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Research article

Dynamic riskscapes for prey: disentangling the impact of human and cougar presence on deer behavior using GPS smartphone locations

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Prey species adjust their behavior along human-use gradients by balancing risks from predators and humans. During hunting seasons, prey often exhibit strong antipredator responses to humans but may develop tolerance in suburban areas to exploit human-mediated resources. Additionally, areas with high human activity may offer reduced predation risk if apex predators avoid such locations. This study examined mule deer *Odocoileus hemionus* behavioral responses to risks from humans and their primary predators, cougars *Puma concolor*, contextualized by differences in risk levels between study sites, individual risk exposure, and human habituation. We framed our investigation using three non-mutually exclusive hypotheses: (H1) neutral impact, (H2) human shielding (human tolerance driven by cougar avoidance), and (H3) super-additive risk (human avoidance dominating behavior). We controlled for deer phenology and diel period, recognizing that deer behavior varies with these temporal dynamics. Spatiotemporal cougar encounter risk was quantified using GPS collar data, while spatiotemporal human encounter risk and use intensity were quantified using GPS smartphone data. Our results supported H2 and H3, emphasizing the significance of site- and individual-level variation in risk exposure and human use intensity. Deer managed cougar risk adaptively, but humans emerged as the dominant perceived risk, varying by study site. At the site with higher cougar density and lower human hunting pressure, deer exhibited antipredator responses to humans based on individual exposure to human activity, except during hunting season, when tolerance for cougars increased. Conversely, humans were the dominant risk at the site with lower cougar density and greater human hunting pressure. Deer behavior varied significantly across

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a gradient of human use, influenced by nuanced human presence and predation risks, which were discernible using human smartphone data.

Keywords: human disturbance, human-use gradients, *Odocoileus hemionus*, predator–prey, *Puma concolor*

Introduction

Animal behavior is driven by localized adaptations (Riotte-Lambert and Matthiopoulos 2020) and physiological requirements (Tracy et al. 2006) but is also influenced by competing risks, such as predation (Gaynor et al. 2019). The variability of predator movements and activity in space and time and hunting success are weighed against various activities of prey (e.g. foraging and mating) to influence decision-making and behavior (Laundré et al. 2001, Gaynor et al. 2019, Palmer et al. 2022). However, human presence elicits antipredator responses in predators and prey, driving behaviors to minimize encounters (Frid and Dill 2002, Gaynor et al. 2018, Doherty et al. 2021, Ordiz et al. 2021). Consequently, the expanding influence of humans on landscapes introduces new complexity into predator–prey interactions.

Prey may adjust their behavior based on the interplay of risks associated with predators and humans (Gaynor et al. 2019, 2022, Prugh et al. 2019). This may be especially true along human-use gradients because mortality risk associated with certain predators may vary in space and time. In wilderness areas, large mammals may be subjected to seasonal human harvest and exhibit strong antipredator responses to humans during this time (Paton et al. 2017, Brown et al. 2020). Outside the hunting season, these responses to humans may weaken (Kays et al. 2016, Brown et al. 2020). In contrast, hunting often does not occur within town and city limits. These environments may offer novel or more predictable food resources and reduced predation pressure from apex predators that avoid urban areas due to persecution (Kuijper et al. 2016, González-Lagos et al. 2021, Ordiz et al. 2021). This reshuffling of risks and rewards can lead to increased tolerance towards humans (Samia et al. 2015, Blumstein 2016, Kuijper et al. 2016, González-Lagos et al. 2021, Ordiz et al. 2021). If inhabiting areas with greater human densities provides a fitness advantage, individuals with genotypes that promote tolerance towards humans may begin to inhabit such areas (Samia et al. 2015, Blumstein 2016, González-Lagos et al. 2021).

Considering the body of work examining predator–prey interactions (Gaynor et al. 2019, Palmer et al. 2022), three broad, non-mutually exclusive hypotheses may explain predator–prey interactions across human-use gradients. Prey and predators may show no behavioral response to humans, with behavior dictated by physiological or environmental cues (Tracy et al. 2006, Riotte-Lambert and Matthiopoulos 2020), suggesting a neutral behavioral impact despite variations in predator and human use and density (H1). In contrast, prey may tolerate humans due to repeated benign interactions, perceiving predators as a greater risk because predator encounters are almost always negative (Samia et al. 2015). This 'human shield hypothesis' suggests that prey reduce overlap with predators that avoid humans while increasing overlap with humans (H2) (Berger 2007, Shores et al. 2019, Abernathy et al. 2023) or human-altered environments, such as locations with bright artificial light (Ditmer et al. 2021). Lastly, under the 'super-additive mortality hypothesis', prey may perceive both predators and humans as risky but attribute humans as a greater threat due to their higher population and broader impact relative to other predators. This aversion would lead prey to weigh human encounters as a greater risk, resulting in increased spatial and temporal overlap with predators that also tend to avoid humans (H3) (Gehr et al. 2020, Murphy et al. 2021, Crawford et al. 2022, Gorczynski et al. 2022). Using these hypotheses as our theoretical framework, we investigated mule deer *Odocoileus hemionus* (hereafter deer) behavioral responses to competing risks from their primary predator – cougars *Puma concolor* (Fig. 1b) – and humans (Fig. 1a). This predator–prey system is ideal for our study because cougars often avoid humans and infrastructure, especially in areas where they are hunted year-round (Kuijper et al. 2016, Nyhus 2016, Ganz et al. 2024). Conversely, deer and other prey species of persecuted apex predators may readily evolve tolerances to humans in benign settings like suburbs and towns (Polfus and Krausman 2012, Sawyer et al. 2017, Ditmer et al. 2021).

Our study focused on two sites with varying human-use gradients and predation risks – varied cougar densities and hunting pressures (Fig. 1c) – where cougars are hunted year-round. This comparison allowed us to evaluate hypotheses under different ecological contexts and understand how deer behavior is influenced by competing risks posed by humans and predators. However, when assessing prey responses to risk across diverse landscapes such as human-use gradients, it is essential to consider behavioral responses relative to the environmental average experienced by an individual. In environments with consistent predation threats, deer may adjust their behavior to balance foraging needs with safety, sometimes accepting higher risks to obtain the necessary energy for survival and reproduction (Van Buskirk et al. 2002, Cherry et al. 2015). Thus, we used a functional response framework to examine how deer modify their selection for risk based on the relative amount of risk experienced (Mysterud and Ims 1998, Holbrook et al. 2019), which likely varies by site and individual (Fig. 1c, e). Moreover, we nested our inquiries within phenological seasons and diel periods (Table 1; Fig. 1d). Controlling for such factors is crucial because deer respond dynamically to spatial and temporal risks, necessitating an understanding of spatially explicit areas and specific periods of vulnerability (Dwinnell et al. 2019,

