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RESEARCH ARTICLE

Legacies of historical population management shape contemporary bear use of anthropogenic spaces

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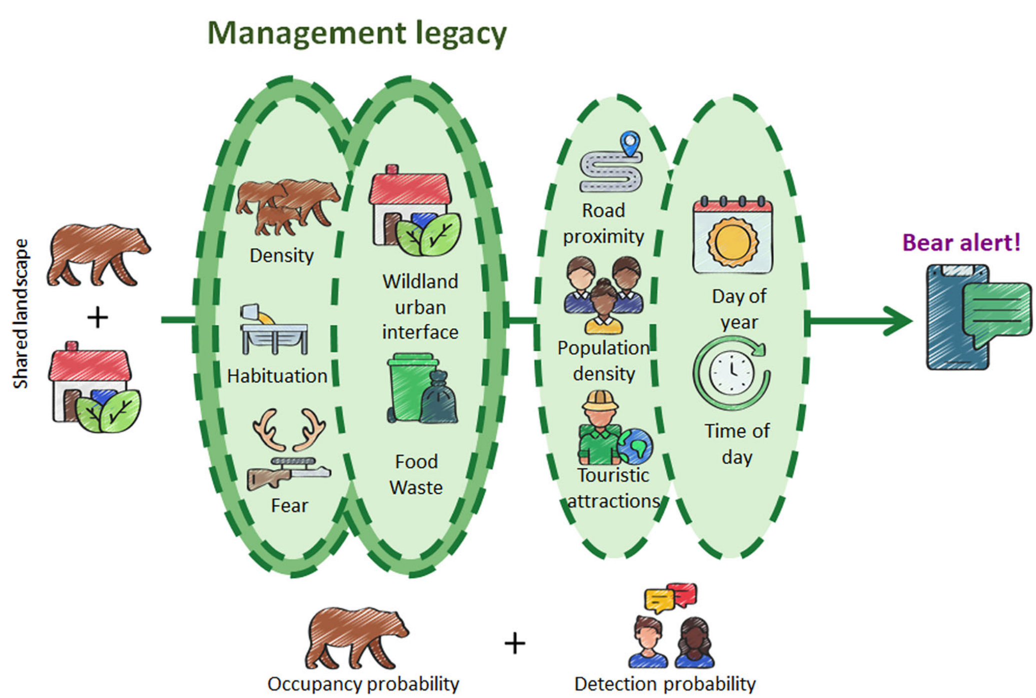
Abstract Romania hosts one of Europe's largest brown bear populations, but rising human-bear encounters and related casualties raise concerns about their drivers and future population management. Using >10 000 encounter reports (2019–2024) in a hierarchical occupancy model accounting for detection processes, we show that bear presence in human-dominated spaces is linked to food conditioning, habituation, and shaped by historical management. Bears occur more often in high wildland-urban interface areas, especially those closer to communist-era elite-hunting grounds with feeding sites. These patterns reflect a long-term legacy of 1960s population management policies interacting with environmental and behavioral processes to shape recent bear behavior. We call for management addressing ecological and social sustainability by phasing out supplemental feeding, reducing habituation and food conditioning, improving public knowledge of bear ecology, and recognizing historical legacies to promote coexistence.

Graphical abstract



Keywords Brown bear · Carpathian region · Coexistence · Historical population management · Human–wildlife interaction · Legacy Effects

INTRODUCTION

As global human population grows, pressure on natural environments intensifies, especially in densely populated regions like Europe (Weber and Sciubba 2019). Despite increasing anthropogenic pressure, Eastern Europe retains large wilderness areas like the Romanian Carpathians, home to one of the largest brown bear (*Ursus arctos,* hereafter *bear*) populations in Europe—alongside other iconic large mammals such as wolf, lynx, European bison or red deer (Chapron et al. 2014; Fedorca et al. 2019; Neagu and Rozylowicz 2025). With a habitat comparable in size to the Greater Yellowstone Ecosystem, the region holds over 15 times more brown bears (Quammen 2003). This abundance results from long-term habitat suitability, historic and recent management, and greater social tolerance toward large carnivores compared to Central Europe (Georgescu 2003; Rode et al. 2021). However, in recent decades, reports of human-bear interactions, including livestock depredation and attacks in urban or peri-urban areas have increased (Bombieri et al. 2019; Pop et al. 2023), raising questions about human-bear coexistence. Amid increasing anthropogenic resistance (Ghoddousi et al. 2021) and declining tolerance, two competing management strategies emerge: reconnecting habitats to support growing populations and promote coexistence (Can et al. 2014; Fletcher and Toncheva 2021; Mayer et al. 2023), or using hunting to reduce numbers, restore fear, limit habituation, and fund conservation (Hertel et al. 2016; Wheat and Wilmers 2016; Stăncioiu et al. 2019a). The success of either approach depends on understanding the socio-ecological drivers of increasing urban and peri-urban bear encounters, and designing and adopting bear management strategies policies that balance conservation success with human safety and inter-specific coexistence.

The recent recovery of large mammal populations is not unique to Romania; many developed countries have seen similar trends due to legal protection and coexistence efforts (Chapron et al. 2014, Carter and Linnell 2016, Mayer et al 2023). However, the intense use of urban and peri-urban habitats by bears is unique to Romania, providing an unprecedented natural experiment on how long-term protection and management can interact to shape ecological responses (Fig. 1). As adaptable omnivores with ranges up to 800 km^2, brown bears typically inhabit extended forested habitats, but can successfully exploit anthropogenic food sources and urban peripheries (Lucas et al. 2025). Their growing urban presence reflects ecological and behavioral responses to human exposure and environmental pressures (Elfström et al. 2014). The shift toward increased use of anthropogenic spaces can be explained by several mechanisms, such as habitat fragmentation, intraspecific competition and displacement of young bears or opportunistic behavior such as human habituation and food-conditioning (Elfström et al. 2014). Hunting can maintain a landscape of fear, discouraging foraging in proximity of humans (Gaynor et al. 2019; Lodberg-Holm et al. 2019; Brown et al 2023; Moleón and Sánchez-Zapata 2023). In fact, if bears associate humans with food sources and loose fear (Gaynor et al. 2019; Brown et al 2023) they can more often cause property damage, livestock losses, or attack humans (Pop et al. 2023), fueling intolerance and fear (Stăncioiu et al. 2019a). However, the time-scales at which the species respond to management practices such as supplemental feeding or hunting remain widely unexplored.

