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The human propensity to kill carnivores is associated with the distribution of spotted hyaenas

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ABSTRACT

Large carnivores are declining globally, making it crucial to understand the factors associated with their distribution for effective conservation. Much conservation research considers resource availability and human presence as key influences on carnivore distribution. However, the human propensity to kill carnivores, rather than mere human presence, may be associated with carnivore distribution. Here, we use the spotted hyaena (*Crocuta crocuta)* as a model species because it occurs in areas with varying levels of human persecution. We evaluate how resource availability (i.e., wild ungulate prey) and livestock herding are associated with spotted hyaena distribution in two Kenyan sites with different propensities to kill carnivores. We conducted 59 calling stations to estimate spotted hyaena density and distribution, and surveyed 396 km of transects to assess the abundance of wild ungulate prey and livestock. We found that in an area with high propensity to kill carnivores, distribution was restricted and associated with wild prey and livestock herding patterns, whereas in an area with low propensity to kill carnivores, spotted hyaenas were widely distributed despite extensive wild prey and livestock herding. This study highlights the importance of considering the human propensity to kill carnivores when examining the impact of wild prey and livestock herding on carnivore distribution. Such understanding is critical to evidence-based wildlife management and to advancing coexistence across diverse social and ecological contexts.

1. Introduction

Large carnivores play a key role in regulating ecosystem structure and functioning through density- and behaviorally-mediated trophic cascades (Ford et al., 2014; Ripple et al., 2014), but their populations and geographic ranges have declined worldwide (Ripple et al., 2014). Persecution by humans has been a major factor contributing to the decline and local extinction of large carnivores from many ecosystems (Ripple et al., 2014). However, humans can also have several non-lethal effects on large carnivore populations (e.g., Bell and Raycraft, 2025). For example, fear (i.e., an emotion triggered in response to a perceived threat to life or risk) can modify carnivore behavior and physiology (Creel and Creel, 2002), and consequently shape their spatial and temporal distribution (e.g., Boydston et al., 2003; Mills et al., 2023;

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Wilkinson, Xu, et al., 2024) at multiple scales (Ripari et al., 2022).

The ecology of fear (Brown et al., 1999), with the derived concept of landscape of fear (Laundré et al., 2010), was initially used to explain spatiotemporal variation in the distribution of prey in response to predators. In the last decade, it has gained scholarly traction in explaining the distribution of carnivores in response to the fear of humans (e.g., Clinchy et al., 2016; Miller and Schmitz, 2019; Suraci et al., 2019; Parsons et al., 2022). Oriol-Cotterill et al. (2015) defined the 'landscape of coexistence' as a subset along the gradient in the landscape of fear where the coexistence of carnivores and prey, or in this case, carnivores and humans, is possible. Importantly, coexistence refers to the persistence of both humans and carnivores within the same landscape despite ongoing conflict and the costs incurred by both, rather than the absence of negative impacts (Oriol-Cotterill et al., 2015). The thresholds that determine human-carnivore coexistence in such landscapes are expected to vary with the species of carnivore, availability of wild prey, environmental conditions (including habitat structure and productivity) and the social characteristics of the landscape, especially with the determinants of human-caused mortality risk, including the human propensity to kill carnivores (Oriol-Cotterill et al., 2015). Since its conceptualization, the landscape of coexistence framework (Oriol-Cotterill et al., 2015) has been influential in illustrating how carnivores respond to multiple human-caused risks across both spatial and temporal scale, mainly in the Global North (e.g., Eurasian lynx *Lynx lynx*; Gehr et al., 2017; Iberian wolf *Canis lupus*; Rio-Maior et al., 2019). Few African studies, particularly on lions (*Panthera leo*), have explicitly operationalized this framework (e.g., Frank, 2023). Nevertheless, many studies engage with similar processes, examining how humans and livestock influence the spatial and temporal behavior of large carnivores (e.g., Dröge et al., 2017; Loveridge et al., 2017; Mills et al., 2023). Most of these studies rely on spatial proxies of human disturbance, such as infrastructures (e.g., villages) or human presence captured on camera traps, without accounting for local variation in human attitudes or tolerance towards carnivores, which may reflect unmeasured differences in local human–carnivore interactions. To the best of our knowledge, no studies have explicitly applied the landscape of coexistence framework to examine how the distribution of large carnivores varies in relation to local variation in the human propensity to kill carnivores, a critical yet often overlooked component of human–carnivore interactions.

Most populations of African large carnivores currently reside within or adjacent to protected areas, wildlife conservancies, and other lands set aside for wildlife (Green and Holekamp, 2019). However, human presence inside wildlife conservation areas has cast doubt on the efficacy of wildlife conservation areas for carnivores' survival and long-term persistence (Lindsey et al., 2017; Loveridge et al., 2017; Kiffner et al., 2022; Wilkinson, Dheer, et al., 2024). For instance, livestock herding can take place legally or illegally in wildlife conservation areas, especially during dry periods when resources are scarce (Butt, 2014; Bedelian and Ogutu, 2017). As a result, several studies have looked at the effects of livestock herding on carnivore ecology and behavior within or nearby wildlife conservation areas (e.g., Ogutu et al., 2005; Broekhuis et al., 2019; Green et al., 2018; Mkonyi et al., 2018; Soofi et al., 2018). On one hand, carnivores could be attracted to livestock as an abundant, higher-quality, easier-to-hunt alternative prey (Sundararaj et al., 2012). On the other hand, carnivores could avoid livestock and change their behavior as a response to behavior by herders, including retaliatory killing (Kolowski et al., 2007; Kissui, 2008). Therefore, the effects of the human propensity to kill carnivores need to be considered when trying to understand anthropogenic influences on carnivore distribution.