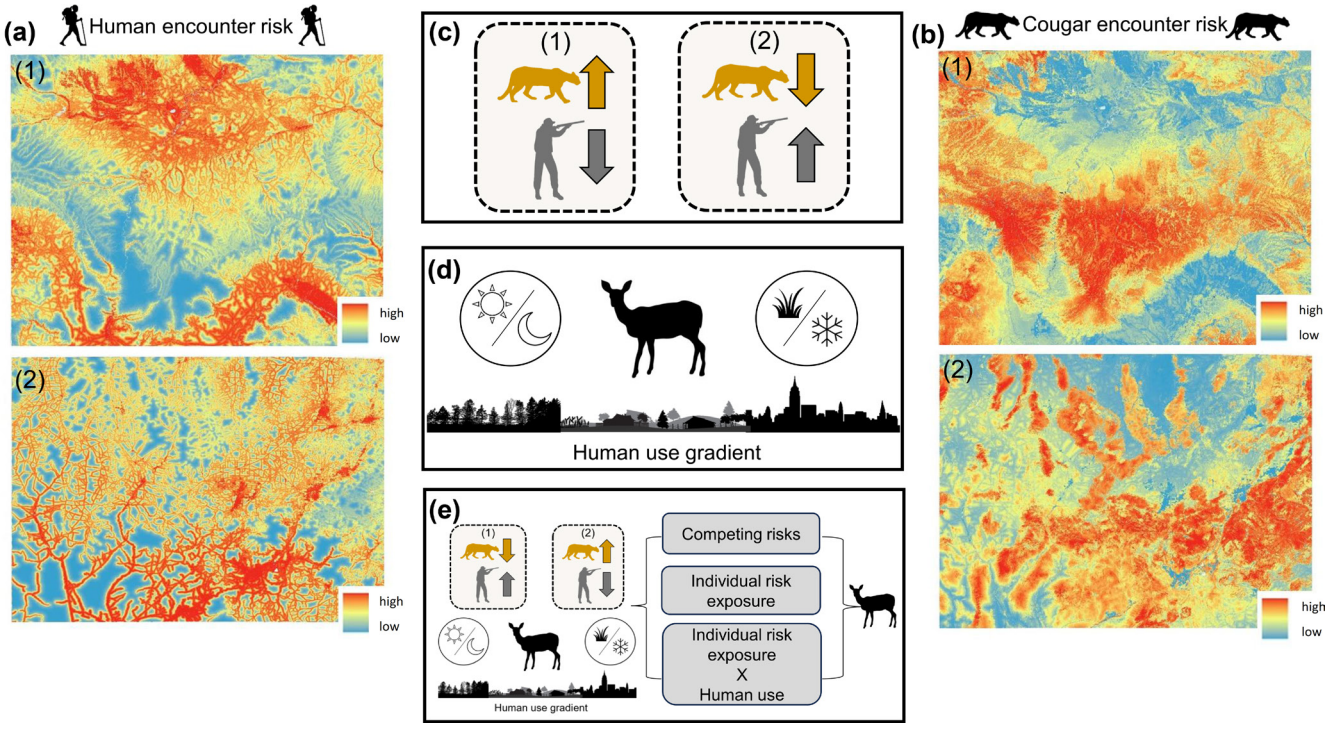

Figure 1. Illustration of competing risks, study areas, and research objectives for understanding mule deer behavior in response to cougar and human encounter risk in the American Southwest, 2019 to 2022. Panels (a) and (b) show spatially explicit estimates of human encounter risk and cougar encounter risk, respectively, for the Book Cliffs (BC; 1) and Pine Valley (PV; 2) study areas. We rescaled risk layers to ensure comparability across sites and between risk types. Panel (c) highlights differences between study areas in cougar densities and human harvest pressure: PV had a lower estimated cougar density (0.54 adults/100 km^2; 95% CI: 0.10–1.90) than BC (1.12 adults/100 km^2; 95% CI: 0.10–4.30), but higher human hunting pressure due to annual female harvests from August to September to address chronic crop damage. Panel (d) represents our first objective: to evaluate mule deer behavioral responses to competing risks along a human use gradient, considering phenological (seasonal) changes and diel activity periods. Panel (e) outlines our second and third objectives, addressed through a functional response framework, which examined how deer adjusted their selection for risk based on individual-level exposure and varying levels of human use. This approach provided insight into how human activity may mediate antipredator behavior through habituation or trade-offs between threats.

Gaynor et al. 2019, Palmer et al. 2022). Phenological seasons, particularly those related to reproduction, modify an animal's energy requirements, and alter its responsiveness to perceived dangers (Cherry et al. 2015, Gulsby et al. 2018). Deer are also more sensitive to certain times of the diel cycle that pose higher risks due to cougar activity. Cougars primarily kill prey where cover and forage overlap, mostly during low-light periods. This causes prey to avoid risky, forage-rich areas during periods of low-light (Lima and Bednekoff 1999, Smith et al. 2019, 2020).

To quantify human presence and intensity of use, we employed GPS smartphone data (hereafter human mobility data) to understand the complex interactions between human activities and wildlife behavior by accounting for temporal human activity patterns (Beumer and Mueller 2023, Ellis-Soto et al. 2023). Instead of static metrics of human density (e.g. roads, buildings), human mobility data allowed us to quantify spatiotemporal probability and intensity of use for humans at fine scales. Using our hypotheses (H1–H3) as the theoretical framework of anticipated behavioral outcomes, we aimed to: 1) understand deer behavioral responses relative to phenological periods (i.e. fetal development, rearing, and hunting seasons) and the competing encounter risks from humans and cougars across sites with differing baseline risk levels (Fig. 1); 2) examine behavioral responses to individual risk exposure across phenological periods and varying levels of competing risks (Fig. 1d, e); and 3) quantify how spatiotemporal human intensity of use influenced deer behavior in response to competing risks (Fig. 1d, e). This approach provided better insights into prey responses to competing risks from humans and predators as human use intensity changed over time and space, helping us understand how habituation might influence antipredator behavior (Ellis-Soto et al. 2023).

Material and methods

Study area

Our study took place across two sites: the Book Cliffs Mountain Range (BC) [39 722.91 km^2, centroid:

Table 1. Predicted outcomes under three hypotheses examininghuman and cougar encounter risk in relation to mule deer biology and diel activity in two study sites in the American Southwest.

Model dataset	Biological significance	Prediction
Late gestation (April–May)	Female mule deer experience significant increases in energy requirements as fetal development peaks, leading them to seek habitats rich in forage (Long et al. 2009, Morano et al. 2019). Human hunting pressure is low to absent, while cougar predation pressure on adult deer remains relatively constant (Engebretsen 2024)	H2 P: Deer tolerate humans due to repeated benign interactions, perceiving cougars as a greater risk because encounters are almost always negative (Sih 2005). Therefore, deer will avoid and display negative functional responses to cougar encounter risk (Sih 2005, Muhly et al. 2011, Gaynor et al. 2019). Deer in areas of higher human use would display stronger cougar avoidance as they may have increased tolerance for humans to offset this risk (Kuijper et al. 2016). Cougar avoidance will be stronger during nocturnal and crepuscular hours of the day when cougar encounters are the most dangerous (Smith et al. 2020, Palmer et al. 2022)
Birthing and rearing (June–August)	Postpartum, the risk to neonates from predators is at its highest, while lactating females face escalating nutritional needs that peak approximately 4–6 weeks after birth (Parker et al. 2009, Roberts and Rubenstein 2014, Dion et al. 2020), posing considerable tradeoffs in maternal care and energy balance (Cherry et al. 2015, Priyadarshini et al. 2022). Human hunting pressure is low to absent, while cougar predation pressure on adult deer remains relatively constant (Engebretsen 2024)	Deer perceive predators and humans as risky but may tolerate or avoid humans depending on their baseline exposure. Under H2 P: deer in areas of higher human use would display stronger cougar avoidance as they may have increased tolerance for humans to offset this risk (Kuijper et al. 2016). Cougar avoidance will be stronger during nocturnal and crepuscular hours of the day when cougar encounters are the most dangerous (Smith et al. 2020, Palmer et al. 2022). Under H3 P: deer less exposed to humans would display aversion, leading deer to weigh human encounters as a greater risk (Crawford et al. 2022). Therefore, deer will avoid and display negative functional responses to humans (Gehr et al. 2018, Gaynor et al. 2019). Human avoidance will be stronger in areas with greater human use and during the diurnal and crepuscular diel periods when humans are mostly active (Gaynor et al. 2018, Palmer et al. 2022)
Hunting (September–October)	Deer are more active as they attempt to accumulate body fat for winter (Hurley et al. 2014) and transition to winter ranges (Merkle et al. 2016, Ortega et al. 2024), increasing their exposure to hunters. Mortality associated with humans is high (Western Association of Fish and Wildlife Agencies 2019, Brown et al 2020), while cougar predation pressure on adult deer remains relatively constant (Engebretsen 2024)	H3 P: deer perceive predators and humans as risky but see humans as a greater threat due to their higher population and broader impact. This aversion would lead deer to weigh human encounters as a greater risk (Crawford et al. 2022). Therefore, deer will avoid and display negative functional responses to humans (Gehr et al. 2018, Gaynor et al. 2019). Human avoidance will be stronger in hunt areas with greater human use and during the diurnal and crepuscular diel periods when humans are mostly active (Gaynor et al. 2018, Palmer et al. 2022)

39°42'15"N, 109°30'18"W] in western Colorado and eastern Utah, and the Pine Valley Mountain Range (PV) [56 556.72 km², centroid: 37°43'44"N, 113°58'28"W] in Utah. We generated a marginal convex polygon around all female mule deer GPS locations in the BC and PV sites to serve as our study area boundaries.