Social-ecological systems and species respond to land use and management decisions with time delays, and impacts can persist from years to centuries (Foster et al. 2003; Kuussaari et al 2009; Polaina et al. 2019; Munteanu et al. 2020). Ecological legacies can be particularly strong after shock-events like wars (Bragina et al. 2018; Barthelme et al. 2024) or under totalitarian regimes, where centralized environmental interventions served political agendas (Brain and Pál 2018). For instance, heavy post–World War II forest harvesting to pay reparations altered forest structures, canopy loss and seed bank diversity in modern Romania and Germany (Nita et al. 2018). Ecological legacies, often modeled by relating contemporary ecological effects to historical drivers,can span decades to centuries (Foster et al. 2003; Kuussaari et al 2009; Polaina et al. 2019; Munteanu et al. 2020) and interact with social legacies, including institutions, norms, and customs that shape management (Tappeiner et al. 2021). Ignoring legacy effects risks misinformed or misguided management and conservation decisions (Munteanu et al. 2020).

In Romania, legacies related to bear populations may stem from communist central planning (1947–1989), which imposed strict wildlife monitoring and management plans emphasizing trophy species like brown bear, wild boar *(Sus scrofa)* and red deer (*Cervus elaphus)* due to leader Nicolae Ceauşescu's hunting interests (Salvatori et al. 2002). Bears were protected, but intensively managed, including supplemental feeding at selected hunting locations since 1974, protected buffer zones around hunting grounds, breeding programs and intensive monitoring (Mooney 1991; Georgescu 2003). Bear protection policies were initiated in 1953 when den hunting was banned, and together with communist population management, likely contributed to Romania being a European bear-abundance hotspot

Fig. 1 Examples of bears exploiting human-dominated landscapes, supporting the conditioning and habituation hypothesis in proximity of restaurants (Foto top left: M. Nita) at garbage dumps (Foto top right: S Munteanu) in Wildland-Urban-Interface (Foto bottom left: C Munteanu) and along roads (Foto bottom right: C Munteanu)

(Quammen 2003). Following the communist regime collapse in 1990, supplemental feeding continued in historical locations and also expanded across the species range (at least 2 km away from forest edge), while hunting resumed under new regulations (Fig. 2). Studies from other temperate systems suggest that if fear of humans dissolves, bears increasingly explore anthropogenic habitats such as agricultural fields, farms, orchards, and especially food waste sites because they provide reliable food sources (Bautista et al. 2017) and refuge from older dominant males (Bellemain et al. 2005). While political discourse and decisions revolve around hunting, supplemental feeding is less often addressed, although bears were actively fed in Romania between 1974 and 2016. In Romania, supplemental feeding continues for non-target species, but only in very few cases, curbing supplemental feeding is acknowledged as a management strategy for brown bear (Neagu and Rozylowicz 2025). This raises the question of whether supplemental feeding has contributed to behavioral and ecological legacies that complicate current coexistence efforts.

Our goal here was to assess if historical population management affects contemporary human–wildlife interactions,particularly the bears' use of urban and peri-urban spaces. Specifically, we asked (a) where and when bear encounters are most likely in Romania (b) what ecological mechanisms drive the use of urban habitats and (c) whether contemporary encounter patterns reflect historical management legacies.

We expected higher rates of human-bear encounters during crepuscular hours, early spring after emergence from winter sleep, and in populated or accessible areas. Bears were expected to use anthropogenic spaces where

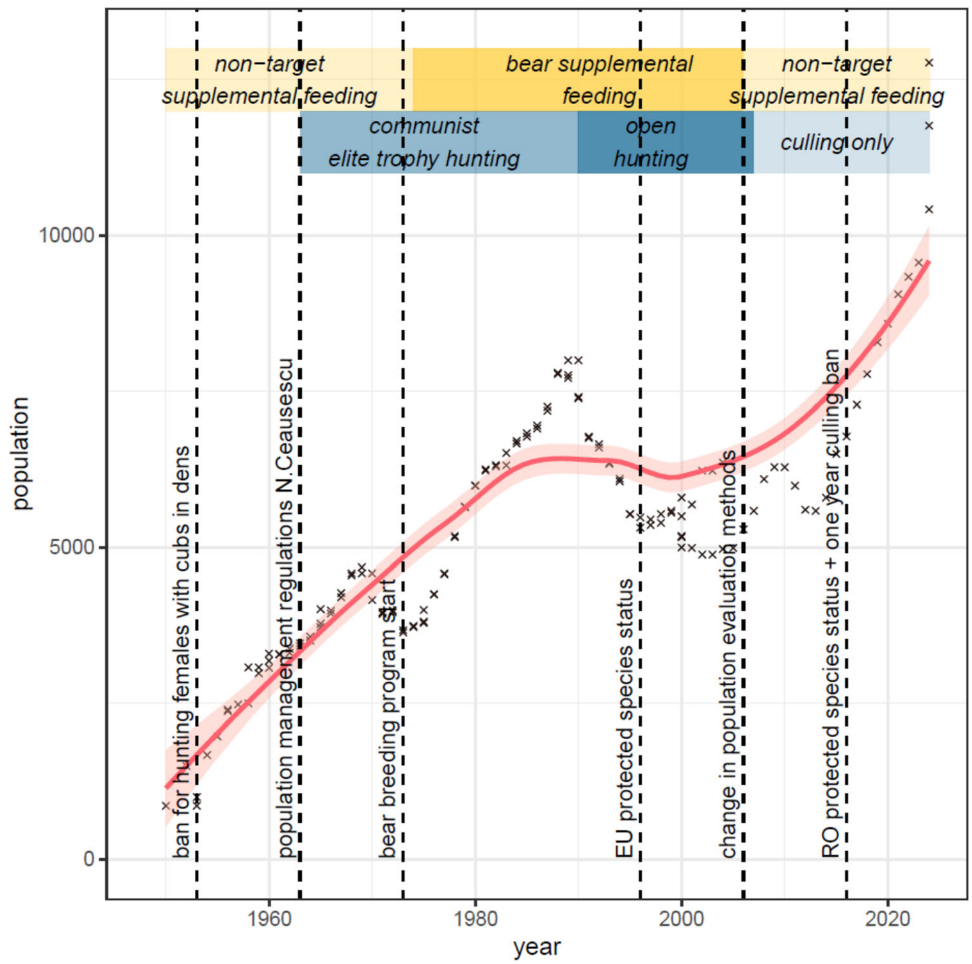


Fig. 2 Bear population trends, as compiled from multiple data sources for Romania between 1940 and 2024 in relation to major political decisions regarding population management. Hunting and supplemental feeding regulations are shown in blue and yellow, respectively. The trendline is computed using a LOESS smoother with a span of 0.85 and 95% confidence interval. Data sources: Mooney (1991), Quammen (2003), MMP (2025), INCDS (2021), Ionescu (2016)