To better understand the effects of the human propensity to kill on carnivores, we use the spotted hyaena *Crocuta crocuta* as a model species. Spotted hyaena adaptations can include shifting their activity patterns to become more nocturnal (Kolowski et al., 2007), increasing their vigilance behavior (Pangle and Holekamp 2010), using dense vegetation to provide cover from people (Kolowski & Holekamp, 2009) and avoiding areas of heavy human use (Boydston et al., 2003; Mbise 2024; Wilkinson, Xu, et al., 2024). The main ecological predictor for spotted hyaena distribution is resource availability (i.e., wild prey: Kruuk 1972; Höner et al., 2005; Watts and Holekamp, 2008, 2009). Human presence, such as livestock herding, might also affect spotted hyaena distribution (Boydston et al., 2003; Kolowski et al., 2007; Holekamp and Dloniak, 2010; Bell and Raycraft, 2025). However, the extent to which livestock herding contributes to spotted hyaena distribution is not clear and may vary not only with their relative densities but also in response to livestock herders' propensity to kill carnivores. While livestock herders carry out little active persecution of spotted hyaenas in some areas, in others, livestock herders pose a direct threat to carnivores both in retaliation for depredation events and in attempts to prevent them in the first place (Mbise, 2024; Hello et al., 2024; Raycraft, 2024; Mramba et al., 2025; Bell and Raycraft, 2025; Raycraft and Bell, 2025). Evidence from human-dominated landscapes, such as the Tarangire ecosystem, suggests that spotted hyaenas can not only survive but may actually thrive under such conditions, with spotted hyaena populations potentially increasing alongside higher human densities (Kiffner et al., 2022; Raycraft, 2024; Raycraft and Bell, 2025). Additionally, it has been suggested that more severe and frequent droughts due to climate change will likely alter distributions of wild prey and increase livestock herding inside wildlife conservation areas, thereby increasing herder-spotted hyaenas interactions (Holekamp and Dloniak, 2010). Therefore, to preserve spotted hyaena populations, it is paramount to understand the variables influencing spotted hyaena distribution, in particular the human propensity to kill them.

To investigate how variation in human propensity to kill carnivores is associated with large carnivores distribution, we document the abundance of resource availability (i.e., wild ungulate prey) and livestock abundance, and the density and distribution of spotted hyaenas across two sites in Kenya where livestock herders have markedly different propensities to kill carnivores (Torrents-Ticó et al., 2023). Overall, we predict that spotted hyaenas will be widely distributed throughout the entire wildlife conservation area where livestock herders have a low propensity to kill carnivores. In contrast, in areas where livestock herders have a high propensity to kill carnivores, we expect spotted hyaenas to be restricted to specific locations far away from livestock herders (i.e., as a spatial avoidance response to a perceived threat). Furthermore, we hypothesize that spotted hyaena distribution responds differently to wild prey and livestock herding in the two sites due to the different human propensity to kill carnivores. We predict that in the site where livestock herders have a high propensity to kill carnivores, the distribution of spotted hyaenas will be better associated with livestock herding rather than wild prey.

2. Methods

2.1. Study sites

We conducted the study in Laikipia conservancies and Sibiloi National Park (hereafter, Sibiloi), Kenya. These two study sites were selected for three main reasons: (1) spotted hyaenas are present in both sites (Frank et al., 2005; Torrents-Ticó et al., 2021); (2) livestock herding occurs on foot in both sites (Mwamidi et al., 2018; Unks et al., 2019; Torrents-Ticó et al., 2023); and (3) the self-reported propensity to kill carnivores by livestock herders differ substantially between the two sites (Torrents-Ticó, 2023; Torrents-Ticó et al., 2023).

Following Torrents-Ticó et al. (2023), we define self-reported human propensity to kill carnivores as a herder's likelihood of engaging in carnivore killing, based on survey responses. This represents one dimension of a complex social-cultural context and reflects an attitudinal component of the local risk landscape that carnivores encounter, which may consequently influence their spatial distribution. Torrents-Ticó et al. (2023) assessed herders' self-reported propensity to kill carnivores using carefully designed questions intended to avoid bias (Nuno and John, 2015), asking about strategies to protect livestock from carnivores and how herders would react to livestock losses caused by carnivores. Responses were categorized as lethal or non-lethal, allowing quantification of the self-reported propensity to kill carnivores at each site (see Torrents-Ticó et al., 2023 for methodological details). The results showed cleared differences between the two sites: in Laikipia, only a small proportion of herders self-reported killing carnivores, reflecting the widespread use of non-lethal strategies. In contrast, in Sibiloi, herders openly reported a high propensity to kill carnivores (see Torrents-Ticó et al., 2023 for more details). Consistent with these findings, Laikipia conservancies were classified as a landscape with a low human propensity to kill carnivores (Frank et al., 2005; Torrents-Ticó et al., 2023), and Sibiloi as a landscape with documented evidence of a high human propensity to kill carnivores (Torrents-Ticó et al., 2022; UNESCO, 2020; Torrents-Ticó et al., 2023). However, we do acknowledge that self-reported propensity to kill carnivores is only a proxy measure and may not accurately reflect actual killing behaviors. Yet, we still believe this proxy offers relevant information about the frequency of killing carnivores on both sites, especially given the absence of direct data on the actual number of animals killed by people (Dickman et al., 2013). Below, we describe the social-ecological characteristics of both study sites, specifically explaining the different factors that may shape human propensity to kill carnivores in each site.

2.1.1. *Laikipia conservancies*

In Laikipia County in central Kenya, we collected data from eleven Laikipia conservancies with a total area of 1603 km^2 (Laikipia North: Loisaba Conservancy, Mpala Ranch, Ol Jogi Wildlife Conservancy, El Karama Wildlife Conservancy, Segera Conservancy, Ol Doingo Lemboro, Mugie Conservancy, Sosian Conservancy, Suyian Conservancy, Ol Maisor Ranch, Jessel Ranch, Fig. 1A). These conservancies are private wildlife conservation areas (also known as private ranches) set up on private land by a private individual or institution for the purpose of wildlife conservation and livestock management (King et al., 2018).

The Laikipia plateau is a semiarid region comprised of Acacia savannah with occasional open grasslands. Annual rainfall is highly variable, averaging 300 mm per year in the more arid northern sections of the county (Heath, 2000). The area experiences a bimodal rainfall distribution, with two rainy seasons occurring between April and June, and October and December, respectively.