The BC site features hot summers with low humidity and cold, dry winters. Mean annual temperatures range from approximately 5°C at high elevations in the north to 15°C in southern deep canyons. Mean annual precipitation is 298 mm, varying from 130 mm in arid canyons to more than 800 mm at high elevations. The topography is characterized by rugged tableland with precipitous sidewalls and abrupt changes in local relief. In contrast, the PV site experiences hot summers and mild winters. Mean annual temperatures vary widely due to elevation differences, ranging from 2°C on high mountains to 14°C in southern lowland areas. Mean annual precipitation is 277 mm, ranging from 4 mm in lower drier areas to over 1000 mm in wetter high mountains. Elevations range from 404 to 3419 m a.s.l., with ruggedness values from flat ground to extremely rugged (range 0–712; Riley et al. 1999).

The BC was estimated to have a higher cougar density, approximately 1.12 (95% CI: 0.10, 4.30) adults per 100 km^2 compared with 0.54 (95% CI: 0.10, 1.90) adults per 100 km^2 in the PV (Stoner et al. 2018). Cougars are the primary predators of adult deer, while coyotes *Canis latrans* and black bears *Ursus americanus* are common predators of offspring in these areas (Salle et al. 2023). While legal harvest is allowed within both study sites, antlerless deer hunting pressure from August to September is relatively higher in the PV. From 2019 to 2022, a total of 941 hunters were reported to be afield (range across years: 37–502) from an allocated 1113 antlerless deer permits (48–741) across all hunt units in the

PV, compared to 196 hunters (42–65) in the BC (275 permits [50–83]). Higher hunters afield lead to noticeable differences in hunter harvest of antlerless deer between the two sites. From 2019 to 2022, 795 antlerless deer (range across years: 33–502) were harvested across all hunt units in the PV, compared to 115 antlerless deer across all hunt units in the BC (14–43). Within both study areas, ranching, livestock grazing, oil and gas production, coal mining, recreation, and tourism were common activities. Larger towns in BC include Vernal, Utah, and Grand Junction, Colorado. Cedar City, Utah, and St. George, Utah, are the largest towns within 200 km of the PV.

Animal capture and GPS data

Cougar captures in the BC were conducted from 2019 to 2021, following the methods outlined in Engebretsen et al. (2023). Once immobilized animals were fitted with GPS collars (ATS G5-2DH GPS-VHF collar; Advanced Telemetry Systems, Inc.) that collected location points at 2-h intervals. In the Delamar Mountains, encompassing the PV Range, cougar captures were conducted from 2019 to 2021 following the methods outlined in Jansen and Jenks (2012). Once immobilized, cougars were fitted with GPS collars (VERTEX PLUS model GPS collar; VECTRONIC Aerospace GmbH) that collected location points at 4-h intervals. All capture methods and handling procedures followed guidelines from the American Society of Mammalogists (Sikes et al. 2011).

Deer in the BC and PV were captured from December 2015 to 2022 (BC: 2017–2022, PV: 2015–2022) following the methods outlined in Van de Kerk et al. (2020). At a central processing site, deer were fitted with GPS collars (model type G2110E2H, G5-2DH Advanced Telemetry Systems) that collected location points at 2-h intervals. We subset our cougar and deer GPS data to phenological periods relevant to deer within our study areas (hereafter deer-season): late gestation (April to May), offspring rearing and birthing (June to August), and hunting (September to October), as described in Table 1. For all GPS locations, we assigned deer-seasons and diel periods (Table 1). Diel periods were defined as crepuscular (start of nautical dawn to sunrise and sunset to end of nautical dusk), day (sunrise to sunset), and night (end of nautical dusk to start of nautical dawn) using ver. 0.5.1 of the 'suncalc' package (Thieurmel and Elmarhraoui 2019). All data manipulation and analyses were performed in R (ver. 4.3.1; www.r-project.org).

Quantifying human intensity of use and competing risks

We used anonymized smartphone GPS location data (hereafter human mobility data) to represent the human intensity of use across the landscape. These data are sourced from software development kits integrated into frequently used mobile applications, collecting location information from anonymized consenting users. Gravy Analytics manages the compilation of these location data, drawing monthly from 10 to 15% of undisclosed data providers who comply with the California Consumer Privacy Act and the European General Data Protection Regulation.

To distinguish human infrastructure from human presence on the landscape, we removed duplicate locations, those on and within 20 m of all roads to filter vehicular traffic (U.S. Geological Survey, National Geospatial Technical Operations Center 2023), those within buildings (Microsoft 2018), and those with speeds over 100 mph to filter air traffic. Using human mobility data, we generated spatiotemporal raster layers to quantify the human intensity of use. To quantify human intensity of use, we summed smartphone detections within 30-m raster pixels across BC and PV. We applied a smoothing technique to address clustering in urban areas, enabling a landscape-scale analysis. We resampled the 30-m rasters to coarser resolutions (240 × 240 m and 510 × 510 m) to better capture human use within deer home ranges (~ 2.59 km²). We applied a moving window focal operation with radial distances of 567 m, 799 m, 978 m, and 1262 m (approximately 1–5 km). This process resulted in spatiotemporal raster layers of human use intensity at multiple scales for each deer season and diel period. These methods are described in greater detail in the Supporting information.

We generated predicted surfaces from resource selection models for each species to represent the risk of encountering either a human or a cougar. We implemented selection models at the second order under a used-available design (Northrup et al. 2022). We developed these models for humans and cougars across all diel periods, deer-seasons (Table 1), and study years, as detailed in the Supporting information. We created binomial generalized linear models appropriate for binary response data, such as used and available locations, using the 'lme4' package (ver. 1.1–35; Bates et al. 2015) in R (ver. 4.3.1; www.r-project.org). All model covariates were scaled and centered, and we verified that variance inflation factors were below 10 to ensure that multicollinearity did not affect model performance (Menard 2002). To assess model fit, we compared species-specific to a null model using Akaike information criterion adjusted for small sample size (AICc) (Anderson and Burnham 2002). From these models, we generated 30-m pixel predicted raster surfaces for each species across the BC and PV study sites, hereafter referred to as the probability of human and the probability of cougar encounter. All spatial analyses were performed using ver. 1.7-46 of the 'terra' package (Hijmans et al. 2024).

Behavioral responses to competing risks

To quantify habitat selection for deer and their behavioral decisions relative to human and cougar encounter risk, we implemented integrated step-selection functions (iSSA) (Avgar et al. 2016) in ver. 0.2.1.0 of the 'amt' package (Signer et al. 2019). ISSAs allow for concurrent inference on movement-free habitat selection and movement parameters. We generated 15 random steps drawn from gamma and von Mises distributions for each deer's used locations to estimate

step lengths and turn angles, respectively. Steps without preceding steps were removed, and for individuals lacking sequential GPS relocations, we resampled data at 2-h intervals, allowing for 30-min deviations.

We assigned diel periods and deer-seasons (Table 1) to all deer used and available locations. We linearly interpolated NDVI (Landsat Spectral Indices products from the U.S. Geological Survey Earth Resources Observation and Science Center) to produce 30-m pixel daily estimates. We extracted 30-m pixel terrain ruggedness (Riley et al. 1999), daily NDVI, categorical cover type (binary 0 or 1 for open, forested, and shrub [Supporting information]; Dewitz 2021), and probabilities of human and cougar encounters for all starting and ending used and available locations. To address collinearity among covariates, we retained NDVI, terrain ruggedness, cover type, and probabilities of human and cougar encounters if their variance inflation factor was < 10 (Menard 2002).