buildings are to a high degree intermixed with forest (Schug et al. 2023), where there is more food waste (food-conditioning hypothesis) (Elfström et al. 2014) and in areas with high bear densities in the core habitat (despotic distribution hypothesis (Elfström et al. 2014)). Distance to historical elite-hunting districts which were once characterized by high densities, strictly enforced supplemental feeding and bait hunting, was used to test for legacy effects. We hypothesized that historical management still shapes bear behavior: historical and long-term food conditioning may have contributed to an increase in contemporary human–bear conflicts. Romania's political and environmental history, and its growing population of brown bears offers a unique natural experiment for understanding how management drives long-term human–wildlife coexistence—a challenge that many countries with growing large mammal populations face today (Can et al. 2014; Fletcher and Toncheva 2021).

MATERIALS AND METHODS

To address our three research questions, we used publicly available, citizen-driven data on bear encounters in Romania (2019–2024). Encounters were reported via emergency line calls and curated by a national text-message warning system (RO-ALERT)—a citizen science dataset on human–wildlife encounters that can provide valuable insights into species space use. We applied a hierarchical species occupancy model separating observational from ecological processes, to disentangle drivers of bear occurrence in human areas from detection biases. Calls were analyzed in a 3×3 km national grid, modeling probability of recorded observation as a function of time, season, and human presence (tourism, population, road density). Once accounting for observation probability, occurrence was modeled based on bear population density, habitat structures (forest, wildland-urban-interface: WUI), human food attractants (human food waste), and historical

Table 1 Variables considered in the final model, the ecological processes that it proxies and the expected directionality of the relationship with bear urban and peri-urban habitat use

Variable	Expected relationship	Mechanism	References
Observation probability variables			
Time of day	+	Bears are crepuscular, most active dawn and dusk	Ordiz et al. (2017)
Time of year	–	Immediately after emergence from hibernation or in the fall when fattening up	Ordiz et al. (2017)
Road density	+	Measure of effort: higher likelihood of encounters due to higher human presence	Brown and Williams (2019)
Population	+	Measure of effort: higher likelihood of observers being present and making calls	Brown and Williams (2019)
Tourism	+	Measure of effort: higher likelihood of observer presence	Brown and Williams (2019)
Occupancy variables			
Maximum bear density in surrounding 9 km area	+	Competition and predation refuge	Elfström et al. (2014), Pop et al. (2023)
Anthropogenic food waste sources	+	Food conditioning and habituation	Smith et al. (2005), Elfström et al. (2014), Powell et al. (2022)
Forest cover	–	Habitat & natural food availability	Elfström et al. (2014), González-Bernardo et al. (2020), Pop et al. (2023)
Wildland-urban-interface (WUI)—proxy for orchards, yards and subsistence farming	+	Food availability from small farms, orchards, bee hives	Blecha et al. (2018), Schug et al. (2023), Kaim et al. (2025)
Distance to historical elite hunting and supplemental feeding areas	–	Management legacy, potentially related to habituation through continued supplemental feeding	Elfström et al. (2014), Selva et al. (2017), Penteriani et al. (2021)

management legacies (distance to historical feeding and hunting grounds).

Study region

We studied the entire range of the brown bearin Romania, focusing on the Romanian Carpathians, the Romanian portion of the Carpathian Ecoregion (135 000 km^2, 57% forested), dominated by deciduous and mixed forests (*Fagus sylvatica, Quercus* spp.) (Munteanu et al. 2022). Romania has a human population of approximately 19.5 million, with 54% living in urban areas and the remainder in smaller rural settlements (Pop et al. 2023). The country harbors the largest brown bear population in Europe outside Russia, estimated at 10 419–12 770 individuals (Fedorca et al. 2019, Ministerul Mediului, Apelor si Padurilor 2025). Following direct persecution and two world wars, Romania's bear population dropped to 860 individuals after WWII (Quammen 2003). Hunting was banned for the general public between 1963 and 1989 but remained permitted for political elites, reflecting Nicolae Ceauşescu's passion for hunting and use of wildlife to display political power (Quammen 2003). During this time Romania was divided in some 2156 hunting districts, with 122 reserved for elite hunting only, and where supplemental feeding was practiced to reduce winter mortality, increase populations, individual fitness and provide predictable locations for bait hunting (Mooney 1991; Georgescu 2003) (Data available at https://doi.org/10.5281/zenodo.18244411). We note that although not documented here, supplemental feeding likely occurred in other areas too. Around these historical elite-hunting management areas, 500 districts were designated for strict species protection. Bear numbers increased from 4000 in 1975 to 8000 in 1989 (Mooney 1991), although Ceauşescu and his elites reportedly hunted a total of some 450 bears until 1989 (Georgescu 2003). After 1990, hunting was opened according to management plans, and by 2000 the bear population was estimated at 5000–6000 (Stăncioiu et al. 2019b). A hunting ban for population management was imposed in 2007, and only culling of human-conflict causing bears was allowed until 2024, with the exception of the year 2016 when a complete ban was active. Human–bear conflicts have risen steadily in Romania, resulting in 26 fatalities and 274 reported injuries since 1995. Comparatively, Romania is characterized by both the largest number of bear attacks on humans worldwide, and the highest brown bear density (Bombieri et al. 2019). In 2024