Laikipia is referred to as one of Kenya's most important areas for biodiversity conservation (Sundaresan and Riginos, 2010; Yurco, 2017). Laikipia has an outstanding international conservation reputation as a result of several decades of conservation efforts especially focusing on carnivores (e.g., conservation projects on endangered species such as African wild dogs and lions, Samburu-Laikipia Wild Dog Project, Lion Landscapes: Woodroffe, 2009; Frank, 2011; Ferguson et al., 2020). It is important to note that there are numerous public and private conservation organizations operating in the area providing appreciable benefits to local communities (e.g., Laikipia Wildlife Forum, Mpala Research Centre, Loisaba Conservancy) (DePuy, 2011; Lamers et al., 2014; Loisaba Conservancy, 2021; Mpala Research Centre, 2021). Most conservation efforts focus on promoting positive human-carnivore relations by helping local communities from adjacent wildlife conservation areas to improve livestock protection and assist when livestock depredation occurs (Gadd, 2005; Sundaresan and Riginos, 2010; Bond, 2014). Maasai pastoralists mostly inhabit Laikipia alongside other ethnic groups (e.g., Samburu). Historically, the Maasai were a semi-nomadic pastoralist community but are now largely sedentary (Seno and Shaw, 2002). Local people in Laikipia tolerate livestock loss, and retributive killing is remarkably uncommon, given predators' impacts (Frank et al., 2005). Additionally, Torrents-Ticó et al. (2023) show low self-reporting of killing carnivores by Maasai in this region.

In Laikipia, herders employ traditional livestock husbandry practices, in which animals are closely herded during the day and confined at night in thornbush enclosures, or *bomas* (Ogada et al., 2003). These herding and *boma* management practices have been maintained over decades, with detailed longitudinal observations spanning 20 years documenting their persistence and evolution (see Frank, 2023). Herders typically sleep in huts adjacent to *bomas*, and many conservancies employ night guards to monitor livestock. When carnivores approach, herders deter them using bright lights, noise, or other deterrents, and some households use guardian dogs to further reduce predation risk. Each conservancy maintains multiple permanent *bomas*, with livestock moved between them every few months to follow seasonal grazing and water availability (Frank, 2023). A technological advance in cattle husbandry occurred around 2004 with the introduction of mobile *bomas*, constructed from interlocking panels of chain-link fencing supported by welded water-pipe frames, which can be relocated as needed. However,

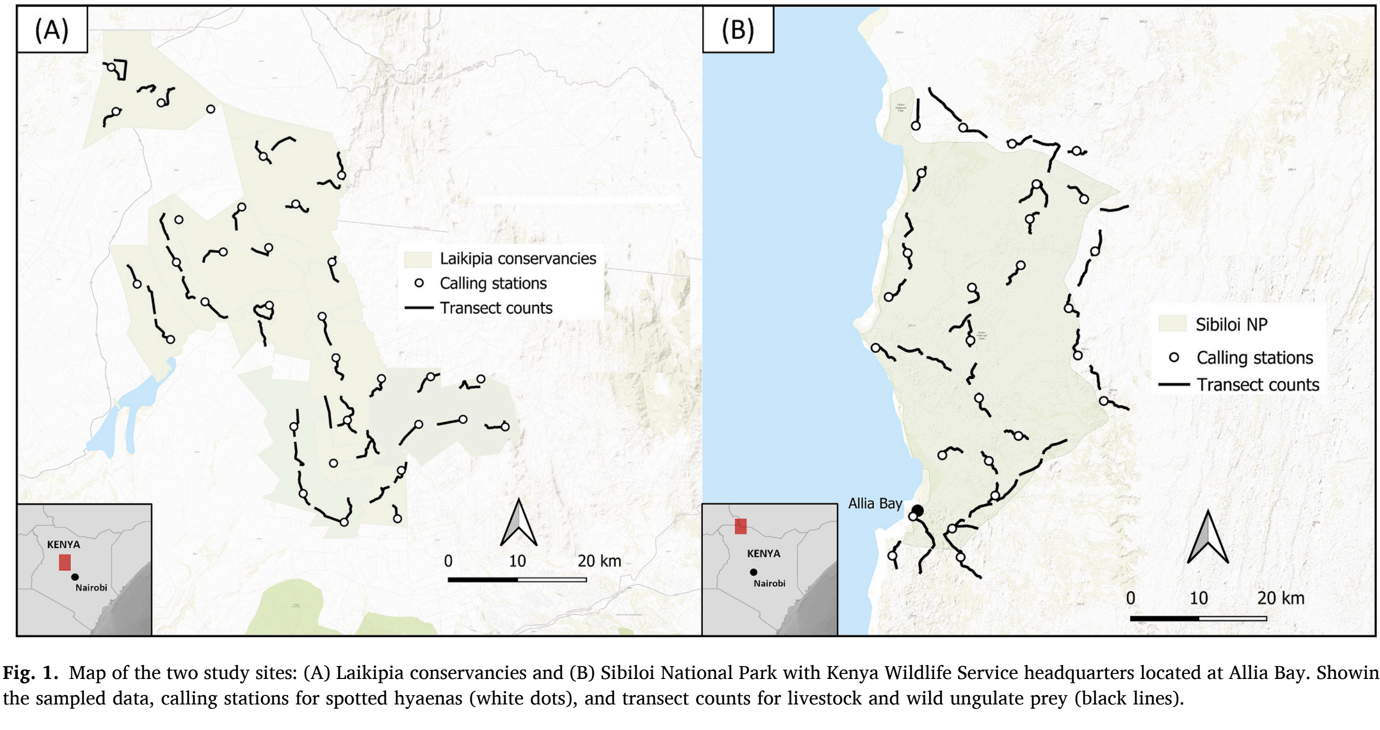

Fig. 1. Map of the two study sites: (A) Laikipia conservancies and (B) Sibiloi National Park with Kenya Wildlife Service headquarters located at Allia Bay. Showing the sampled data, calling stations for spotted hyaenas (white dots), and transect counts for livestock and wild ungulate prey (black lines).

the high cost of these mobile *bomas* substantially limits their adoption. Livestock holdings are typically mixed, keeping cattle alongside goats and sheep ("shoats") (Unks et al., 2019; Hoffmann et al., 2022). However, Laikipia conservancies are primarily cattle-focused, with smaller numbers of shoats (Frank, 2023). Historical records and surveys indicate that livestock depredation in Laikipia has primarily targeted cattle but also occasionally shoats (Frank, 2023). Depredation occurs both during grazing and near *bomas*, with attacks historically increasing when livestock are dispersed during dry seasons (Ogada et al., 2003; Frank, 2023). Human population densities within Laikipia conservancies are generally low, and within nearby Maasai communities, they vary across locations: in 2009, Koija (7,605 ha) had 2,267 residents, while Il Motiok (3,651 ha) had 999 residents (Kaye-Zwiebel and King, 2014).