To address our first objective, we generated competing selection and movement models for each deer for each deer-season for each study site. The selection component included 1) the base model (terrain ruggedness + daily NDVI + cover type), 2) a cougar encounter model (terrain ruggedness + daily NDVI + cover type + probability of cougar encounter), 3) a human encounter model (terrain ruggedness + daily NDVI + cover type + probability of human encounter), and 4) a combined risks model (terrain ruggedness + daily NDVI + cover type + probability of cougar encounter + probability of human cougar encounter). The movement component incorporated the interactive effects of competing risks on movement rates (step lengths) and movement patterns (turn angles). We used the logarithm of step lengths for movement rates, and for directionality, we used the cosine of turn angles. The movement component of the cougar encounter model assessed cougar encounter effects on deer movement (cosine[turn angle] × cougar encounter probability + log[step length] × cougar encounter probability), the human encounter model (cosine[turn angle] × human encounter probability + log[step length] × human encounter probability) examined human encounter effects on movement, and the cougar and human encounter model (cosine[turn angle] × cougar encounter probability + log[step length] × cougar encounter probability + cosine[turn angle] × human encounter probability + log[step length] × human encounter probability) evaluated separate two-way interactions on movement for each risk type. The base model served as a control.

Our modeling framework assesses deer responses to human and predator risks using an environmental model as a neutrality benchmark (Table 1). Apparent neutrality can occur when risk mitigation strategies, like human shielding and avoidance, counterbalance each other at the population level. Consequently, some deer may exhibit human shielding while others focus on avoidance, leading to an overall neutral response. Therefore, we emphasize that neutral responses should be interpreted cautiously, as they may represent risk trade-offs rather than genuine insensitivity to risk (Supporting information).

We used the Akaike information criterion adjusted for small sample size (AICc) for each deer's candidate model set to determine the top model explaining deer habitat selection and movement (Anderson and Burnham 2002). We selected the most parsimonious model if multiple models competed (ΔAICc < 2). Given our analysis aimed to reveal broader population-level trends amid these competing risks, we retained deer iSSA data from deer-season combinations where the cougar and human encounter model was the top, most parsimonious model.

Using these subsets of data, we developed models for each site. We divided data into subsets for each diel period and generated cougar and human encounter models for each deer-season combination. From these individual models, we calculated population-level mean beta estimates and 95% confidence intervals for each study site, running 10 000 bootstrap iterations using ver. 1.3–28.1 of the 'boot' package (Davison and Hinkley 1997, Canty and Ripley 2024).

Functional response to competing risks and human intensity of use

To address our second objective in the context of individual risk exposure, we used a functional response framework, which assesses the selection of an environmental variable based on the availability of that variable (Mysterud and Ims 1998, Holbrook et al. 2019). By including the availability of competing risks, we could understand how changes in these risks influenced deer selection at the finest scale (i.e. the movement step) (Ditmer et al. 2021). We utilized data from deer-season combinations where the cougar and human encounter model was identified as the most parsimonious (lowest ΔAICc).

We created human and cougar encounter risk selection ratios for each individual deer across retained deer-seasons. We calculated these ratios by dividing the continuous estimates of human and cougar encounter probability at each used location (used risk) by the mean probability of each respective risk at the corresponding available locations (available risk). A selection ratio greater than one indicates selection for areas with higher encounter risk than what was available at the movement step, whereas a ratio less than one indicates selection for areas with lower encounter risk compared to the average available locations.

We created generalized linear mixed effects models to test how deer responded to competing risks at each movement step. In separate models for humans and cougars, the log of the risk selection ratio at each movement step for each respective species served as the response variable. The probability of encounter risk served as a fixed effect in the models. For human encounter risk models, we used the mean probability of human encounter at the associated available movement step. For cougar encounter risk models, we used the mean probability of cougar encounter at the associated available movement step.

Our model sets for competing risks comprised three models: 1) null model as a control to provide a baseline for

measuring the effects of the functional response (cougars and humans: ~ 1), 2) 'risk model' consisting of the mean probability of risk encounter at associated available steps (cougars: mean cougar encounter probability, humans: mean human encounter probability), and to address our third objective 3) 'human intensity of use and risk model' consisting of the mean probability of risk encounter at associated available steps interacted with human intensity of use (cougars: mean cougar encounter probability × human intensity of use, humans: mean human encounter probability × human intensity of use). For each candidate model set, we used AICc to determine if fluctuations in risk at the movement step and human intensity of use best explained an animal's functional response compared to a null model (Anderson and Burnham 2002). We selected the most parsimonious model if multiple models were competing (ΔAICc < 2).

Before testing competing models for human and cougar risks, we evaluated multiple combinations of spatial resolution (240 m and 510 m) and smoothing windows (1–5 km) of the human intensity of use rasters. We did this for each study site, deer-season, and diel period, selecting the best configuration using AICc (Anderson and Burnham 2002). This methodology is fully described in the Supporting Information. Moreover, we anticipated that study sites, deer-seasons, and diel periods would influence the functional response to risks (Table 1). Therefore, before testing these models within candidate sets, we used AICc to determine if dividing our data into subsets based on study site, deer-season, and diel period was necessary for the best inference relative to each encounter risk (Anderson and Burnham 2002). All generalized linear mixed effects models included a random intercept for animal identification number to account for individual variation and were implemented in ver. 1.1-35.1 of the 'lme4' package (Bates et al. 2015).

Results

Measuring dynamic competing risks

In both BC and PV, humans selected areas closer to improved roads, less rugged terrain, and lower elevations, and selected urban areas more compared to agricultural, forested, open, and shrub habitats consistently across deer-seasons and diel periods (Fig. 1a, Supporting information). In contrast, cougars selected higher elevations, rougher terrain, and shrub and forested habitats. Selection of unimproved roads and trails, open habitats, and improved roads varied across study sites and diel periods for cougars (Fig. 1b, Supporting information).

Across all years and deer-seasons considered, the highest human intensity of use was in the PV (mean: 53

