Title - Species-specific interactions with apex carnivores yield unique benefits and burdens for mesocarnivores

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WB, JWR, DRS, and SC conceptualized the study, raised resources, and oversaw project completion. WB, DRS, CL, and GS conducted fieldwork and collected the data. WB, JWR, and SC developed the methodology and analytical approaches. WB, JWR, ZL, GS, and EK curated the data and performed the analyses, with inputs from SC and DRS. WB, JWR, and SC wrote the manuscript, with help from GS. All authors reviewed subsequent drafts and approved the final version.

Statement on Inclusion:
Our study brings together authors from diverse career stages, including scientists based in the country where the study was carried out. All authors were engaged early on with the research to ensure that the diverse sets of perspectives they represent was considered from the onset. Whenever relevant, literature published by scientists from the region was cited.

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The authors declare no conflicts of interest.

ABSTRACT

1. Mesocarnivores must balance the negative (competition) and positive (carrion provisioning) effects of dominant apex carnivores to coexist in shared landscapes. How mesocarnivores navigate such top-down effects have typically been examined through a *risk-reward* lens. However, the risks accrued by mesocarnivores might not be even across all apex-mesocarnivore pairings in multi-carnivore systems, and instead can be mediated through species-specific interactions.

2. Using remote-camera surveys from 2021–2023, we estimated apex (wolf, cougar) and mesocarnivore (red fox, coyote) spatial overlap, occupancy, temporal activity, and fine-scale behaviors in northern Yellowstone National Park, USA. Additionally, we monitored GPS-collared wolf and cougar predation from 2016–2023 and recorded red fox and coyote mortalities and scavenging events at these locations.

3. Red foxes and coyotes were ubiquitous in our study area with high naïve occupancy, despite abundant wolves and cougars. Coyote occupancy was positively associated with wolf occupancy, but exhibited marginal avoidance of cougars. Photo-detection probabilities of both mesocarnivores doubled in the 24 hours following apex carnivore detections, with the exception of coyotes following cougars. Overall latency of coyote detections was longest following cougar detections and shortest following wolves, while foxes exhibited no such difference. Further, coyotes were most active when wolves and cougars were collectively least active. Red foxes were nocturnal and appeared less sensitive to wolf and cougar activities, but avoided coyote peak times.

4. Coyotes were more prevalent scavengers than red foxes at apex carnivore kills, but scavenging often had lethal consequences. We found that when wolves kill coyotes, it

was typically when coyotes attempted to scavenge from wolf kills, while cougars killed and consumed coyotes as prey. Thus wolves act as competitors for coyotes, while cougars are both predators and competitors. This distinction possibly explains coyote avoidance of cougars but attraction to wolves.

5. Mesocarnivores in Yellowstone leverage foraging benefits from associating with apex carnivores. However, these benefits are burdened by associating with wolves and cougars whose contrasting hunting modes and habitat preferences yield separate risks. Disparate costs to mesocarnivores contingent upon apex carnivore behavior offer novel insights into carnivore community ecology, and call for a more nuanced analysis of trophic interactions.

KEYWORDS: community ecology, intra-guild competition, landscape of fear, mesopredator release, occupancy analysis, resource facilitation, trophic-mediated behavior, Yellowstone

INTRODUCTION

Intraguild carnivore interactions have crucial bearings on the functional ecology of an ecosystem (Caro & Stoner, 2003; Schuette et al., 2013) and the management of multi-carnivore systems (Brook et al., 2012; Creel & Creel, 1996). Interactions between carnivores range from lethal confrontations and competitive exclusion to facilitation, and can proximately alter the abundance, distribution and behavior of all the species in the guild (Diserens et al., 2022; Palomares & Caro, 1999; Prugh & Sivy, 2020). Such interactions can ultimately affect the structure and function of entire ecosystems through trophic-mediated effects (Brashares et al., 2010; Elmhagen et al., 2010; Elmhagen & Rushton, 2007; Terborgh et al., 2001). Apex carnivores, through their direct (lethal) and indirect (exploitation competition and behavioral suppression) effects, often determine where, when, and how frequently subordinate/mesocarnivores use resources (Gordon et al., 2015; Newsome et al., 2017). For instance, African wild dogs (*Lyacon pictus*) are often excluded from areas of high preferred-prey density by larger, more dominant lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) due to both direct killing and kleptoparasitism (Creel & Creel, 1996; Mills & Gorman, 1997). Similar effects have also been observed in other carnivore systems (see Caro & Stoner, 2003; Curveira-Santos et al., 2021; Dyck et al., 2022; Fedriani et al., 2000).