2.1.2. *Sibiloi national park*

Sibiloi has an area of 1570 km^2 and is located on the remote north-eastern shore of Lake Turkana, North Kenya (Fig. 1B). Sibiloi National Park was established in 1973 and was declared a UNESCO World Heritage site in 1993 (IUCN, 2020; Mbaluka and Brown, 2016; NMK and KWS, 2019). Sibiloi was inscribed in 2018 on the UNESCO List of World Heritage in Danger (UNESCO, 2018). Kenya Wildlife Service is an extension of the national government that co-manages Sibiloi and provides security to wildlife with permanent headquarters at Allia Bay, in the southern section of Sibiloi (Fig. 1B).

The region's environment is characterized by a semi-desert with an arid climate, with mean annual temperatures around 32 °C (Mbaluka and Brown, 2016). Mean annual rainfall is around 150 mm distributed along two rainy seasons: from March to May and October to December (Mbaluka and Brown, 2016). The landscape is dominated by dwarf shrubland and grassland vegetation, with some riparian forests along ephemeral streams that carry underground water (Mbaluka and Brown, 2016).

Sibiloi has a lack of public infrastructure, low literacy levels, and limited telecommunication networks (IUCN, 2020). Conservation initiatives (e.g., Sibiloi Management Plan 2018–2028) are meagre at best (UNESCO World Heritage Centre, 2020). In 2019, it was reported that the park was significantly under-resourced and understaffed, with the limited funding available for management being obtained from tourism revenues from other sites in Kenya (IUCN, 2020). The Daasanach community, a subsistence-based group (Junqueira et al., 2021), extends between the northern shores of Lake Turkana (Kenya), and the lower stretch of the Omo River valley and its delta (Ethiopia). Although the Daasanach are considered a semi-nomadic agro-pastoralist group, agriculture is practiced sporadically among Kenyan Daasanach (Bethancourt et al., 2021).

Daasanach pastoralists maintain traditional livestock husbandry systems that are closely tied to seasonal resource availability and customary territorial management. In this semi-arid landscape, livestock herding depends strongly on the distribution of pastures sustained by seasonal rainfall, with herders accompanying animals throughout grazing and moving between communal grazing areas according to wet and dry season cycles (Mwamidi et al., 2018; Junqueira et al., 2021). Livestock are kept in *bomas* at night, which generally consist of thorn-bush enclosures. Most herders do not use additional deterrents or guardian dogs, and protection relies primarily on traditional bush fencing, nighttime guarding and extensive use of firearms (Torrents-Ticó et al., 2023). Settlement patterns reflect these seasonal movements, with pastoralists practicing semi-nomadic mobility (Mwamidi et al., 2018; KNBS, 2019). According to the Ileret Ward Veterinary Officer, the Daasanach community maintains approximately 31,000 cattle, 50,000 goats and sheep (shoats), 3,000 donkeys, and 400 camels (Mwamidi and Renom, 2018). Ileret Ward, which includes Sibiloi National Park, covers 1,973 km^2 and had 18,233 residents in 2019 (KNBS, 2019). Historical patterns indicate frequent livestock depredation, and retaliatory or preemptive killings of carnivores, including spotted hyaenas, are common (IUCN, 2020; UNESCO, 2020). For example, a ranger reported that "youth kill all the wildlife they encounter when they are encroaching in Sibiloi with their herds of livestock" (UNESCO, 2020). Self-reported surveys indicate that the Daasanach openly acknowledge a high propensity to kill carnivores, particularly hyaenas (Torrents-Ticó et al., 2023). We do not believe that attitudes towards carnivores, and the propensity to kill hyaenas specifically, vary substantially within the study area and we therefore assume that the attitudes and behaviors are relatively homogeneous across each study area.

2.2. *Data collection*

We conducted fieldwork between February–March 2018. We carried out calling stations to determine the density and distribution of spotted hyaenas. We conducted transect counts to assess the abundance of livestock and wild ungulate prey.

Calling stations (also known as 'call-ins' or 'call-ups'). We carried out 32 calling stations in Laikipia conservancies (Fig. 1A) and 27 calling stations centered on Sibiloi (Fig. 1B). We took GPS coordinates of calling station locations, which were mostly located along the roads to avoid impacting the fragile equilibrium of the savannahs. We prioritized open areas with good visibility and stations were at least 6 km apart to avoid double counting of hyaenas (Yirga et al., 2014; Aebischer et al., 2020). Neighboring stations were sampled consecutively on the same night to minimize the probability of duplicate counts (Cozzi et al., 2013). The calling stations survey effort covered approximately 54% of the Laikipia conservancies and 46% of Sibioi, well above the 20% minimum area coverage recommended for estimating population densities in an area by Ogutu and Dublin (1998).

Calling stations were set up at night, starting at least half an hour after sunset, when spotted hyaenas are most active (Cozzi et al., 2013). At the beginning of each calling station, we recorded the wind with the PCE-MAM 2 Mini Anemometer and we only carried out calling stations when the wind speed was below 3.7 m/s (Mbise et al., 2020). To attract spotted hyaenas, we used playback sounds broadcast at 110 dB (measured at 1 m from the speaker with a PCE-MSL1 Sound Level Meter) through a digital audio player connected to a 12 V FS-75U amplifier connected to two PEM-81 speakers mounted onto the roof of a car (approximately at 1.5 m above ground). We used a set of 6-min calls particularly suitable for attracting spotted hyaenas and successfully used for this purpose (Mills, 1998; Mills et al., 2001; Creel and Creel, 2002; Cozzi et al., 2013). Calls consisted of several sounds representing the distress bleating of a wildebeest (*Connochaetes taurinus*) calf, spotted hyaenas competing over a kill, a fight between two neighboring spotted hyaena clans, and spotted hyaenas mobbing lions. The broadcasting time was set to 30 min. 6-minute-long spotted hyaena calls were separated by 4 min intervals of silence and repeated three times (Mills et al., 2001; Creel and Creel, 2002; Graf et al., 2009). While broadcasting the playback sounds, the speaker was rotated to ensure 360° sampling (Mills et al., 2001; Kiffner et al., 2007; Cozzi et al., 2013). Two observers (Laikipia: E.M., M.T.-T; Sibiloi: T.T.K., M.T.-T.) scanned for all large carnivores during calling stations and recorded the species and number of individuals approaching each station. However, analyses in this study focus exclusively on spotted hyaenas, as detections of other large carnivore species were too infrequent to allow meaningful statistical analysis.