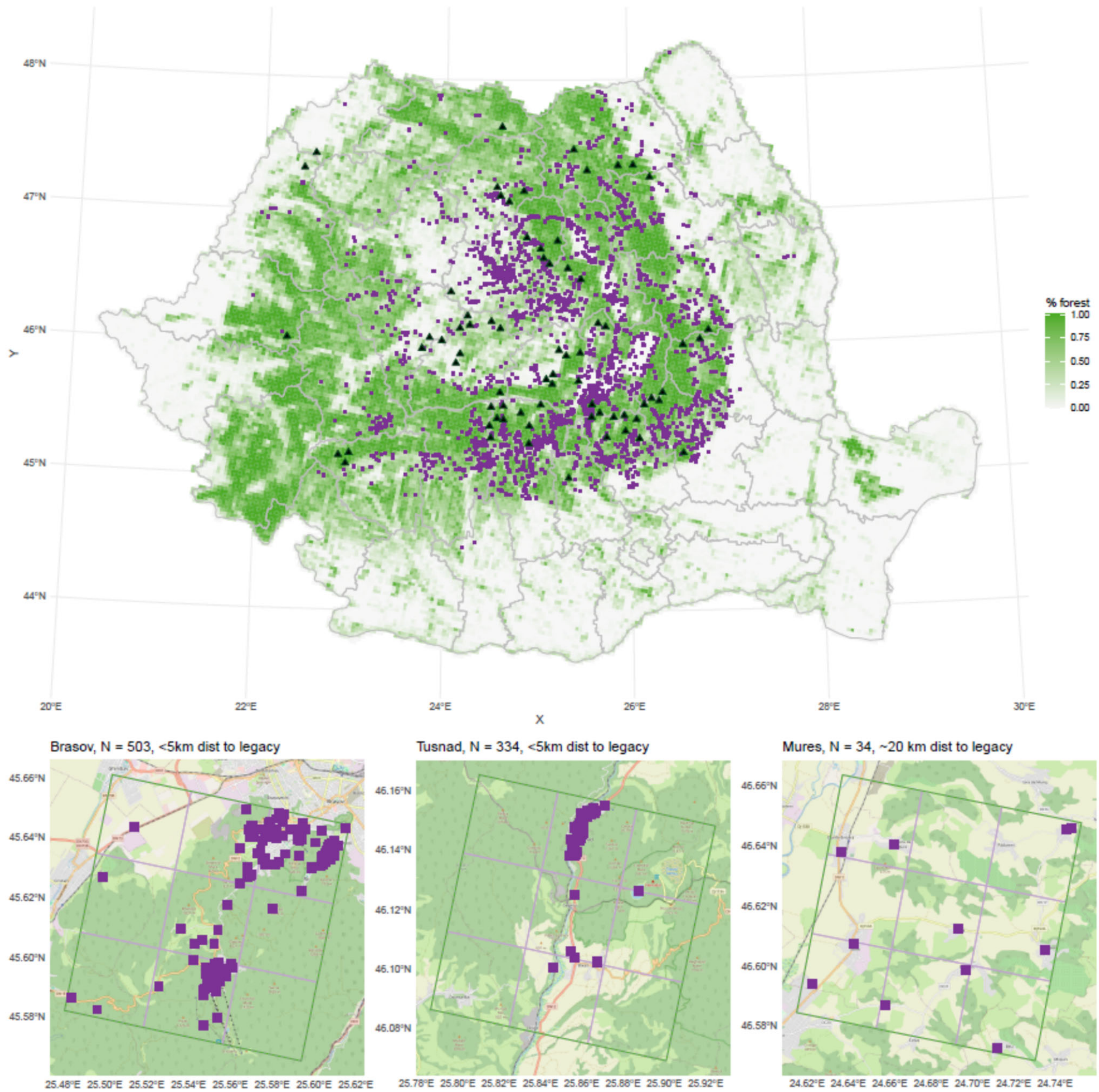


Fig. 3 Study area. Romania, with its forest cover and the distribution of human-bear encounters. Each purple point represents a 3×3 km grid cell where bear encounters have been reported at least once between 2019–2024 (N=1548 cells, N=10 472 calls, range: 1:443 calls/grid cell). The entire country of Romania is covered by a total of 27 197 grid cells. The black triangles represent approximate locations of historical bear feeding and hunting areas 1963–1984. Bottom row: Distribution of bear-encounter calls in three subset regions a 9×9 km (point locations may overlap). N represents the number of calls for the entire 9×9 km grid cell. The listed distance is the distance from the cell center to the nearest historical feeding and hunting district

a level of intervention of culling 450 was approved to prevent human–wildlife conflicts. To analyze bear-human interactions and their drivers, we covered the entire study area with a 3×3 km grid (N=27 197 cells) with all data reported at the grid-cell level (Fig. 3).

Bear encounters data

We used data from the RO-ALERT system, which broadcasts emergency warnings via mobile networks under the Romanian Ministry of Internal Affairs and the Inspectorate for Emergency Situations (IGSU) (Ordonanta de urgenta privind operarea sistemului de avertizare a populatiei in situatii de urgenta "RO-ALERT" 2017). Data were pre-filtered by data providers on messages that involved bears (hereafter bear-alerts). The bear-alert system was launched in late 2018, and it has since curated and disseminated wildlife encounter reports based on emergency calls, primarily from populated areas. The system collects wildlife encounter reports from emergency calls, mainly in populated areas. We retrieved 10 716 bear-alerts recorded between January 2019 and December 2024. Each message included location, date, and time, and occasionally the number of individuals (2.84%). We geolocated the messages using the pandas package and OpenStreetMaps OSM in python, assigning exact coordinates when specific addresses (street, house number) were available and using commune or village centroids when addresses were missing. All locations were cross-checked against message text and broadcast area, and 623 mislocated points were manually corrected. Messages lacking sufficient detail for geolocation were excluded, resulting in 10 476 georeferenced bear encounters across 1548 unique 3×3 km grid cells. For each bear-alert, we extracted time of day and day of year, classifying them into seasons and crepuscular periods using the 'suncalc' package in RStudio (Thieurmel and Elmarhraoui 2022).