Consequently, mesocarnivores avoid competition and confrontation through fine-scale spatiotemporal segregation and resource partitioning. Fedriani et al. (1999) found that when lynx (*Lynx lynx*) were more active, red fox (*Vulpes vulpes*) avoided habitats frequented by lynx. In Southern India, while leopards (*P. pardus*) and tigers (*P. tigris*) showed very little temporal partitioning in their activity patterns, leopards hunted in areas with significantly lower vegetation cover than tigers, and both selected different prey types and size-classes (Karanth & Sunquist,

1995). In contrast, fine-scale temporal avoidance of lions by cheetahs (*Acinonyx jubatus*) has been observed in multiple systems of Tanzania to reduce kleptoparasitism and/or lethal confrontations (see Durant, 2000; Swanson et al., 2014).

Quantifying the complex fine-scale strategies employed by mesocarnivores to coexist with competitively dominant carnivores is of particular relevance in the Anthropocene because humans have disproportionately affected apex carnivores. We have either caused severe population declines and local extinctions (Ripple et al., 2014), or promoted the recovery of apex carnivores through reintroduction and conservation efforts (Bangs & Fritts, 1996; Chapron et al., 2014; Lotze et al., 2011). Such scenarios can have intriguing consequences—in some places mesocarnivores have been released from competitive suppression (Crooks & Soulé, 1999; Prugh et al., 2009), while in other areas they face rising competition from recovering apex carnivores (Berger & Gese, 2007; Jiménez et al., 2019). However, while apex carnivores may limit mesocarnivores through direct and indirect effects, they can also offer scavenging opportunities from carcasses of killed prey (Brunet et al., 2022; Sivy et al., 2017; Wilmers et al., 2003). Thus, the distribution and behavior of mesocarnivores with respect to their apex counterparts are contingent upon the *risks* (interference competition) and *rewards* (carcass provisioning) of associations in space and time (Ruprecht et al., 2021).

This risk-reward spectrum for mesocarnivores can be further nuanced by the type of interactions with apex carnivores and seasonality. For instance, the magnitude of risks for a mesocarnivore that primarily competes over resources with an apex carnivore is arguably different than when the mesocarnivore, in addition to resource competition, is also hunted as prey (Broekhuis, 2015; Carbone et al., 2005). Additionally, in mountainous environments, ungulate migrations and snow conditions influence the distribution and availability of prey for

both apex and mesocarnivores. In these systems, ungulate birth pulses and changes to body condition lead to seasonal variation in the average size of apex carnivore kills, with larger carcasses (and thus opportunities for mesocarnivores to scavenge) more readily available during winter months (Wilmers et al., 2003). Large carcass availability in winter might shift the dynamics of spatiotemporal cohabitation within carnivore guilds. Thus, interactions between apex and mesocarnivores are mediated by a suite of local ecological conditions and inter-specific interactions.

Yellowstone National Park is the largest intact, temperate ecosystem in the USA that hosts a diverse community of mammalian carnivores and ungulates. In the Northern Range of Yellowstone National Park, apex carnivores such as wolves and cougars (*Puma concolor*) are abundant, particularly in the winter when they are supported by large ungulate prey that congregate at high densities (Anton, 2020; MacNulty et al., 2020; Smith et al., 2020). Given the abundance of wolves and cougars and their potential dominating/top-down effects in the system, we assessed two competing hypotheses with respect to mesocarnivore (coyote and red fox) distribution and behavior:

1. Mesocarnivores will avoid apex carnivores, both spatially and temporally, to minimize direct (lethal) risks (*risk aversion hypothesis*).
2. Mesocarnivores will be spatially and temporally attracted to apex carnivores to leverage scavenging opportunities from apex carnivore kills (*facilitation hypothesis*).