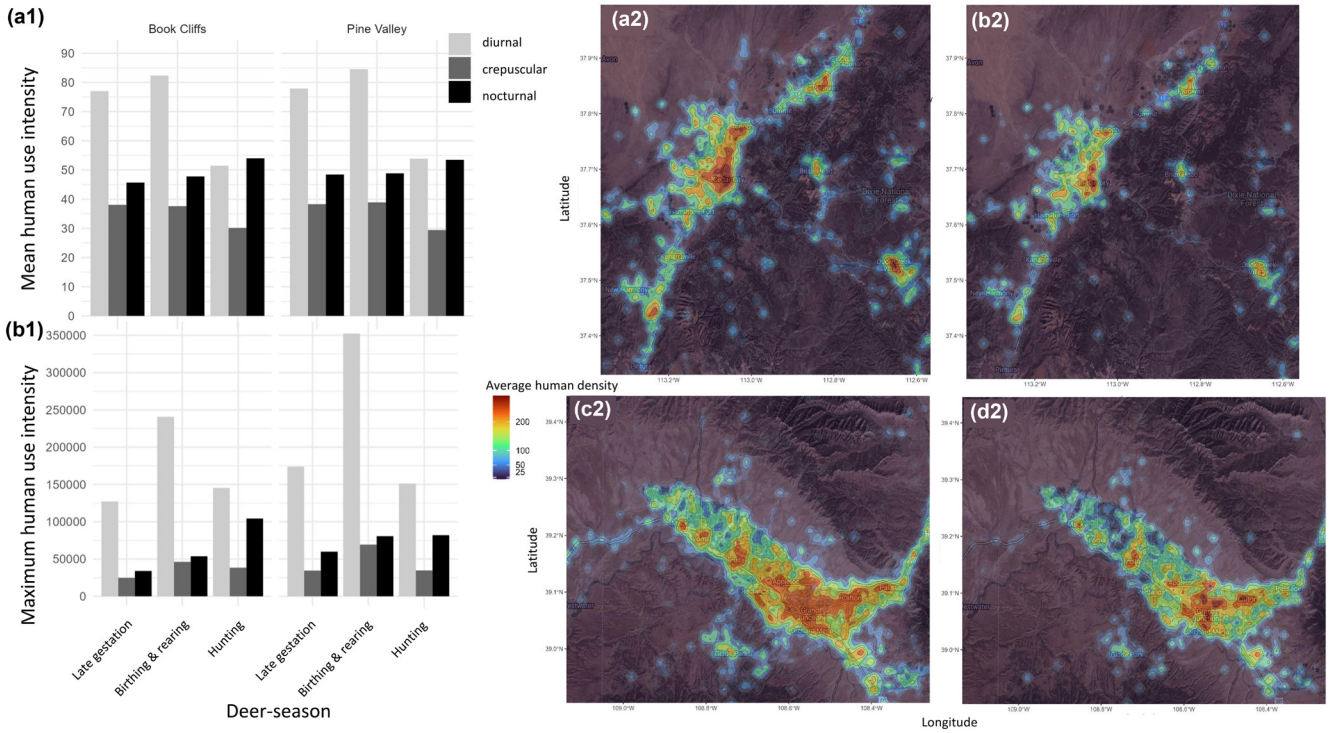

Figure 2. Human intensity of use patterns in the Book Cliffs and Pine Valley, in the American Southwest, from 2019 to 2022. We summarized these patterns to display the mean (a1) and maximum (b1) human GPS smartphone detections (detections/900 m^2) during our study period. Illustration of the changes in human intensity of use patterns from day to night (a2 and c2 for daytime and b2 and d2 for night-time) during birthing and rearing for mule deer (June through August) within our study areas, Book Cliffs (c2, d2) and Pine Valley (a2, b2).

detections/900m^2, range: 1–115 331) compared to BC (mean: 52 detections/900m^2, range: 1–90 488). Still, both sites experienced similar human use on average (Fig. 2a1). Human detections varied across deer-seasons, with the most detections occurring during birthing and rearing, followed by late gestation and hunting (Fig. 2a1). Most detections occurred during the day across deer-seasons, with the highest diurnal detections during birthing and rearing and the highest nocturnal detections during the hunting season (Fig. 2b1). During the day, human intensity of use was more diffuse and spread across the landscape (Fig. 2a2, c2). The spatial extent of human intensity of use decreased at night, with areas of high use mostly in residential areas (Fig. 2b2, d2).

How does deer activity change across phenological seasons?

During late gestation and birthing–rearing seasons, deer had the greatest daily movements during the crepuscular period. During the hunting season, deer in the site with the lower hunting pressure but the greater cougar density (BC) moved more during the day (Supporting information). In contrast, deer in the site with the lower cougar density (PV) and higher hunting pressure moved more during the crepuscular period during this season (Supporting information). Across study sites and deer-seasons, movement rates were always faster in areas with greater human encounter risk than cougar encounter risk (Supporting information).

How do phenological seasons influence the selection of competing risks?

Integrated step selection models included 563 deer-seasons. We incorporated data from 159 female deer across 308 deer-seasons in BC and 122 female deer across 255 seasons from PV. Across all phenological seasons, most top models for individual deer included the combined risk of encountering both cougars and humans for both the BC (range: 41–42% of top models across seasons) and the PV (41–52% of top models with the least during hunting season and the most during birthing and rearing). Human encounter risk was included in 63% of top seasonal models for both the BC and the PV sites, when considering both models containing only human risk and combined risk (human + cougar encounter risk). The BC site exhibited more variability across seasons in response to human risk (variance: BC = 6.35, PV = 3.46); human encounter risk was among the top models most frequently during late gestation (66% of deer-seasons) and least during birthing and rearing (59% of deer-seasons). Models for deer in the PV site included human encounter risk at nearly the same percentage across biological seasons (62–64% of top models; Supporting information).

Cougar risk encounter, was included in top deer seasonal models at similar percentages within the BC (66% average across seasons) and PV (67% average across seasons), when considering both models containing only cougar risk and combined risk (human + cougar encounter risk). However, responses to cougar encounter risk fluctuated among seasons, with both sites having the highest percentage of top models with cougar risk during the late gestation (BC: 71%; PV: 71%), followed by the hunting season (BC: 63%; PV: 69%), and the birthing and rearing (BC: 64%; PV: 62%). Neither human nor cougar encounter risk (base model only) was included in the top model for 13% of BC and 16% of PV deer-seasons, with the highest percentage occurring in the birthing and rearing for both sites (BC: 19%; PV: 26%), and the least during the late gestation in the BC (6% of top models), and the hunting in PV (10% of top models; Supporting information).

How do competing risks influence individual deer behavior?

Addressing our first objective, we examined the beta coefficients for deer-seasons where the top model was the aggregated risk of encountering both cougars and humans. This subset included 91 female deer across 128 deer-seasons from BC and 71 individuals across 119 from PV. Deer adjusted their movement patterns in response to the type and timing of risks posed by humans and cougars (Supporting information). For instance, BC deer exhibited more tortuous movements during high-risk times in high-risk areas for both cougars and humans (Supporting information). The influence of human presence on deer behavior, such as greater activity in areas of high human encounter risk (Supporting information) and more directional and quicker movements in these areas (Supporting information), highlight how humans may be perceived as a greater competing risk. However, the contrasting behaviors observed at the two study sites (Supporting information) indicate that local predator densities influence prey behavior. See full movement results in the Supporting information.

We found distinct antipredator behavior across study sites (Supporting information). The step selection analysis showed intriguing patterns in how individuals selected or avoided competing risks (Fig. 3, Supporting information); however, there was significant individual variation, leading to population-level beta estimates that included zero in relation to the risk of encountering humans (Fig. 3). Such variation emphasizes the importance of a functional response framework. Indeed, a functional response to competing risks was evident in 32 of the 36 deer-season diel period combinations (hashed lines in Fig. 3). We discuss our most prevailing findings below by considering the results from the integrated step selection and the functional response analysis. Habitat selection patterns relative to environmental variables are discussed in the Supporting information. Functional response results were interpreted by study site, phenological season, and diel period (Supporting information).

How do deer living in areas with higher densities of natural predators respond to competing risks?

At the site with higher cougar density and less hunting pressure (BC), deer exhibited varied antipredator responses during late gestation and birthing and rearing. Step selection

