard Panthera pardus saxicolor in Bamu National Park, Iran. Oryx 44 (4), 551–557.
Ghoddousi, A. and Khorozyan, I., 2023. *Panthera pardus ssp. tulliana. The IUCN Red List of Threatened Species 2023: e. T15961A50660903* [online].
Ghorbanalizadeh, A., Akhani, H., 2022. Plant diversity of Hyrcanian relict forests: an annotated checklist, chorology and threat categories of endemic and near endemic vascular plant species. Plant. Divers. 44 (1), 39–69.
Habibullah, M.S., Din, B.H., Tan, S.H., Zahid, H., 2022. Impact of climate change on biodiversity loss: global evidence. Environ. Sci. Pollut. Res. 29 (1), 1073–1086.
Hamidi, A., Ghoddousi, A., Soufi, M., Ghadirian, T., Jowkar, H., Ashayeri, S., 2014. Camera trap study of Persian leopard in Golestan National Park, Iran. Cat. N. 60, 12–14.
Hinde, K., Wilkinson, A., Tokota, S., Amin, R., O'Riain, M.J., Williams, K.S., 2023. Leopard density and the ecological and anthropogenic factors influencing density in a mixed-use landscape in the Western Cape, South Africa. Plos. One 18 (10), e0293445.
Johnson, C.N., Balmford, A., Brook, B.W., Buettel, J.C., Galetti, M., Guangchun, L., Wilmshurst, J.M., 2017. Biodiversity losses and conservation responses in the Anthropocene. Science 356 (6335), 270–275.
Karami M., Ghadirian T., Faizolahi K., 2016. The Atlas of Mammals of Iran.p.180.
Karanth, K.U., Nichols, J.D., 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79 (8), 2852–2862.
Khorozyan, I., Ghoddousi, S., Soufi, M., Soofi, M., Waltert, M., 2018. Cattle selectivity by leopards suggests ways to mitigate human–leopard conflict. Ecol. Evol. 8 (16), 8011–8018.
Khorozyan, I.G., Malkhasyan, A.G., Abramov, A.V., 2008. Presence–absence surveys of prey and their use in predicting leopard (Panthera pardus) densities: a case study from Armenia. Integr. Zool. 3 (4), 322–332.
Khosravi, R., Julaie, L., Fandos, G., Kuemmerle, T., Ghoddousi, A., 2024. Determinants of livestock depredation risk by Persian leopards in southern Iran. Biol. Conserv. 291, 110510.
Kolowski, J.M., Oley, J., McShea, W.J., 2021. High-density camera trap grid reveals lack of consistency in detection and capture rates across space and time. Ecosphere 12 (2), e03350.
Kuipers, K.J., Hilbers, J.P., Garcia-Ulloa, J., Graae, B.J., May, R., Verones, F., Huijbregts, M.A., Schipper, A.M., 2021. Habitat fragmentation amplifies threats from habitat loss to mammal diversity across the world's terrestrial ecoregions. One Earth 4 (10), 1505–1513.
Kumbhojkar, S., Yosef, R., Mehta, A., Rakholia, S., 2020. A camera-trap home-range analysis of the Indian leopard (Panthera pardus fusca) in Jaipur, India. Animals 10 (9), 1600.
Li, G., Fang, C., Watson, J.E., Sun, S., Qi, W., Wang, Z., Liu, J., 2024. Mixed effectiveness of global protected areas in resisting habitat loss. Nat. Commun. 15 (1), 8389.
Loveridge, A.J., Sousa, L.L., Seymour-Smith, J.L., Mandisodza-Chikerema, R., Macdonald, D.W., 2022. Environmental and anthropogenic drivers of African leopard Panthera pardus population density. Biol. Conserv. 272, 109641.
Mann, G.K., O'Riain, M.J., Parker, D.M., 2020. A leopard's favourite spots: habitat preference and population density of leopards in a semi-arid biodiversity hotspot. J. Arid. Environ. 181, 104218.
Marchese, C., 2015. Biodiversity hotspots: a shortcut for a more complicated concept. Glob. Ecol. Conserv. 3, 297–309.
Martins, Q., Harris, S., 2013. Movement, activity and hunting behaviour of leopards in the C ederberg mountains, South Africa. Afr. J. Ecol. 51 (4), 571–579.