These hypotheses might not be mutually exclusive, instead mesocarnivores may employ a mix of proactive and reactive strategies at different spatiotemporal scales that can partially align with both hypotheses (Creel, 2018; Swanson et al., 2014). Furthermore, long-term anecdotes

from Yellowstone suggest that while coyotes and red foxes are killed by both wolves and cougars, the mechanisms of such lethal actions differ. Cougars appear to *hunt* coyotes as prey, while wolves kill them *opportunistically* at ungulate-carcass sites. Thus, the magnitude of risks (versus rewards) for mesocarnivores in this system is expected to differ as a function of the apex carnivore in question, arguably resulting in separate spatiotemporal and behavioral effects. Alternatively, mesocarnivores may not be affected by top-down regulation from apex carnivores, instead their distribution and behavior might be mediated by bottom-up processes such as habitat structure and other eco-geographical covariates (Cano-Martínez et al., 2024). To understand these complex relationships, we estimated spatial overlap, occupancy, diel activity patterns, and fine-scale temporal responses between carnivore detections through winter camera-trapping surveys. We also monitored predation events of GPS-collared wolves and cougars to quantify mesocarnivore scavenging at apex carnivore kills, as well as direct killings of mesocarnivores.

MATERIALS AND METHODS

Study Area

We conducted this study in the Northern Range of Yellowstone National Park (Figure 1). Our study area ranges in elevation between 1500–2400m and includes a mix of rugged and rocky terrain along with open, rolling hills where the common vegetation types are Douglas-fir (*Psuedotsuga menziesii*), sage brush (*Artemisia* spp.), and juniper (*Juniperus* spp.). The area experiences long, cold winters with average snow-water-equivalents ranging from 2–30 cm (Plumb et al., 2009). Wolves, grizzly bears (*Ursus arctos horribilis)*, black bears (*U. americanus*), and cougars exist in relatively high numbers as apex carnivores, while coyotes, red fox, bobcats, and martens (*Martes americana*) form the prominent mesocarnivore strata.

Camera Trap Surveys

Camera surveys were done in a 580-km^2 area delineated by a 5-km buffer around our camera-trap grid that was originally developed to estimate cougar densities. We deployed camera stations in a "checkerboard" pattern (to increase variability in the spacing between stations; Sun et al., 2014) with a grid of 3.2-km^2 cells (Anton, 2020). Within each selected grid cell, we deployed two camera stations at locations chosen to maximize detections, with a minimum distance of 1 km between stations.

Camera stations were active for 15-week winter sampling periods (i.e., sessions) between December and March of 2020-21, 2021-22, and 2022-23 (hereafter 2021, 2022, and 2023, respectively). We used Browning Spec Ops trail cameras with motion-activated passive infrared detectors. During 2021, we deployed 90 cameras across 60 stations, such that half of the stations had one camera while the remaining stations had two opposite-facing cameras. In 2022 and 2023, two cameras were deployed at each station for a total of 120 cameras. Each camera was set for long-range motion detection and recorded 20-second videos with one-minute delays between each recording. We manually examined all videos, classified species, and extracted meta-data using the *timelapse2* image analyzing software (Greenberg et al., 2019).