Transect counts. We (Laikipia: E.M., M.T.-T.; Sibiloi: T.T.K., M.T.-T.) surveyed a total of 184 km (Fig. 1A) and 212 km (Fig. 1B) in Laikipia conservancies and Sibiloi respectively, during the evening before sunset and before carrying out the calling stations. For each transect, a driver/navigator drove the vehicle along 4 km at a maximum speed of 15 kph with one observer scanning for livestock and wild ungulate prey on each side of the transect. We recorded the species observed, the group size, and the angle and distance to the animal (Buckland et al., 1993). A GPS coordinate was taken for every sighting. We focused on wild ungulate prey (see Supplementary Material 1 for a complete list of species recorded) and livestock (large livestock: camel *Camelus bactrianus*, cattle

Bos indicus, donkey *Equus africanus;* small livestock: shoat due to the difficulty in distinguishing the two species in large mixed herds *Ovis aries, Capra hircus*). We counted livestock numbers and used the abundance of livestock as a proxy for the number of livestock herders because, in general, a higher number of livestock is associated with more herders herding livestock. Since livestock herds often included both cattle and shoats in the two study, we treated them collectively.

2.3. Data analysis

Spotted hyaena density. To calculate density estimates, we used the number of spotted hyaena individuals approaching each calling station. We could not calibrate response distance and likelihood experimentally for spotted hyaenas due to time and logistical limitations. Therefore, following Cozzi et al. (2013), that used the same playback sounds and broadcasting time, we applied a response likelihood of 0.6 and used a response distance of 2.93 km per calling station, thus, giving a sampling area of 27 km^2 per calling station.

Livestock and wild ungulate prey encounter rate and relative abundance index. In Sibiloi, our wild prey observations were below recommended minimum sample size of 20 (Isaac et al., 2011), 40 (Buckland et al., 1993), and 60 observations (Buckland et al., 2015) to assess species detectability. Therefore, we used the encounter rate (frequency of observation events of each species per unit survey effort: e.g., a herd of gazelles was counted as one event) and relative abundance index (total number of individuals sighted per unit survey effort) as proxies of the wild ungulate prey. For consistency, we applied the same approach to livestock, calculating both encounter rate and relative abundance index using identical definitions. These metrics provide a descriptive overview of the local abundance, availability and distribution of livestock and wild prey at each study site.

Predictors of spotted hyaena distribution. To model the spotted hyaena distribution as a function of livestock herding and wild prey, we estimated livestock and wild ungulate prey local abundance at calling stations using the Inverse Distance Weighting method (IDW, e.g., Björklund et al., 2016) applied to raw transect-based group-size observations of livestock and wild ungulates:

$$(x_0) = \frac{\sum_{i=1}^{n} \frac{Z_i}{D_i^2}}{\sum_{i=1}^{n} \frac{1}{D_i^2}}, \quad D_i < 24\,\text{km}$$

where $\widehat{Z}(x_0)$ corresponds to the local livestock or wild herbivore abundance estimation at each focal calling station at coordinates x_0. Z_i represents the group size of each livestock/herbivores record along transects observation *i,* and D_i is the distance between each record *i* and the calling station at x_0. Each observation was weighted by the inverse of the squared distance ($1/D_i^2$), such that observations closer to a calling station contributed more strongly than distant observations. This is a commonly used distance-decay function used in ecological applications of IDW; for example, one gazelle at one km from the calling station has the same weight as a group of 100 gazelles at 10 km from the calling station. The weighted values were summed across all *n* observations and standardized by the sum of the weights to provide the distance-weighted mean. Only observations within 24 km of the calling station were included in the calculation. The 24 km radius accounts for movement distances documented in arid, low-productivity regions where hyaenas may travel 23–27 km per day (Kruger National Park, South Africa: Henschel & Skinner 1987; southern Kalahari, South Africa: Mills 1990).

To assess the effects of livestock and ungulate abundance on spotted hyaena numbers across sites, we fit a negative binomial regression model. Specifically, we modeled spotted hyaena abundance as a function of livestock abundance, ungulate abundance, site, and the interactions between site and each predictor. The model was specified as follows:

$$Y_i \sim \mathrm{NB}(\mu_i, \theta), \quad i = 1, \cdots, n,$$

$$\begin{aligned}\log(\mu_i) = {} & \beta_0 + \beta_1\,(\text{IDW livestock}_i) + \beta_2\,(\text{IDW wild ungulates}_i) \\ & + \beta_3\,\text{Site}_i + \beta_4\,(\mathit{IDW}\text{livestock}_i \times \text{Site}_i) \\ & + \beta_5\,(\mathit{IDW}\text{wild ungulates}_i \times \text{Site}_i),\end{aligned}$$

where Y_i is the observed spotted hyaena abundance in the *i*th calling station count, μ_i is the expected spotted hyaena abundance, θ is the dispersion parameter, β_0 is the intercept, representing the site Laikipia with zero IDW of Livestock and zero IDW of wild prey, and β_1 through β_5 are the regression coefficients. In this parameterization, the main effects for Livestock and Ungulates represent their influence in the reference site Laikipia, while the interaction terms quantify how these effects differ between sites.

The model selection was guided by the Akaike Information Criterion (AIC). We compared a set of candidate models that varied in the inclusion of predictors and interaction terms. The model validation, including e.g., heteroscedasticity and outliers, was performed using visual diagnostics and formal tests with the DHARMa R package version 0.4.6 (Hartig, 2022). We used the ggpredict function in ‘ggeffects’ R package version 1.6.0 (Lüdecke et al., 2020) to plot predicted spotted hyaena counts based on the effects of predictor variables, livestock and wild ungulate prey, for each site. All statistical analyses were performed in R 4.4.2 (R Core Team, 2024).

3. Results

3.1. Spotted hyaena density

We counted 133 spotted hyaenas in the Laikipia conservancies, giving a density of 0.26 per km^2. Spotted hyaenas were observed at 84% of the calling stations across the study site (Table 1, Fig. 2A). The mean number of spotted hyaenas responding per calling station was four, ranging between 0 and 15.

In Sibiloi, we counted 22 spotted hyaenas, giving a density of 0.04 per km^2. Spotted hyaenas were observed at 26% of the calling stations, mostly in the south of the park (Table 1, Fig. 2B). The mean number of spotted hyaenas responding per calling station was one and ranged between 0 and 8.