Environmental variables

We selected environmental variables expected to influence both bear detectability and their use of urban and peri-urban areas (Table 1). To account for variation in probability of observation, we included time of day and day of year, as bears exhibit crepuscular activity patterns and increased movement during periods of hyperphagia in spring and fall (González-Bernardo et al. 2020). We also considered human population density, touristic facility density, and road density as potential factors affecting detection. We calculated human population density per grid cell based on GEOSTAT 2011 grid data (Eurostat 2011). We extracted road length and the number of touristic facilities (hotels, restaurants, pensions) per grid cell from OpenStreetMap using the OSMDownloader plug-in in QGIS. We focused on five environmental variables that captured the availability of anthropogenic food sources, potential for habituation, and habitat characteristics and which we expected could affect bear use of urban spaces (Table 1). Forest cover was extracted from (Hansen et al. 2013) and the proportion of the wildland–urban interface (WUI) per grid cell was calculated to identify areas with high human–wildlife conflict potential (Schug et al. 2023; Kaim et al. 2025). We quantified the density of food-related attractants per grid cell by extracting the number of potential food source locations (restaurants, hotels, supermarkets, waste containers, and food stands) from OpenStreetMap using the OSMDownloader plug-in in QGIS. To represent intra-species competition and predator avoidance, we used bear density estimates for most Romanian hunting districts (INCDS: Institutul National de Cercetare-Dezvoltare in Silvlicultura 2021). We spatially allocated the average density values for the hunting district to only forested areas, extracted them to each grid cell, imputed missing values using the 'MuMIn' package in R, and calculated the maximum bear density within a 9×9 km moving window. The size of the moving window was meant to capture the approximate size of a wildlife management unit (ca. 100 km^2). To assess potential time-delayed effects (Foster et al 2003; Kuussaari et al 2009; Munteanu et al 2020), we used a 1986 hunting district map identifying 122 elite-hunting areas (average 85 km^2) along with their respective buffer/protection zones, noting that all these units are located within the bear range but some were managed for other wildlife. We geolocated each district's centroid and computed the distance from each grid cell to the nearest hunting district as a proxy for potential legacy effects. Although we cannot fully distinguish legacy effects from persistent spatial structure or non-random historical feeding site selection, we assume the existence of a legacy effect of historical hunting, if the proxy for historical supplemental feeding location has a significant effect on the contemporary bear use of anthropogenic spaces. We examined all variables for collinearity using Spearman's rho and retained only predictors that did not exceed a correlation of 0.7. We log-transformed the waste and tourism variables, and normalized all predictors to mean 0 and standard deviation 1 using the 'bestNormalize' package in RStudio (Peterson 2023).

Occupancy models

To investigate the drivers of brown bear presence in urban and peri-urban areas, we used a Bayesian hierarchical framework and a single-species spatial occupancy model implemented in the spOccupancy package in R (Doser et al. 2022). Our data reflects structural characteristics typically used to assess human–wildlife interactions, such as citizen science observations, damage reports, emergency calls, or compensation claims (Ravenelle and Nyhus 2017; Pop et al. 2023).

To reduce artificial clustering, all bear encounter records were aggregated to the 3 km $\times$ 3 km grid, and for the modeling, we retained presence-only information per grid cell and year, assuming a closed bear population between 2019 and 2024. For each year and presence cell, we summarized the median minute of the day and day of the year in the most frequent time of day and season, as well as the total number of bear-alert messages per grid cell. Multiple observations within the same grid cell and year were reduced to a single bear observation event. Reports at the same location from different years were treated as repeated samples. We compiled annual presence–absence data across 1533 grid cells with confirmed bear presence and 3467 randomly selected cells with no bear reports located within the species' known range (Chapron et al. 2014), resulting in a total sample of 5000 grid cells. To account for spatial autocorrelation between the 3×3 km grid cells, we included the x and y coordinates of each cell location in the occupancy modeling framework, which relies on a gaussian process with an exponential decay function to account for the fact that nearby grid cells are more similar and this similarity decreases with distance (Doser et al. 2022). To generate the pseudo-absence data, we first selected all grid cells for which no bear encounter was reported within the species range since 2019. We then randomly assigned time of day and day of year values to all pseudo-absence cells, and further randomly selected 3467 cells of these for the modeling exercise to avoid oversampling and speed up computing.

In a hierarchical modeling approach, observation probability was modeled as a function of time of day, day of year, human population, tourism potential, and road density (Table 1). Further, bear occurrence probability incorporated the detection processes and additionally included the percentage of wildland–urban interface (WUI), forest cover, potential food waste sources, local maximum bear density (9×9 km), and distance to historical supplemental feeding sites (Table 1). Among possible interactions, only the interaction between WUI and distance to feeding sites showed a significant effect and was retained in the final model. The final model was calibrated using five Markov Chain Monte Carlo (MCMC) chains with 2000 iterations, a burn-in of 2000, and a thinning rate of 20.

We used the Bayesian posterior distributions of the coefficient estimates to assess the effects of predictors on bear site occupancy. We considered variables to have a strong effect when the 95% credible interval (CI) of the estimate did not overlap zero, and a weak effect when the 50% credible interval (CI) did not overlap zero. To evaluate model convergence, we calculated Gelman–Rubin diagnostic statistics (Rhat <1.1) and effective sample sizes (ESS >100) for all variables (Doser et al. 2022). We obtained $\hat{R}$ values below 1.1 and ESS values above 300 for all parameters, and visually inspected trace-plots, all indicating good model convergence and mixing. To assess model fit, we conducted posterior predictive checks using the Freeman–Tukey statistic and calculated the Bayesian p-value (Doser et al. 2022), which was 0.65, suggesting very good model fit. To further explore legacy effects of historical supplemental feeding sites, we analyzed the relationship between the number of bear-alert messages per grid cell and the distance to historical elite hunting districts, transforming both variables using a Yeo-Johnson transformation and applying a simple linear model applied only to cells with reported bear presence. We conducted all data analyses in R (R Core Team, 2020) using the packages tidyr, dplyr, sf, suncalc, terra, bestNormalize, and MuMIn for data preparation, spOccupancy for modeling and diagnostics, and ggplot2 and cowplot for visualization. Grid data with explanatory variables and model outputs are available at https://doi.org/10.5281/zenodo.18244411.