Data Analysis

Spatial Overlap

We assessed the spatial overlap between the four carnivore species (wolf, cougar, coyote, and red fox) using Pianka's niche overlap index (Pianka, 1973). We calculated the mean relative abundance index (RAI), also known as the photo-capture rate (Carbone et al., 2001) across all three sessions for each species at each camera station. Detections of the same species within 30 minutes of one another were omitted to minimize duplicate records of the same individual

(Tanwar et al., 2021). Camera stations were treated as spatially independent to calculate RAI. Pianka's index measures overlap in space use for each species pair and ranges from 0–1 (Justa & Lyngdoh, 2023; Pianka, 1973). We also ran 100,000 bootstrap samples to generate 95% confidence intervals (CI) around the mean.

Multi-Species Occupancy Models

To evaluate how habitat covariates and spatial interactions with other carnivores influenced the occurrence of apex and mesocarnivores, we constructed multi-species occupancy models (Rota et al., 2016) using the *unmarked R* package (Fiske & Chandler, 2011; R Core Team, 2023). Occupancy models incorporate binary presence-absence (1/0) data through likelihood-based approaches to estimate species occurrence at site *i* in a latent *z* (occupancy) "state" model, while accounting for imperfect detections through a separate "detection" model. Multi-species occupancy models are an extension of the single-species occupancy model (MacKenzie, 2006) that apply a hierarchical modeling framework to estimate the effect of covariates (first-order) and species co-occurrence (second-order) on occupancy.

We used 1-km^2 grid cells for modeling occupancy, with each cell containing no more than one camera station. Because wolves, cougars, coyotes, and potentially red foxes typically occupy ranges larger than 1 km^2, the close spacing of our cameras may violate assumptions of spatial independence. Hence, our occupancy estimates more aptly describe patterns of "space use" rather than distribution (Steenweg et al., 2018). For estimating detection probabilities of each species, we considered three covariates. First, the number of active cameras at a station (ranging from 0–2 as a product of how many cameras were active and for how long during week-long occasions). As the number of active cameras increased, we expected an increase in detection probability. Second, we used ratios of topographic roughness and percent tree cover at

camera stations by dividing fine-scale (30 m) values by the average values from a 1-km^2 buffer around the station for each covariate. For estimating species occupancy, we included three landscape covariates at a 1-km spatial resolution: topographic roughness, percent tree cover, and average snow depth. These habitat covariates were included because they are known to affect the occupancy, movement, and detection of carnivores. Please refer to Table S1 for covariate details.

We used a multi-stage build-up strategy to select the top multi-species occupancy models (Twining et al., 2024) for each of our three sessions. Models only included univariate effects on detection or occupancy, unless multiple covariates had significant effects ($p < 0.05$), at which point we added additional significant covariates (no more than two). We began by constructing single-species models to evaluate which covariates best explained detection probabilities while keeping occupancy as constant ($\Psi(.)$). The top detection models were selected for each species based on the significance of beta estimates and Akaike Information Criterion (AIC), after which we included covariates on occupancy to find the top overall first-order model by again using AIC. After selecting the top first-order model, we added second-order species interactions to develop multi-species models that tested the effects of species co-occurrence on occupancy. Since we were interested in ecological co-occurrence, we elected to report results from the second-order multi-species occupancy models even if they performed worse than the top single-species model. Please refer to Table S3 and S4 for a list and comparison of candidate models.

Temporal Activity Patterns

To maintain independence of detections, photo-captures of the same species within 30 minutes were omitted (Tanwar et al., 2021). We used the *activity* package in R to estimate diel activity patterns for wolves, cougars, coyotes, and red foxes using non-parametric kernel density estimation (Rowcliffe, 2023). To quantify temporal niche partitioning between species and

identify potential coexistence strategies that extend beyond broad-scale occupancy, we used the *overlap* package in R to assess overlap of diel activity patterns between each species-pair (e.g., wolf-coyote, coyote-red fox) by calculating the area under the combined activity curves, $\widehat{\Delta_4}$ (Ridout & Linkie, 2009). We generated 10,000 bootstrap samples of the activity overlap coefficient, $\widehat{\Delta_4}$, for each species-pair to estimate 95% confidence intervals of overlap.