Mohammadi, A., Lunnon, C., Moll, R.J., Tan, C.K.W., Hobeali, K., Behnoud, P., Moghadas, P., Macdonald, D.W., Farhadinia, M.S., 2021. Contrasting responses of large carnivores to land use management across an Asian montane landscape in Iran. Biodivers. Conserv. 30 (13), 4023–4037.
Olhnuud, A., Wen, J., Yu, J., Lyu, F., Zhang, Q., 2025. Responses of insect pollinators to habitat fragmentation: a global meta-analysis. J. Appl. Ecol.
Parchizadeh, J., Arias, M.G., Belant, J.L., 2024. Livestock predation patterns by gray wolves and persian leopards in Iran. Sci. Rep. 14 (1), 26899.
Petridou, M., Benson, J.F., Gimenez, O., Kati, V., 2023. Spatiotemporal patterns of wolves, and sympatric predators and prey relative to human disturbance in northwestern Greece. Diversity 15 (2), 184.
Pokheral, C.P., Wegge, P., 2019. Coexisting large carnivores: spatial relationships of tigers and leopards and their prey in a prey-rich area in lowland Nepal. Ecoscience 26 (1), 1–9.

Powers, R.P., Jetz, W., 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nat. Clim. Change 9 (4), 323–329.
Ray-Brambach, R.R., Stommel, C., Rödder, D., 2018. Home ranges, activity patterns and habitat preferences of leopards in Luambe National Park and adjacent Game Management Area in the Luangwa Valley, Zambia. Mamm. Biol. 92 (1), 102–110.
Reyes, A., Rodríguez, D., Reyes-Amaya, N., Rodríguez-Castro, D., Restrepo, H., Urquijo, M., 2017. Comparative efficiency of photographs and videos for individual identification of the Andean bear (Tremarctos ornatus) in camera trapping. Therya 8 (1), 83–87.
Rogan, M.S., Balme, G.A., Distiller, G., Pitman, R.T., Broadfield, J., Mann, G.K., Whittington-Jones, G.M., Thomas, L.H., O'Riain, M.J., 2019. The influence of movement on the occupancy–density relationship at small spatial scales. Ecosphere 10 (8), e02807.
Rouse, S., Behnoud, P., Hobeali, K., Moghadas, P., Salahshour, Z., Eslahi, H., Ommatmohammadi, M., Khani, A., Shabani, A., Macdonald, D.W., Farhadinia, M.S., 2021. Intraspecific interactions in a high-density leopard population. Ecol. Evol. 11 (23), 16572–16584.
Sagheb Talebi, K., Sajedi, T., Pourhashemi, M., 2014. Forests of Iran: A Treasure from the Past, a Hope for the Future (No. 15325). Springer Netherlands.
Salmanpour, F., Shakoori, Z., Kia, M., Eshaghi, R., Ghaderi, M., Ghomi, S., Kaveh, R., Rabie, K., Kiabi, B.H., Farhadinia, M.S., 2023. Mineral lick use by a community of large herbivores in northern Iran. Ecol. Evol. 13 (1), e9731.
Salmanpour, F., Shakoori, Z., Langevelde, F.V., Kiabi, B.H., Sayahnia, R., Ahmadzadeh, F., 2026a. Phenological responses to climate change: advancing mating and calving in wild and semi-captive Caspian red deer. Wildl. Biol. 2026 (3), e01486.
Salmanpour, F., Shakoori, Z., Tizrouyan, M., Salmanpour, M., Nouri, S., Kia, M., Eshaghi, R., Ebrahimi, A., 2026b. Divergent temporal trends in brown bear survival and reproductive indices shaped by seasonal vegetation dynamics and urban expansion. Environ. Manag. 76 (8), 257.
Sanei, A., Zakaria, M., Daraei, L., Besmeli, M.R., Esfandiari, F., Veisi, H., Absalan, H., Fasihi, F., 2020. Countrywide distribution modelling of the persian leopard potential habitats on a regional basis in Iran. Research and Management Practices for Conservation of the Persian Leopard in Iran. Springer International Publishing, Cham, pp. 81–107.
Seddon, N., Mace, G.M., Naeem, S., Tobias, J.A., Pigot, A.L., Cavanagh, R., Mouillot, D., Vause, J., Walpole, M., 2016. Biodiversity in the anthropocene: prospects and policy. Proc. R. Soc. B Biol. Sci. 283 (1844), 20162094.