RESULTS

Where and when bear encounters are most likely

We analyzed N=10 472 bear-alert messages (1–443 calls per 3×3 km grid cell). Bears were most often observed during crepuscular hours, which coincides with feeding times (Fig. 3) but among crepuscular time encounters were more common in evening and afternoon hours when both bears and humans are active (Fig. 3). Reports peaked in late summer-early fall, aligning with hyperphagia when bears accumulate resources prior to hibernation. We identified 1533 grid cells where bears were reported at least once and treated these as positive observationss:the detection model showed a positive effect of time of day and day of year on the probability of observing a bear (M: 0.33, 95% CI 0.28–0.38, respectively M: 0.28, 95% CI 0.23–0.34). Road density (M: 0.16, 95% CI 0.07–0.24), the density of tourist attractions (restaurants, hotels, M: 0.15, 95% CI 0.02–0.19), and population density (M: 0.13, 95% CI 0.04–0.21) significantly increase detectability. In short, bears are most often observed on summer evenings, along roads and in the proximity of tourist attractions (Fig. 4).

Ecological mechanisms driving the use of urban and peri-urban habitats

We found that the percentage of wildland-urban interface (WUI) was the strongest predictor of bear occurrence in urban and peri-urban areas (M: 2.87 95% CI 2.32–3.72) (Fig. 5). Bears were more likely to occur in WUI cells closer to historically elite hunting grounds, indicating that the proximity to these areas modulates contemporary space-use-patterns of bears (interaction term M: −0.58, 95% CI −0.98 to −0.24) (Fig. 5). Bear occurrence also increased with the number of anthropogenic food-waste sites per cell (M: 0.61, 95% CI 0.35–0.91) (Fig. 5), supporting the food-conditioning hypothesis. In contrast, bear density within a 9×9 km area had no significant effect (M =0.06, 95% CI −0.28 to 0.43) (Fig. 5), providing no evidence for the despotic distribution hypothesis. Occurrence probability was higher when forest cover was low or intermediate (M: −0.57, 95% CI −0.91 to −0.27). The distance to historical elite-hunting districts had no significant effect on occurrence alone (M: 0.07, 95% CI −0.50 to −0.66), but only in an interactive effect with WUI (Fig. 5). Overall, bears preferentially used human-dominated areas with mixed habitat and abundant food waste, especially near historical hunting and feeding sites.

Contemporary space use is modulated by historical management legacies

Our hierarchical occupancy models suggest that, after accounting for observation probability, bears are more likely to use human-dominated areas where housing is interspersed with wildland habitat. This relationship is further modulated by proximity to historical elite-hunting districts where supplemental feeding was common: bear occupancy is higher in WUI areas nearer to these sites (interaction term M:−0.58, 95% CI −0.98 to −0.24), suggesting a long-term food conditioning effect. Supporting this, the number of bear-alerts per grid cell was significantly higher near former feeding grounds (R=−0.16 $p<$ 0.001, Fig. 6). Together, these results point towards a persistent legacy of historical bear management, observed in contemporary bear space use (Fig. 6).

DISCUSSION

Our study shows that both contemporary habitat conditions (high WUI) and historical management legacies (hunting and supplemental feeding regulations) continue to shape human-bear encounters in Romania. Yet, these long-term socio-ecological dynamics remain largely overlooked in recent bear conservation and management debates (Can et al. 2014; Stăncioiu et al. 2019a; Braczkowski et al. 2023). A key sustainability challenge is balancing human wellbeing with biodiversity protection and ecosystem service provision to sustain coexistence (Braczkowski et al. 2023). The Romanian case provides valuable insights into how politically driven decisions, if disregarded, may have long-term impacts on species and their interaction with humans. Decisions made over 50 years ago still influence present human–bear interactions, especially in high WUI areas near former elite-hunting sites. Furthermore, our results provide compelling evidence for the food conditioning and the habituation hypothesis, showing that anthropogenic food sources (proxied by waste locations and habitat intermix) drive bear use of urban and peri-urban areas. These results hold after accounting for detection biases: encounters were most frequent in summer evenings, near roads, and tourist sites. Taken together, our results stress the need to make far-sighted conservation and management decisions today, as today's actions may shape wildlife behavior for decades.

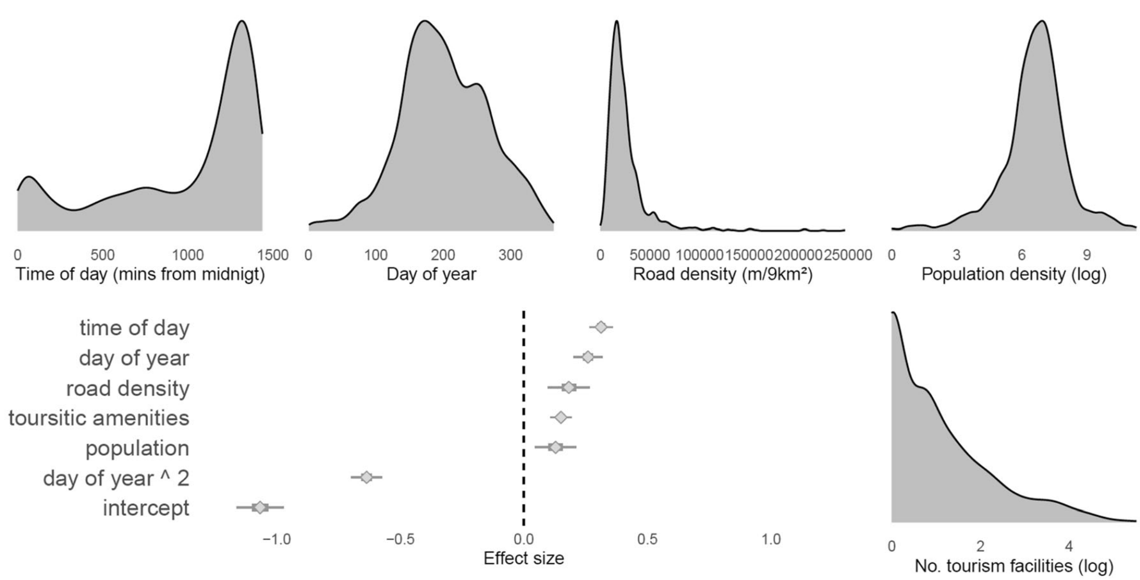


Fig. 4 Effect size (posterior mean, 50 and 95 CI) of 5 potential proxies for bear observation by humans. Observation probability can be affected by bear activity patterns (tod:time of day, doy:day of year) as well as by human activity and presence (population, number of tourist attractions, density of roads). All variables have a large effect on encounters, which are more likely later in the day, later in the year in areas with higher road density and more touristic attractions. The doy has a humped-shaped effect with encounters more likely to occur in late summer. Grey histograms represent the distributions of all (N=10472) bear calls in Romania recorded between 2019-2024.