Time-to-event

We examined fine-scale mesocarnivore activity in response to apex carnivore movements using time-to-event analysis (Cusack et al., 2017; Davis et al., 2021). The elapsed time between a mesocarnivore detection following an apex carnivore detection was recorded at each camera station for a given session. Subsequently, we combined data across all sessions for each apex and mesocarnivore pairing. We truncated apex carnivore detections to only include events that were followed by a mesocarnivore detection (i.e., apex carnivore detections followed by another apex carnivore detection were omitted). Detections of mesocarnivores were recorded for 5 days following an apex carnivore detection, with elapsed time differences binned into 24-hour periods. Thereafter, we estimated detection probabilities by dividing the number of mesocarnivore detections in each 24-hour period by the total number of detections across all sessions (Cusack et al., 2017; Davis et al., 2021). These detection probabilities were compared to random iterations (n = 1,000) of mesocarnivore detections to derive expected detection probabilities for each 24-hour period by using standard two-tailed permutation tests (Davis et al., 2021). If the risk aversion hypothesis was true, we would expect coyote and red fox detection probabilities to be significantly lower following an apex carnivore detection. The converse would be in effect if the facilitation hypothesis was true.

Monitoring of Apex Carnivore Predation Events

To assess mesocarnivore scavenging at apex carnivore kills and direct killing of mesocarnivores, we monitored predation by GPS-collared wolves (n = 26 from 8 packs) and cougars (n = 17) during 30-day winter sampling periods (November to March) from 2016–2023. Monitored wolves and cougars were fitted with Vectronics or Telonics GPS-Satellite collars that were programmed to collect hourly fixes. We searched GPS-location clusters (Anderson & Lindzey, 2003) to identify kill sites and conducted necropsies on prey remains. At each kill, we ascertained the likely cause of death, the species, sex, age of prey when possible, and the presence of scavengers through visual observations and sign (e.g., scat, tracks, hair).

RESULTS

Spatial Overlap

Mean spatial overlap between apex and mesocarnivores was 0.57 ± 0.02 for coyote-wolf, 0.24 ± 0.005 for coyote-cougar, 0.67 ± 0.01 for red fox-wolf, and 0.53 ± 0.01 for red fox-cougar across the 3 sessions (Figure 2, Table S2). Overlap between mesocarnivores (red fox-coyote) was relatively high across all sessions (0.54 ± 0.01), while overlap between apex carnivores (wolf-cougar) was comparatively lower (0.33 ± 0.02).

Multi-Species Occupancy Models

Mean naive occupancy across all three sessions was 0.89 for red fox, 0.59 for coyote, 0.59 for wolf, and 0.52 for cougar (Figure 3a). In 2021, the best-performing model had poor convergence with inflated standard errors, possibly due to high naive occupancy estimates (Figure 3a). We re-fitted the top model by imposing an optimized penalty (0.5) on the calculated likelihood through K-fold cross-validation. We acknowledge that adding a likelihood penalty introduces bias to parameter estimates. Therefore, results from the 2021 model should be interpreted with caution. Given this, cover ratio best explained variation in both red fox (β = -

0.19, P = 0.02) and cougar detection probability in 2021 (β = -0.16, P = 0.4). The effect of cover ratio on cougar detections became insignificant when moving from the detection-only model to the full, penalized model. No predictors explained significant variation in coyote or wolf detections. Topographic roughness had a significant positive effect on cougar occupancy probability (β = 1.71, P = 0.001), but there were no covariates that influenced red fox, coyote, or wolf occupancy.

In 2022 (Table S3 and S4, Figure S1), variation in red fox detection probability was best explained by roughness ratio, with red fox detection increasing as roughness ratio increased (β = -0.25, P = 0.09). Cover ratio had a significant, positive effect on coyote detection probability (β = 0.14, P = 0.01) and a negative effect on cougar detection probability (β = -0.11, P = 0.37). Roughness ratio for red fox and cover ratio for cougars had significant effects in the detection-only model. However, these effects on detection became insignificant once occupancy covariates were included in the model. There was no covariate that explained variation in the probability of wolf detection better than the null model. Habitat covariates only helped explain variation in cougar occupancy, while the null model performed best for red fox, coyote, and wolf. Cougar occupancy probability increased as mean snow depth decreased, (β = -0.94, P = 0.05) and roughness increased (β = 1.16, P = 0.04) (Figure S2).