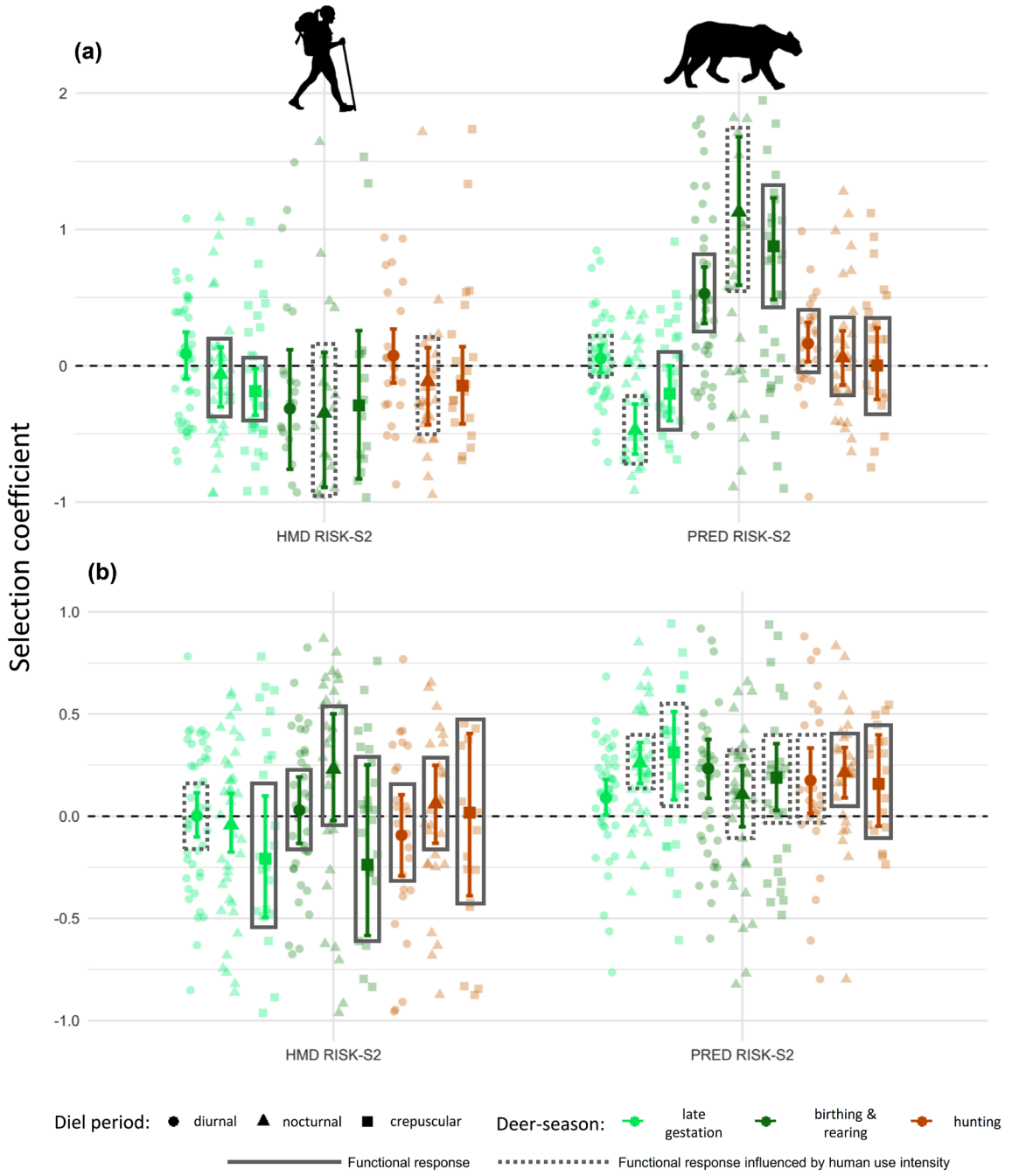

Figure 3. Individual and population-level integrated step selection models for mule deer in response to competing risks. We estimated selection coefficients across deer-seasons relevant to mule deer in two study sites -- the Book Cliffs (a) and Pine Valley (b) -- in the American Southwest, from 2019 to 2022. 'HMD RISK-S2' denotesselection patterns relative to the probability of encountering a human, while 'PRED RISK-S2' reflects selection relative to the probability of encountering a cougar. Larger solid points and associated bars represent population-level mean selection coefficients with 95% confidence intervals; semi-transparent points indicate individual-level coefficients. Box outlines and line styles indicate whether functional responses were detected and whether those responses varied with human use intensity. Symbols are colored by deer season and shaped by diel period.

alone suggested mixed responses to human risk across these phenological seasons, but population-level estimates overlapped zero. During late gestation, deer avoided cougar risk during the crepuscular period and night while selecting this risk during all periods during birthing and rearing (Fig. 3a, Supporting information). However, the functional response analysis highlighted that deer displayed a negative functional response to human risk in late gestation during the crepuscular period (Fig. 4a), when deer at this site are the most active (Supporting information). Deer also had a negative

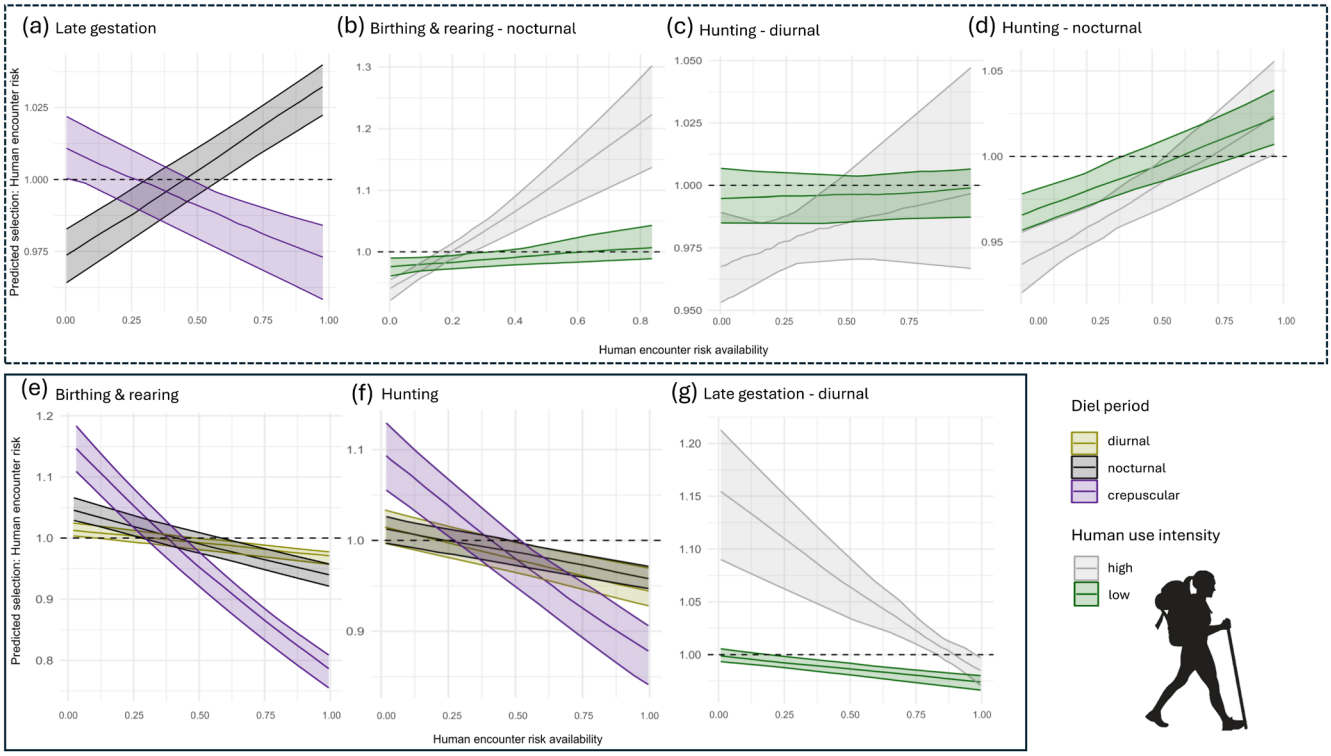

Figure 4. Significant functional response curves for mule deer in relation to human encounter risk across deer-seasons and diel periods from 2019 to 2022. Plots depict results from the Book Cliffs (a)–(d); dashed bounding box) and Pine Valley (e)–(g); solid bounding box) study sites in the American Southwest, USA. Functional responses are shown across deer-season and diel period combinations either without accounting for human use intensity (a), (e), (f) or with human use intensity incorporated into the models (b)–(d), (g). Solid center lines represent model predictions; outer lines and shaded ribbons denote 95% confidence intervals. Line and shading colors reflect diel periods and levels of human use intensity.Deer-season and diel period combinations not shown were not significant.

functional response to cougars during the day and crepuscular period during the birthing and rearing period (Fig. 5b), suggesting that deer avoid both encounter risks during their most active period – the crepuscular period.

We found evidence that deer had different antipredator strategies for each risk type. Deer displayed a positive functional response to cougar and human encounter risk at night during late gestation (Fig. 4a, 5a). This may be related to deer living in areas with greater human use changing their behavior to adaptively modulate risk exposure based on the time each risk is most likely active on the landscape. Deer occupying areas with greater human use had a negative functional response to cougars during the crepuscular period (Fig. 5e), a time when they are most active and the risk from cougar mortality likely increases; simultaneously, deer living in areas with greater human use displayed a positive response to cougar encounter risk during the day, a time when humans are most active (Fig. 5d). During birthing and rearing, deer occupying areas with greater human use intensity may also be using humans to offset risk from cougars because they displayed a positive functional response to human encounters at night (Fig. 4b) while having a negative functional response to cougars at night (Fig. 5f).