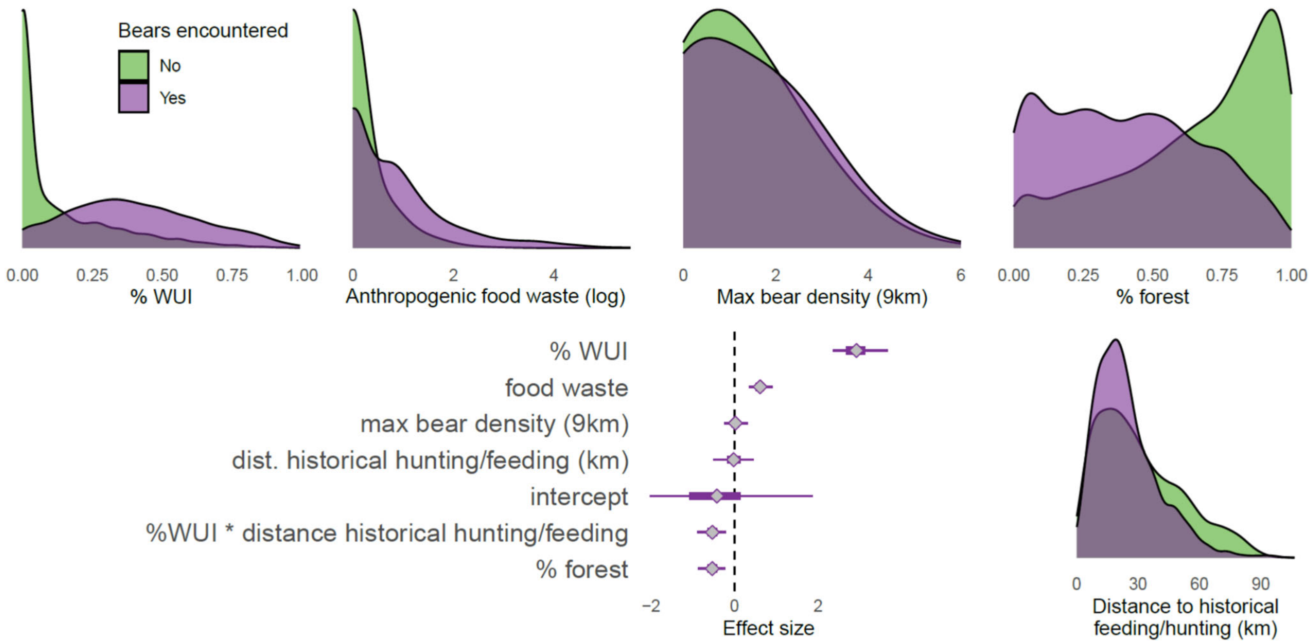


Fig. 5 Density distribution of variables included in the occupancy model for the grid cells where bears were reported (N=1548) in purple, and for areas without bear reports in green (N=25 649). Bear encounters are more frequent in areas with higher percentage of Wildland-urban-interface, intermediate forest cover, higher number of amenities, in areas with higher bear densities in the surrounding region and closer to the historical bear breeding spots. The last panel shows the relationship between the frequency of reported bears per grid cell in relation to the distance from the historical feeding grounds. Central figure: Effect size (posterior mean, 50 and 95 CI) of 4 potential direct (percent WUI, percent forest cover, no. of amenities and bear density in surrounding area) and one legacy driver (distance to historical elite hunting districts) for bear occurrence in human-dominated areas. The percentage of WUI and number of sources of anthropogenic food waste indicate a strong positive relationship with bear occurrence. No effect is observed for the density of bears in the surrounding landscape or for the distance to historical hunting/feeding grounds. The percent forest cover has a negative effect on bear encounters, while the distance to the historical elite-hunting and feeding grounds has a modulating effect on the WUI

Fig. 6 **A** The number of bear-alert calls per 3 × 3 km grid cell is decreasing with increasing distance from historical supplemental feeding locations (Spearman's Rho −0.16, p<0.001, variables are transformed using a Yeo-Johnson normalization). **B** Interaction plot highlighting that a higher number of bear-alerts are recorded in areas with high WUI that are close to historical feeding stations. % WUI is depicted on the y-axis and distance to historical elite hunting districts on the x-axis.) Darker colors indicate a higher average number of bear-alerts per grid cell. **C** Female and 3 cubs feeding on supplemental corn feed at a location is situated within < 3 km of historical supplemental feeding locations (Photo C.Munteanu 2024)

Ecological mechanisms and legacy effects

Our results confirm that bears in Romania effectively exploit human-dominated landscapes for food, supporting the habituation and food-conditioning hypotheses. Globally, food-related habituation is a key driver of human-bear interactions (Smith et al. 2005; Elfström et al. 2014; Carter and Linnell 2016; Powell et al. 2022). In Romania, food conditioning appears to be linked to two potential food sources: orchards, agricultural fields (esp. corn) and small farms for fruit and honey (proxied by WUI) and importantly, anthropogenic food waste (proxied by garbage dumps, restaurants and hotels). Similar to findings in Poland, bears frequent WUI areas to find fruit, honey and occasionally livestock (Kaim et al. 2025). Indeed, WUI is also used by other large carnivores globally (Odden et al. 2014; Blecha et al. 2018). Over time, anthropogenic food sources lead to food conditioning and habituation behaviors (Kaim et al. 2025; Neagu and Rozylowicz 2025). Besides WUI, food waste abundance was a major predictor of bear occurrence. Although waste-management policies have existed since 2003, poor infrastructure, coordination, and awareness limit implementation (Nastase et al. 2019). Consequently, bears and related conflicts are most frequent near restaurants, hotels and other food-waste sites (Figs. 1, 4). Overall, the most important drivers of bear occurrence in human-dominated landscapes are related to food availability—and the long-term persistence of food sources in the wildland-urban interface (Kaim et al. 2025). In Romania, bears have long been exposed to human-related food since targeted supplemental feeding began in 1974, driven partly by the authoritarian regime's management practices. Indeed, many authoritarian regimes display political supremacy through control of nature (Brain and Pál 2018). To display political supremacy through international trophy hunting, Nicolae Ceauşescu implemented a program combining elite hunting, large-scale supplemental feeding (carcasses, pellets, fruit, sweets), and bear breeding and translocation (Mooney 1991; Quammen 2003). These measures rapidly boosted populations—from about 1000 bears in the 1950s to 8000 by 1989—despite 450 individuals hunted by elites (Fig. 2) (Georgescu 2003).