In 2023 (Tables S3 and S4, Figure S1), active cameras were positively-associated (β = 0.63, P = 0.005) and cover ratio was negatively-associated (β = -0.1, P = 0.03) with red fox detection probability. As cover ratio increased, coyote detection probability also increased (β = 0.16, P = 0.007). Roughness ratio had a positive effect on wolf detection probability (β = -0.78, P = 0.002), while active cameras were positively-associated (β = 2.57, P = 0.04) and cover ratio negatively-associated (β = -0.34, P = 0.006) with cougar detection probability. Once again,

covariates only helped explain variation in cougar occupancy, with occupancy probability increasing as roughness increased (β = 1.6, P = 0.007) (Figure S2) and cover decreased (β = -1.1, P = 0.06).

After incorporating second-order species interactions on occupancy, we found that the majority of species occurred independent of each other (Table S5). However, coyote occupancy was conditional on wolf occupancy, with coyote occupancy being significantly higher where wolves were present in 2021 (β = 1.35, P = 0.006) and 2022 (β = 2.3, P = 0.03), and marginally significant in 2023 (β = 1.23, P = 0.07) (Figure 3b). Possibly due to bias from the penalized model in 2021, we also found positive associations between red fox and coyote (β = 1.47, P < 0.0001), red fox and wolf (β = 1.14, P = 0.001), and red fox and cougar (β = 1.2, P = 0.003), and a near significant negative association between coyote and cougar (β = -1.0, P = 0.07).

Temporal Activity Patterns

Cougars (n = 341 detections) exhibited unimodal diel activity, being most active around dusk peaking at 1800 and least active from morning (0800) to midday (1400) (Figure 4). Wolves (n = 443 detections) had bimodal, crepuscular activity patterns, with peak activity shortly after dawn (~0800–0900) and a secondary peak at dusk (1700–1800) (Figure 4). Wolves were least active during midday (~1100–1500). Coyotes (n = 541 detections) had more consistent activity across the diel cycle and were more diurnal, with peak activity occurring from late morning (0900) to midday (1400) and lowest activity before dawn (0500) and after dusk (2100) (Figure 4). Red foxes (n = 1520 detections), on the other hand, exhibited highly nocturnal patterns, being most active shortly after dusk (1800–2100) and sustaining high activity until before dawn (2100–0600) before plummeting to little or no activity during daylight hours (0800–1600) (Figure 4). Temporal overlap between apex and mesocarnivores was $\widehat{\Delta_4}$ = 0.86 (CI: 0.81 – 0.89) for wolf-

coyote, 0.68 (CI: 0.61 – 0.7) for wolf-red fox, 0.81 (CI: 0.74 – 0.85) for cougar-coyote, and 0.72 (CI: 0.66 – 0.76) for cougar-red fox across the three sessions (Figure 4a). Overlap between mesocarnivores (red fox-coyote) was $\widehat{\Delta_4}$ = 0.61 (CI: 0.53 – 0.62), while overlap between apex carnivores (wolf-cougar) was $\widehat{\Delta_4}$ = 0.86 (CI: 0.8 – 0.91) (Figure 4b).