However, during the hunting season deer had varied responses to humans based on use intensity, increasing tolerance for cougar encounter risk as human-related mortality risk increased. Step selection alone suggested deer selected areas with higher human encounter risk during the day and avoided these areas during the crepuscular period and night. Still, these population-level results overlapped zero (Fig. 3a, Supporting information). For cougar risk, step selection alone suggested deer selected areas with higher cougar encounter risk during the day and night, but these population-level results overlapped zero (Fig. 3a, Supporting information). Yet, while deer demonstrated a positive functional response to human encounter risk at night across intensities of use (Fig. 4d), they simultaneously showed a positive functional response for cougar encounter risk across all diel periods (Fig. 5c, Supporting information).

How do deer living with greater hunting pressure and higher human use respond to competing risks?

In contrast to the BC, deer modulated their risk from cougars adaptively during all phenological seasons. Step selection alone suggested deer had mixed responses to human encounter risk, but these population-level results overlapped zero. For cougar risk, step selection alone suggested deer generally selected areas with higher cougar encounter risk during most diel periods and seasons, but some of these population-level

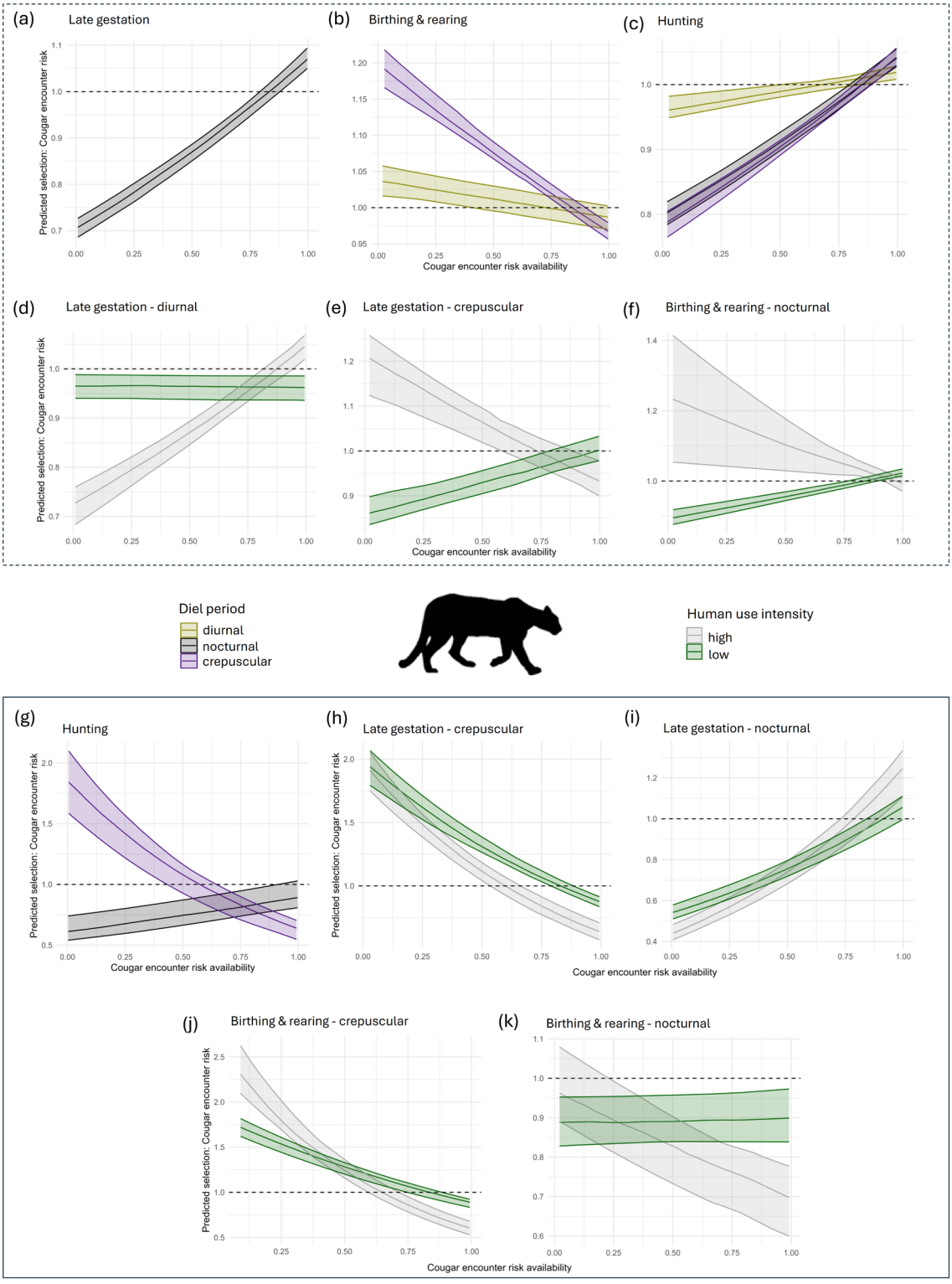

Figure 5. Significant functional response curves for mule deer in relation to cougar encounter risk across deer-seasons and diel periods from 2019 to 2022. Plots depict results from the Book Cliffs (a)–(d); dashed bounding box) and Pine Valley (e)–(g); solid bounding box) study sites in the American Southwest, USA. Functional responses are shown across deer-season and diel period combinations either without accounting for human use intensity (a)–(c), (g) or with human use intensity incorporated into the models (d)–(f), (h)–(k). Solid center lines represent model predictions; outer lines and shaded ribbons indicate 95% confidence intervals. Line and shading colors reflect diel periods and levels of human use intensity. Deer-season and diel period combinations not shown were not significant.

results overlapped zero (Fig. 3b; Supporting information). However, deer avoided human encounter risk as individual exposure increased, demonstrating a negative functional response during all diel periods throughout birthing and rearing and the hunting season (Fig. 4e and f). In areas of high human use, deer avoided humans more strongly during the day, during the relatively low-risk phenological period–late gestation (Fig. 4g).

Modifying behavior based on the diel period, deer avoided cougar encounter risk more strongly during their most active period – the crepuscular period – during all deer-seasons (Fig. 5g h, and j). However, they displayed an increased tolerance for cougar encounter risk at night during the hunting season (Fig. 5g). During birthing and rearing, deer in areas of greater human use intensity avoided cougar encounter risk more strongly than deer in areas with lower human use (Fig. 5j, k; Supporting information).

Discussion

We examined antipredator behavior in mule deer across a gradient of human use within sites with varying predator densities and human hunting pressure, focusing on the competing risks of cougars and humans. Our findings support previous research indicating that these risks strongly influence prey behavior across phenological seasons and diel periods (Gaynor et al. 2019, Palmer et al. 2022). By leveraging human mobility data, we successfully quantified human encounter risk and intensity of use at both fine and broad spatiotemporal scales (Fig. 1–2). In doing so, we found support for both the human shield (Berger 2007, Shores et al. 2019, Abernathy et al. 2023, Ganz et al. 2024) and super-additive predation hypotheses (Gehr et al. 2020, Murphy et al. 2021, Crawford et al. 2022, Gorczynski et al. 2022); however, we found the most support for the super-additive predation hypotheses, wherein humans were the greatest perceived threat. We note, support for multiple hypotheses emphasizes the importance of baseline predator densities and individual exposure to humans to fully contextualize prey responses to competing risks. Finally, our findings emphasize that deer behavior varies across a gradient of human use, driven by differing levels of human presence and mortality risks across study sites – a finding that would have been obscured without leveraging human GPS smartphone data (Fig. 4b–d, g, 5d–f, h–5k).