3.2. Livestock and wild ungulate prey encounter rate and relative abundance index

While in Laikipia most of the sightings were from wild ungulate prey, in Sibiloi there were more sightings of livestock than wild ungulate prey (Table 2, Fig. 2B). In Sibiloi, small livestock (i.e., sheep and goats) and large livestock were encountered at similar rates (0.066 for both). However, shoats were relatively more abundant than large livestock, as indicated by a higher relative abundance index (3.863 vs. 1.538). In contrast, livestock observations in Laikipia were dominated by large livestock, while shoats were rare (encounter rate: 0.092 for large livestock vs. 0.005 for shoats; relative abundance index: 9.750 vs. 0.179).

3.3. Predictors of spotted hyaena distribution

In Laikipia conservancies, where there is low propensity to kill carnivores, spotted hyaena distribution was not significatively associated with either livestock abundance ($\beta = 0.003$, SE $= 0.0035$, $z = 0.905$, $p = 0.366$) or wild ungulate abundance ($\beta = -0.085$, SE $= 0.053$, $z = -1.618$, $p = 0.106$; Fig. 3). However, the significant interaction terms indicate that these relationships differ in Sibiloi. Specifically, the interaction between livestock and site Sibiloi ($\beta = -0.040$, SE $= 0.013$, $z = -3.054$, $p = 0.002$) implies that the effect of livestock abundance in Sibiloi is negative; $0.003 - 0.040 = -0.037$. That is, an increase in livestock abundance in Sibiloi is associated with a significant decline in spotted

Table 1
Response of spotted hyaenas to calling stations. Abundance refers to the total number of individuals that approached the calling stations. Presence (%) refers to the percentage of calling stations where the carnivore was observed.

	Callingstations		Abundance	Presence (%)	Density (individuals/km^2)
Laikipia conservancies	32	Spotted hyaena	133	84	0.26
Sibiloi	27	Spotted hyaena	22	26	0.04

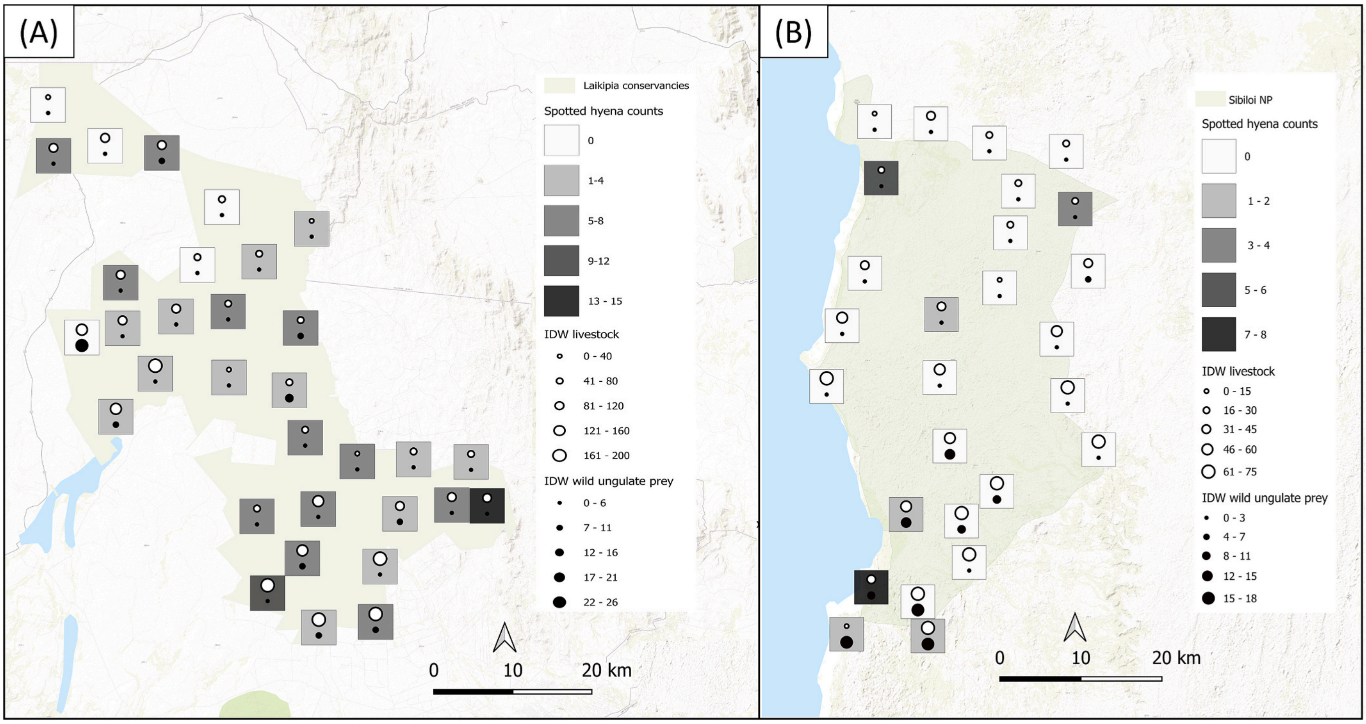

Fig. 2. Spotted hyaenas are exposed to spatial variations in livestock (IDW of livestock, white circle) and wild ungulate prey (IDW of wild ungulate prey, black circle). The squares represent the locations where we carried out calling stations. (A) Laikipia conservancies and (B) Sibiloi.

Table 2
Encounter rate and relative abundance index for livestock and wild ungulate prey from transect counts in both study sites.

	Transect counts (km)		Encounter rate	Relative abundance index
Laikipia conservancies	184			
		Livestock	0.10	9.93
		Wild ungulate prey	1.43	8.11
Sibiloi	212			
		Livestock	0.13	5.40
		Wild ungulate prey	0.10	1.09

hyaena abundance. In contrast, the interaction between wild ungulate abundance and the site Sibiloi ($\beta = 0.190$, SE = 0.07, $z = 2.697$, $p = 0.007$) suggests that the net effect of ungulates in Sibiloi is $-0.085 + 0.190 = 0.105$, meaning that hyaena abundance increases with higher wild ungulate numbers in Sibiloi (Fig. 3). Model selection based on AIC revealed that none of the reduced models were below or within two AIC units of the full model (AIC = 234.39). The intercept, representing the expected log hyaena abundance in Laikipia when both livestock and ungulate values are zero, was $\beta = 1.584$ (SE = 0.438, z = 3.615, $p < 0.001$), and the dispersal parameter was $\theta = 1.36$. Model assumptions were not violated.