Time-to-event

Compared to the mean values derived from random iterations of detection probabilities, red foxes and coyotes were both over twice as likely to be detected in the 24-hour period following a wolf detection (red foxes: 0.034 compared to 0.015, P = 0.001; coyotes: 0.05 compared to 0.018; P = 0.001; Figure 5). However, their detection probabilities following cougar detections differed. While red foxes were over twice as likely to be detected in the 24-hour period following a cougar detection (0.024 compared to 0.011; P = 0.001), coyote detection rates were not affected. Additionally, red foxes were more likely to be detected in the 72-hour period following a wolf detection (0.01 compared to 0.007; P = 0.04) and the 96-hour period following a cougar detection (0.009 compared to 0.004; P = 0.001). Overall, the time interval between detections of a mesocarnivore subsequent to an apex carnivore detection was shortest for wolf-coyote (median = 17.67 hours) and longest for cougar-coyote (median = 57.35 hours). Foxes showed similar latency to wolf and cougar detections, with medians of 21.11 and 24.69 hours, respectively (Figure 5 b).

Monitoring of Apex Carnivore Predation Events

We detected 327 wolf kills and 257 cougar kills during winter sampling periods. Coyote presence was recorded at 222 (68%) wolf kills and 80 (31%) cougar kills (Figure 6a). Red fox presence was recorded at 67 (20%) wolf kills and 46 (18%) cougar kills (Figure 6a). From this predation monitoring, we documented 18 coyotes and one red fox killed by wolves (Figure 6b).

Of the coyotes killed by wolves, 11 (61%) occurred at wolf feeding sites (i.e., ungulates killed or scavenged by wolves), while the red fox mortality did not occur at a wolf-killed prey site. Cougars killed eight coyotes and three red foxes during this time (Figure 6b). None of these mortalities were associated with cougar-killed prey sites, rather they were fully consumed and generally found in cache piles - suggestive of cougar consumption.

DISCUSSION

Red foxes and coyotes, mesocarnivores that frequently scavenge from wolf and cougar kills, were ubiquitous in our study area (Figure 1). Aside from coyote and wolf overlap with cougars, we found a high degree of spatial overlap between mesocarnivores, as well as apex-mesocarnivore pairs (Figure 2). Our multi-species occupancy models revealed no significant effect of habitat covariates on mesocarnivore occupancy, an unsurprising result given their relatively high naïve occupancy estimates (Figure 3). Our analysis suggests a positive relationship between wolf and coyote occupancy for all years, as well as evidence of negative impacts of cougar occupancy on coyote space-use (Table S4). Notably, coyotes and cougars also had the lowest spatial overlap of all species pairs (Figure 2), indicating a likely avoidance of cougars by coyotes in our system. However, potential pitfalls of this analysis should be considered.

Our camera-trapping study was designed to estimate cougar density rather than apex and mesocarnivore occupancy, leading to camera spacing closer than the average home range size of each species, with the potential exception of red fox (Main et al., 2020). While similar camera spacings have been used to assess occupancy of apex and mesocarnivores (Justa & Lyngdoh, 2023), this may violate assumptions of spatial independence, and hence our results are more indicative of carnivore space-use patterns as opposed to occupancy (Steenweg et al., 2018).

Further, competition between species is often more nuanced than the binary “occupied” versus “unoccupied.” Instead, species may coexist in broad space by mitigating finer-scale overlap in space and time. The fact that each apex and mesocarnivore species was detected at the majority of sites during the course of our study (Figure 1) supports this notion and further demonstrates the limitations of using occupancy analysis to study species interactions in saturated systems. These analytical constraints, however, do not limit the scope of our conclusions which are drawn at a very high resolution of space use for most of the species. In fact, they provide stronger support for the saturation of this system. As such, fine-scale temporal approaches were required to disentangle these complex intra-guild relationships.

Despite having considerable temporal overlap with wolves and cougars, diel activity plots indicated that coyotes were most active mid-day when apex carnivores were collectively the least active in our study area (Figure 4). This peak in activity differs from those of coyotes inhabiting adjacent areas of the Greater Yellowstone Ecosystem with lower apex carnivore densities, where coyotes were found to be more active in the early morning and at night (Smith et al., 2023). In contrast, red foxes appeared less sensitive to the diel activity of apex carnivores. Not only did their peak in activity closely align with that of cougars, but they also displayed the same nocturnal patterns as red foxes across the Greater Yellowstone Ecosystem (Smith et al., 2023). However, red foxes exhibited high temporal segregation from coyotes which was evident in having the lowest temporal overlap of any species pair (Figure 4). Studies elsewhere have shown that coyotes and red foxes compete severely, with coyotes competitively excluding and/or killing red foxes (Fedriani et al., 2000; Levi & Wilmers, 2012). Thus, the nocturnal activity of red foxes might also be to avoid coyote peak activity during the day that is in turn modulated by wolf and