Deer must balance the frequent, often non-lethal risk of human encounters during non-hunting seasons with the rarer yet lethal encounters of cougars. Understanding how deer navigate these spatial and temporal challenges sheds light on the strategies prey use to enhance fitness under diverse risks. Across three key seasons, female deer somewhat adjusted their risk exposure and activity patterns in alignment with life history phenology (Table 1) and the competing risks they face (Lima and Bednekoff 1999, Van Buskirk et al. 2002, Dwinnell et al. 2019). For example, during the hunting season, deer within the site with high cougar density (BC) increased tolerance for cougar encounters as human-related mortality risks rose, highlighting their ability to prioritize more immediate threats (Table 1, Fig. 5c). During birthing and rearing, deer used human presence as a potential shield from predators while caring for their offspring (Table 1), avoiding cougar risk while displaying positive responses to human encounters at night (Fig. 4b, 5f). These strategies highlight how deer can align risk mitigation with life history phenology to balance frequent, non-lethal human risks and rarer but lethal predator encounters (Gaynor et al. 2019, Palmer et al. 2022).

Deer adapted their behavior to the type and timing of risks from humans and cougars, modifying their activity patterns in response to seasonal and diel variations (Supporting information). At the site with higher cougar density and lower hunting pressure (BC), deer displayed more tortuous movements during high-risk periods – nocturnal hours, birthing and rearing, and daytime hours during the hunting season (Supporting information) – suggesting a balancing act between foraging and safety, consistent with findings from other studies (Lima and Bednekoff 1999, Palmer et al. 2022). However, our results indicate that humans have a stronger influence on deer activity patterns than cougars, as seen in increased movement rates (Supporting information) and more directed movement in areas with higher human encounter likelihood (Supporting information). In some cases, deer increased activity in areas of high cougar encounter risk, potentially increasing their vulnerability to cougar predation (Supporting information; Gehr et al. 2020, Mills and Harris 2020, Murphy et al. 2021). Even in BC, where our results suggest deer may be habituated, deer generally exhibited increased tolerance for cougar encounter risk during the hunting season (Fig. 5c).

The differences in deer behavior across the two sites suggest that local predator densities and human hunting pressures also shape prey responses and habituation. In BC, where cougar density is higher, and human hunting pressure is lower, deer exhibited selection patterns that suggest habituation for deer living in areas of greater human use. In areas with high human use, deer selected areas of increased cougar encounter risk during the day but avoided these areas at night and during crepuscular times (Fig. 5d–f) while preferring areas with higher human encounter risk at night when rearing their offspring (Fig. 4b). These findings suggest that deer have different antipredator responses to humans that vary with exposure, supporting the notion of human tolerance (Blumstein 2016) and the varied effects of human presence on wildlife antipredator behavior (Geffroy et al. 2020). In areas where hunting is limited or absent (e.g. cities and towns), deer may tolerate human presence due to habituation from repeated non-threatening interactions and potentially lower cougar predation success (Samia et al. 2015, Blumstein 2016, Kuijper et al. 2016, González-Lagos et al. 2021, Ordiz et al. 2021). Indeed, the mean and variability in antipredator responses change based on the duration of contact with humans (Geffroy et al. 2020), resulting in deer adjusting their behavior to accommodate living alongside humans,

as suggested elsewhere (Gaynor et al. 2018). For example, when harvest by humans was low, deer selected areas with a higher probability of human encounter at night – a time when locations of humans may not represent a high probability of encounter as they are in buildings (Fig. 3, 4a, b, d). This is likely driven by the benefits of living in human-dominated environments, such as the 'predator release' effect (Kuijper et al. 2016) and higher breeding success compared to rural counterparts (Carrete and Tella 2017). Such behavioral differences can be reinforced by the heritability of 'fear' of humans and antipredator behavior, which may have initially resulted from selection pressures (Carrete and Tella 2017). Such adaptability suggests not merely a reactive but an anticipatory behavior, deeply tuned to biological rhythms and environmental pressures (Gaynor et al. 2019, Palmer et al. 2022, Weiss and Marshall 2023).

In contrast, human presence appeared to be the primary risk factor in the PV, which had lower cougar density and higher hunting pressure. Deer consistently **avoided** humans throughout two risk-sensitive seasons (birthing and rearing and hunting; Table 1) and across all diel periods (Fig. 4e, f), with even stronger avoidance during the day in areas with high human use (Fig. 4g). Nevertheless, deer at the PV site managed their risk from cougars adaptively, modifying their behavior across diel periods. For example, deer exhibited the strongest avoidance of cougar encounter risk during crepuscular periods – their most active time – across all seasons (Fig. 5g, h, j). Deer in areas with high human use displayed even stronger avoidance of cougar encounter risk when rearing offspring, compared to deer in areas with lower human use (Fig. 5k). The latter may suggest a shift in tolerance toward human risk when traveling with offspring because, during this period, deer must navigate tradeoffs associated with heightened predation risks to neonates and increased nutritional demands associated with lactation (Table 1; Sadleir et al. 1982, Clutton-Brock et al. 1989). This interplay between deer, cougars, and human activity illustrates how prey exploit temporal refuges to mitigate risks from multiple predators, reflecting a complex adaptive response to fluctuating threats (Brown et al. 2020, Kautz et al. 2022, Abernathy et al. 2023, Ganz et al. 2024).

Human mobility data allowed us to overcome the spatial and temporal limitations of traditional ecological methods of capturing spatiotemporal human use, such as trail counters (Costello et al. 2013), camera traps (Abernathy et al. 2023), and recreational GPS units (Olson et al. 2018), which often fail to capture fine-scale behavioral responses across large, complex areas with appropriate sample sizes (Beumer and Mueller 2023, Ellis-Soto et al. 2023). Moreover, unlike approaches that leverage remotely sensed artificial light as a dynamic proxy for human presence, our approach also captured human daytime behaviors, such as recreation and using natural (unbuilt) areas relevant to wildlife (Ditmer et al. 2021). These data allowed us to investigate how human activity and usage intensity differences affected deer behavior. They provided detailed insights that were previously unattainable; they enabled us to test hypotheses such as the human shield and super-additive mortality effects in a new way (Beumer and Mueller 2023, Ellis-Soto et al. 2023). Using these data, we could better understand how more habituated deer respond differently to risks than their less habituated counterparts, demonstrating behavioral plasticity influenced by the degree of human presence and baseline risks within a site.

Our study is a pioneering effort to use human mobility data in ecological research, offering a replicable model to understand the complex interactions between human activities and wildlife behavior (Beumer and Mueller 2023, Ellis-Soto et al. 2023). These data provide a basis for more effective wildlife management and conservation strategies (Oliver et al. 2024). Managers and conservationists can identify distinct spatial and temporal periods to apply actions, such as informing hunting regulations and promoting access to control over-objective herds (Brown et al. 2020), structuring natural area access to accommodate sensitive phenological periods, and reducing human–wildlife conflicts (Young et al. 2019). As ecology adopts more digitally integrated approaches, such data will be invaluable in designing management and conservation measures finely tuned to more realistic human activity patterns (Ellis-Soto et al. 2023, Oliver et al. 2024). Integrating human mobility data into ecological research exemplifies the potential for innovative technologies to enhance our understanding of human–wildlife interactions and foster adaptive, data-driven practices.

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Author contributions

Heather N. Abernathy: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (lead); Software (supporting); Supervision (supporting); Validation (lead); Writing – original draft (lead); Writing – review and editing (lead). **Mark A. Ditmer**: Conceptualization (supporting); Data curation (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Resources (lead); Software (supporting); Supervision (lead); Visualization (supporting); Writing – review and editing (equal). **David C. Stoner**: Project administration (supporting); Writing – review and editing (equal). **Kent R. Hersey**: Data curation (lead); Investigation (lead); Writing – review

and editing (supporting). **Katherine A. Schoenecker**: Investigation (lead); Writing – review and editing (supporting). **Pat J. Jackson**: Investigation (lead). **Kristin N. Engebretsen**: Data curation (supporting); Investigation (lead); Writing – review and editing (equal). **Julie K. Young**: Data curation (lead); Investigation (lead); Writing – review and editing (equal). **George Wittemyer**: Conceptualization (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (lead); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/ecog.07626.

Data availability statement

Data are available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.51c59zwkg (Abernathy et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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