4. Discussion

Our results suggest that spotted hyaena distribution across the two Kenyan landscapes reflects a complex interplay between wild prey availability, livestock herding, and variation in human propensity to kill carnivores. While wild prey and livestock herding were associated with spotted hyaena distribution in Sibiloi, these relationships differed markedly from those observed in Laikipia, where spotted hyaenas were widely distributed despite extensive wild prey and livestock herding. These contrasting patterns are consistent with the idea that local variation in human propensity to kill carnivores may be associated with how spotted hyaenas respond to livestock herding and wild prey across landscapes.

This study provides the first density estimate of spotted hyaenas in both study sites. The density found for spotted hyaenas in Laikipia conservancies overall (0.26 individuals/km^2) is comparable to the minimum density of 0.24 hyaenas/km^2 found in Lewa Wildlife Conservancy (Laikipia: Dheer, 2016), and higher than areas such as the Okavango Delta (Cozzi et al., 2013), Kruger National Park and Central Kalahari Game Reserve (Holekamp and Dloniak 2010). Given the limited information on spotted hyaenas in central Kenya, our estimate provides a valuable reference point for future monitoring. However, there are still gaps in knowledge that need to be filled relative to clan sizes, home ranges and movement patterns. In Laikipia conservancies, where herders have a low propensity to kill carnivores (Frank et al., 2005; Torrents-Ticó et al., 2023), spotted hyaenas have a wide distribution occupying the entire wildlife conservation area regardless of

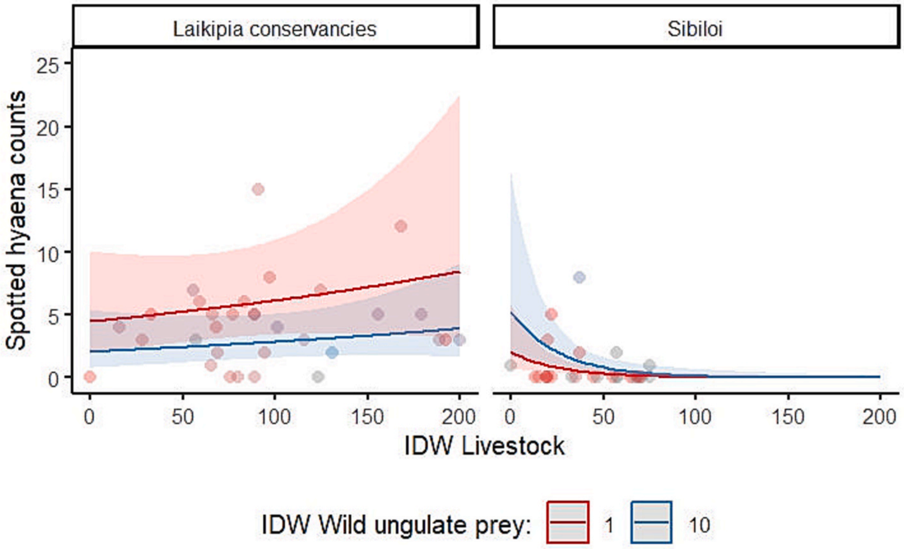

Fig. 3. Predicted counts of spotted hyaena in relation to Inverse Distance Weight (IDW) of livestock and to IDW of wild ungulate prey (Low = 1 and High = 10) in both study sites. Shaded areas represent 95% confidence intervals.

herder activity (i.e., livestock abundance) and resource availability (i.e., wild prey), likely because a low propensity to kill carnivores may reduce the importance of food availability as a limiting factor.

In Sibiloi, spotted hyaena density was estimated at 0.04 individuals/km^2, a value comparable to densities reported for other arid or semi-arid regions with clumped resource distributions, such as Majete Wildlife Reserve, Malawi (0.039 individuals/km^2; Retief, 2016) and Etosha National Park, Namibia (0.05 individuals/km^2; Trinkel, 2009). Lower spotted hyaena density estimates were only reported for the Kalahari, South Africa (0.009 individuals/km^2; Mills, 1990), the Namib desert, Namibia (0.004–0.0085 individuals/km^2; Tilson and Henschel, 1986), and the Dinder National Park, Sudan (0.018 individuals/km^2; Mohammed et al., 2019). This low density may partly reflect harsh climatic conditions and low wild prey availability. However, our analyses cannot disentangle the relative importance of prey limitation from other ecological and social factors, such as livestock herding and human propensity to kill carnivores. We therefore refrain from associating the low density of spotted hyaenas in Sibiloi to any single factor. Although spotted hyaena abundance in Sibiloi was positively associated with wild ungulate availability, this pattern was evident only in areas with lower levels of livestock herding, and thus lower propensity to kill carnivores, suggesting that access to wild prey may be spatially constrained by human-related factors rather than prey availability alone. This may help explain why spotted hyaenas are being largely constrained to the southernmost region of the park, near the Kenyan Wildlife Service headquarters (i.e., Allia Bay), where there is spatially restricted patrolling that reduces the presence of livestock herding, as well as other human activities that may affect wildlife, including poaching (UNESCO, 2020). The negative association in Sibiloi between spotted hyaenas and livestock herding indicates that the presence of herders with a high propensity to kill carnivores, many of whom possess firearms, may represent a direct threat to spotted hyaenas (IUCN, 2020; UNESCO, 2020). Consequently, the presence of herders with a high propensity to kill carnivores may have serious fitness implications for spotted hyaenas in that effective habitat loss might be associated with loss of access to also limited but more widely spread wild prey resources. Overall, our results suggest that in Sibiloi, spotted hyaena distribution may be associated with the interaction of wild prey availability and high levels of human propensity to kill carnivores, which could have implications for their local persistence. This may have broader ecological consequences for the whole ecosystem, particularly since other large carnivore species, including lions and leopards (*Panther pardus*), are absent or present only at very low abundances (Torrents-Ticó et al., 2021).

We acknowledge some potential limitations in our study, which also highlight opportunities for future research. Our analyses cannot disentangle ‘push’ effects (avoidance of areas with high livestock or human activity) from ‘pull’ effects (attraction to remaining wild prey), nor can they isolate these interactions from broader landscape-level factors. Nonetheless, these proximal mechanisms likely operate simultaneously and may be associated with spotted hyaena distribution. Consequently, carnivore distribution still serves as a valuable indicator of human propensity to kill carnivores. Furthermore, while our study offers only a single snapshot in time, it highlights patterns suggesting how the continuous and ongoing presence of livestock herding, and the associated human propensity to kill carnivores, in the landscape is consistent with where spotted hyaenas occur. Future research could evaluate spotted hyaena movement patterns at finer spatial and temporal resolution in relation to wild ungulate prey and livestock herding.