Soofi, M., Ghoddousi, A., Zeppenfeld, T., Shokri, S., Soufi, M., Jafari, A., Ahmadpour, M., Qashqaei, A.T., Egli, L., Ghadirian, T., Chahartaghi, N.R., 2018. Livestock grazing in protected areas and its effects on large mammals in the Hyrcanian forest, Iran. Biol. Conserv. 217, 377–382.
Soofi, M., Ghoddousi, A., Zeppenfeld, T., Shokri, S., Soufi, M., Egli, L., Jafari, A., Ahmadpour, M., Qashqaei, A., Ghadirian, T., Filla, M., 2019. Assessing the relationship between illegal hunting of ungulates, wild prey occurrence and livestock depredation rate by large carnivores. J. Appl. Ecol. 56 (2), 365–374.
Soofi, M., Qashqaei, A.T., Mousavi, M., Hadipour, E., Filla, M., Kiabi, B.H., Bleyhl, B., Ghoddousi, A., Balkenhol, N., Royle, A., Pavey, C.R., 2022. Quantifying the relationship between prey density, livestock and illegal killing of leopards. J. Appl. Ecol. 59 (6), 1536–1547.
Szabó, Z., Gombkötő, P., Aranyi, S.C., Patkó, L., Patkó, D., Barta, Z., 2024. Camera trapping of forest mammals in Bükk Mountain, Hungary. Community Ecol. 1–9.
Taghdisi, M., Mohammadi, A., Nourani, E., Shokri, S., Rezaei, A., Kaboli, M., 2013. Diet and habitat use of the endangered Persian leopard (Panthera pardus saxicolor) in northeastern Iran. Turk. J. Zool. 37 (5), 554–561.
Tizrouyan, M., Salmanpour, F., Mofrad, K.A., Ardani, P., Sadati, E., Hedayatpour, O., Yasari, M., Gohardehi, A., Salmanpour, M., 2026. Spatiotemporal patterns of brown bears with cubs compared to lone bears. Mammal Res. 71 (1), 1.
Trew, B.T., Maclean, I.M., 2021. Vulnerability of global biodiversity hotspots to climate change. Glob. Ecol. Biogeogr. 30 (4), 768–783.
Tucker, M.A., Santini, L., Carbone, C., Mueller, T., 2021. Mammal population densities at a global scale are higher in human-modified areas. Ecography 44 (1), 1–13.
van Vliet, J., 2019. Direct and indirect loss of natural area from urban expansion. Nat. Sustain. 2 (8), 755–763.
Vinks, M.A., Creel, S., Rosenblatt, E., Becker, M.S., Schuette, P., Goodheart, B., Sanguinetti, C., Banda, K., Chifunte, C., Simukonda, C., 2022. Leopard Panthera pardus density and survival in an ecosystem with depressed abundance of prey and dominant competitors. Oryx 56 (4), 518–527.
Wattegedera, M., Silva, D., Sooriyabandara, C., Wimaladasa, P., Siriwardena, R., Piyasena, M., Marasinghe, R.M., Hathurusinghe, B.M., Nilanthi, R.M., Gunawardena, S., Peiris, H., 2022. A multi-point identification approach for the recognition of individual leopards (Panthera pardus kotiya). Animals 12 (5), 660.
Williams, J.J., Freeman, R., Spooner, F., Newbold, T., 2022. Vertebrate population trends are influenced by interactions between land use, climatic position, habitat loss and climate change. Glob. Change Biol. 28 (3), 797–815.
Yildiz, F., Uzun, A., 2024. Daily activity patterns and overlap activity of medium–large mammals in Sülüklü Lake Nature Park, Western Black Sea Region, Türkiye. Ecol. Evol. 14 (12), e70654.
Yuan, R., Zhang, N., Zhang, Q., 2024. The impact of habitat loss and fragmentation on biodiversity in global protected areas. Sci. Total. Environ. 931, 173004.
Yusefi, G.H., Brito, J.C., Soofi, M., Safi, K., 2022. Hunting and persecution drive mammal declines in Iran. Sci. Rep. 12 (1), 17743.
Zhang, H., Chase, J.M., Liao, J., 2024. Habitat amount modulates biodiversity responses to fragmentation. Nat. Ecol. & Evol. 8 (8), 1437–1447.