Our analyses indicate greater bear use of WUI areas near historical hunting districts, suggesting decades-long food conditioning and habituation, but we note estimates of feeding locations are both approximate and likely conservative. Here, we use the centroids of historically hunting districts as proxies for historical hunting and feeding locations, acknowledging uncertainty since district size (100 km^2) likely obscures true feeding locations. Furthermore, supplemental feeding persisted at these locations and even extended beyond them (but no accurate data on more recent feeding locations was available to us). The observed effects may also be partially confounded by the fact that historical elite-hunting grounds were typically established in areas with already high baseline bear populations. Due to these limitations, we expect that our estimates of the effect of the supplemental feeding sites is rather conservative. Incorporating historical population data, historical bear density estimates and updated feeding-site locations (which anecdotally increased threefold between 1990 and 2016) would likely strengthen model explanatory power and increase estimated effect sizes.

Legacy effects for human–wildlife interactions

Curbing supplemental feeding is one of several evidence-based conservation practices that have contributed to reducing human–widlife conflicts worldwide, but it has been adopted thus far in only 13% of the protected area management plans in Romania (Neagu and Rozylowicz 2025). In Romania, supplemental feeding was historically tied to bait hunting and elite hunting drives (Mooney 1991; Georgescu 2003). After the fall of communism, hunting became more broadly accessible (Salvatori et al. 2002), which slowed population growth (Fig. 2) and likely maintained a landscape of fear (Gaynor et al. 2019; Lodberg-Holm et al. 2019). While legally approved and practiced in some parts of the world (Bischof et al. 2008; Candler et al. 2019; Lafferty et al. 2024), bait hunting remains ethically controversial (Carter and Linnell 2016) and reinforces habituation in target and non-target species (Selva et al. 2017; Penteriani et al. 2018). While globally bait hunting can generate revenue for management and conservation (Salvatori et al. 2002), it also incentivizes continued feeding, which in turn can lead bears to selectively exploit locations where food is predictably provided (Kavčič et al. 2015; Powell et al. 2022), irrespective of the species targeted by feeding (Selva et al. 2017). Furthermore, supplemental feeding, whether diversionary, for bait hunting, or for wildlife watching, causes bears exposed to predictable food sources to reduce their home ranges and alter feeding habits or space use (Kavčič et al. 2015; Penteriani et al. 2021). Historically, these behavioral effects may have been offset by hunting pressure maintaining a landscape of fear (Gaynor et al. 2019; Lodberg-Holm et al. 2019). However, Romania's hunting bans in 2007 and 2016 could have reduced perceived risk from people, allowing bears to expand into anthropogenic spaces, similar to patterns observed in Alaskan brown bears (Wheat and Wilmers 2016).When the landscape of fear dissolves and the number of habituated bears increases, conflicts, damages, and economic losses increase too (Bautista et al. 2017; Pop et al. 2023), alongside public distrust in policies (Neagu et al. 2022) and negative perceptions of the species (Stăncioiu et al. 2019a). Over time, these feedback loops can reinforce conflict, increase anthropogenic resistance (Ghoddousi et al. 2021) and contribute to rising biophobia (Soga and Gaston 2016). Our results provide further evidence that historical management legacies persist long after political change, continuing to shape wildlife behavior and the prospects for coexistence (Carter and Linnell 2016).

Global studies on bear behavior suggest that increased bear densities can alter habitat use, particularly among females with cubs, making high density a potential mechanism for food conditioning (Elfström et al. 2014). Our data did not support the hypothesis that high bear density in core habitats drives bear occurrence in urban or peri-urban areas, even though conspecific pressure is often cited as a factor in bears exploiting human food sources (Gunther and Wymann 2008; Powell et al. 2022). Romania has one of the highest bear densities globally, and this may mask effect sizes overall. Furthermore, to best assess this effect, we would need to include both information on change in density over time, as well as sex-ratios, both of which were not available to us. We examined the proportion of RO-ALERT messages reporting females with cubs, cubs alone, or young bears and found that less than 10% of 10 672 records mentioned cubs (5.7%) and or females (3.6%), but we caution these values are unlikely to indicate true demographics, because reports heavily depend on observer species knowledge and local conditions, introducing large reporting biases.

CONSERVATION AND MANAGEMENT IMPLICATIONS

With the largest brown bear population in Europe west of Russia (Neagu and Rozylowicz 2025), Romania holds the potential to become a poster child for ecologically and socially sustainable bear conservation, but this requires confronting historical management legacies. Ongoing debates about conservation and population management (Kutal et al 2025) could provide opportunities to break reinforcing cycles of food conditioning and habituation induced by supplemental feeding and waste management, and focus on emphasizing behavioral adaptation in both bears and humans to foster coexistence (Carter and Linnell 2016; Fletcher and Toncheva 2021; Mayer et al 2023). In 2016, targeted feeding for hunting was banned in Romania, but it is still sparsely implemented in management plans (Neagu and Rozylowicz 2025), and since November 2025 feeding bears in human-dominated spaces for tourism is fined, but supplemental feeding for wildlife watching continues. However, we suggest that further management actions could include phasing out non-target supplemental feeding (esp corn) and securing food-waste sources to reduce bears' attraction to people. Lowering encounter rates also depends on re-establishing a landscape of fear. Equally, addressing human habituation to bears, such as feeding or close approaches, requires targeted education in schools and popular media.

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Author contributions CM conceptualized the study analyzed and interpreted the data and wrote the manuscript, NMD and SR compiled and analyzed data, all authors interpreted the results, IS and CM acquired funding, and all authors revised and agreed with the manuscript.

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Data availability All data created and used in the analyses as well as the model outputs are available via the following link: https://doi.org/10.5281/zenodo.18244411.

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