Additional ecological and environmental factors, such as vegetation (Boydston et al., 2003) and distance to water sources (Kolowski & Holekamp, 2009) may influence spotted hyaena distribution. Interspecific interactions with other large carnivores, particularly lions, can also affect spotted hyaena behavior through kleptoparasitism, direct competition, and territorial dynamics (Périquet et al., 2015, 2016; Kiffner et al., 2022). Lions were absent in Sibiloi (Torrents-Ticó et al., 2021), and recorded at low numbers in Laikipia, and were therefore not included in our models. Nevertheless, both the absence of lions in Sibiloi and their presence in Laikipia may further shape spotted hyaena spatial patterns. Consequently, while livestock herding seems to be associated with spotted hyaena distribution in areas with high propensity to kill carnivores, it likely interacts with other ecological variables (e.g., water sources, habitat structure, and interspecific interactions) to shape overall habitat use (Wilkinson, Xu, et al., 2024). For instance, recent work on lions shows that their avoidance of human disturbance varies with site-level environmental characteristics, including vegetation productivity (e.g., Normalized Difference Vegetation Index, NDVI), highlighting how the combined effects of human activities and environmental change can simultaneously compromise the ecological function of large carnivores (Mills et al., 2023). Therefore, future studies that integrate both anthropogenic and ecological factors (see Mills et al., 2023; Wilkinson et al., 2024; Bell and Raycraft, 2025) will provide a more comprehensive understanding of the factors associated with large carnivores distribution across these landscapes.

The human dimensions of our study are inherently complex and multi-faceted. Self-reported measures of human propensity to kill carnivores may be biased and serve only as proxy indicators, which may not fully reflect actual killing behaviors. This discrepancy can arise because livestock herders may not openly report retaliatory killings, a prohibited and illegal activity, due to law enforcement and legal repercussions (Kissui et al., 2019; Kiffner et al., 2022; Raycraft 2024), as is often the case in Laikipia and other East African pastoralist landscapes. In contrast, in other pastoralists context such as Sibiloi, where conservation presence and law enforcement are extremely limited, herders may experience fewer constraints in openly reporting behaviors that would be more strongly restricted elsewhere (Torrents-Ticó et al., 2023). In such pastoralist contexts, self-reporting to kill carnivores may serve as a form of social signaling, reflecting bravery or responsibility in defending livestock, a behavior that is strongly shaped by perceived normative expectations, what individuals believe others in their community do or approve of (Treves and Karanth 2003). Nevertheless, self-reported propensity to kill carnivores remain a valuable proxy for understanding human–carnivore interactions, particularly given the absence of official data (Dickman et al., 2013).

Furthermore, self-reported propensity to kill carnivores reflect only one manifestation of a broader and culturally embedded social context. Ethnically grounded differences between the Maasai and Daasanach pastoralist communities, including norms surrounding livestock protection and herd composition, moral evaluation of carnivore killing, and culturally sanctioned responses to wildlife threats, are likely to play an important role in shaping human–carnivore interactions across the two study sites. These cultural differences are also reflected in livestock husbandry practices and herd composition, which can further influence the distribution of spotted hyaenas. Because spotted hyaenas primarily prey on small livestock rather than large livestock (Kissui, 2008), variation in herd composition and *boma* structure may determine where spotted hyaenas occur. Our analyses, which were based on total livestock abundance, did not fully capture these effects; future studies that disaggregate livestock data could provide a more precise understanding of how human livelihoods interact with carnivore spatial patterns.

Previous research from East Africa suggests that Maasai pastoralist societies have historically maintained cultural institutions, norms, and value systems that can promote comparatively higher tolerance toward large carnivores, even in the face of livestock losses, whereas other pastoralist groups may hold different normative expectations regarding the legitimacy or necessity of killing wildlife to protect livelihoods (e.g., Kissui, 2008; Dickman, 2010; Fernández-Llamazares et al., 2020; Cabeza et al., 2024). Such culturally mediated differences can influence not only actual killing behavior, but also how individuals report intentions, perceive risk, and interpret coexistence. Thus, coexistence includes feedback loops, where carnivore impacts on humans (e.g., livestock depredation, safety risks) influence human responses, which then affect carnivore survival and spatial distribution. Consequently, measures of human propensity to kill carnivores should be interpreted as situated within these broader social-cultural frameworks rather than as purely individual or ecological factors. Recognizing this cultural heterogeneity is critical for understanding spatial variation in carnivore distribution and for designing context-specific strategies aimed at supporting human-carnivore coexistence across culturally-diverse pastoralist landscapes.

Overall, our study suggests that spotted hyaena distribution is associated with a complex interplay between prey availability, livestock herding and human propensity to kill carnivores, which Suraci et al. (2021) noted that can vary across carnivore species. The presence of herders with a high propensity to kill carnivores is associated with the patterns of spotted hyaena distribution, interacting with wild prey availability, as well as other ecological and social factors. These results emphasize the importance of acknowledging the complex role of livestock herding in shaping carnivore habitats, which can provide a starting point for developing strategies to support both carnivore conservation and human livelihoods (Oriol-Cotterill et al., 2015; Gehr et al., 2017; Kiffner et al., 2022).

5. Conclusion

Our study suggests that human propensity to kill carnivores is one component of a multidimensional landscape associated with spotted hyaena distribution. In areas with a low propensity to kill carnivores, spotted hyaenas were observed across areas with both wild prey and livestock herding, whereas in areas with a higher propensity to kill carnivores, their distribution tended to be more restricted, potentially reflecting attraction to wild prey and avoidance of livestock herding areas perceived as risky. These patterns highlight the importance of incorporating local human propensity to kill carnivores into assessments of large carnivores spatial ecology. Understanding such social–ecological dynamics can inform targeted conservation strategies and support coexistence between humans and large carnivores.

CRediT authorship contribution statement

Miquel Torrents-Ticó: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Álvaro Fernández-Llamazares:** Writing – review & editing, Supervision. **Mar Cabeza:** Writing – review & editing, Supervision. **Emmanuel Miliko:** Methodology, Investigation. **Thomas Titiay Komoi:** Methodology, Investigation. **Daniel Burgas:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis.

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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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2026.127279.

Data availability

Data will be made available on request.

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