cougar activity (Figure 4). Temporal sympatry amongst the carnivore guild appears to be layered with apex carnivores affecting coyotes, and coyotes affecting red foxes.

Our findings add to a growing body of work that demonstrate how inferences concerning apex and mesocarnivore interactions depend on the spatiotemporal scale at which analyses are conducted. For example, Prugh et al. (2023) found that coyotes avoided areas with greater wolf utilization when using step-selection analyses. Mesocarnivores may indeed avoid possible encounters with apex carnivores when moving throughout their landscape, yet scavenging opportunities from apex carnivore kills likely drive temporary attraction. In our study, both coyote and red fox detection probabilities at camera stations doubled in the 24 hours following wolf detections (Figure 5), and this pattern also held true for red fox detections following cougars. In conjunction with frequent mesocarnivore scavenging signs recorded at wolf and cougar kill sites (Figure 6a), these results suggest that the benefits from such scavenging opportunities perhaps facilitate broad mesocarnivore space-use despite high densities of apex carnivores in our study area.

It is, however, noteworthy that coyote detection probabilities were not affected by cougar detections. This possible lack of attraction is corroborated by our occupancy and temporal activity results that collectively indicate coyotes exhibit some proactive avoidance of cougars. Additionally, our predation monitoring provides evidence of cougars killing and consuming coyotes, a key distinction from wolves that typically kill, but do not consume coyotes attempting to scavenge from their kills (Figure 6b). Based on our results and relevant earlier research from the study system (Ruth et al., 2019), we propose that coyote avoidance of cougars could be a result of coyotes serving as prey for cougars in addition to being a competitor, thereby facing higher risks. This is unlike coyote-wolf interactions, where coyotes are only a competitor of

wolves. Furthermore, the ambush hunting style of cougars, combined with the forested and topographically rough terrain they inhabit, could lead to coyotes being more vulnerable in those habitats and/or at cougar kill sites (Perrig et al., 2023). In contrast, the open and flatter terrain preferred by wolves could provide more visual and olfactory cues for coyotes to assess (and escape) immediate risks of lethal encounters. Such disparate risk-effects might have also manifested in coyote-scavenging to be over twice as prevalent at wolf kills than cougar kills in our study area (Figure 6a).

Red fox detection probabilities were affected by both wolf and cougar detections, suggesting attraction to apex carnivore movements. Coupled with their highly nocturnal activity that is offset from peak coyote activity, these patterns suggest foxes may be operating along a risk-reward continuum to seek scavenging opportunities from apex carnivore kills while minimizing exposure to competitively-dominant coyotes. While relatively few fox mortalities were detected through monitoring apex carnivore predation, we speculate similar relationships as with coyotes; foxes are more likely to be preyed upon and consumed by cougars, whereas risk from wolves is based on resource competition. Yet, foxes exhibited more attraction to cougars compared to coyotes, indicating that they may be more adept at avoiding immediate risks of cougar predation. Owing to their relatively large foot:body ratio, foxes are better at maneuvering on top of snow (Van Etten et al., 2007), possibly explaining their increased ability to escape cougar predation.

The availability of alternative resources may also influence these relationships. The limitations of prey acquisition during winter months may increase mesocarnivore reliance on scavenging opportunities (Jensen et al., 2022; Smith et al., 2023). However, lower detections of fox sign at wolf and cougar kills in winter compared to coyotes suggests foxes may be able to

meet energetic demands from alternative food sources, presumably due to their smaller body size. For example, compared to coyotes and wolves, foxes in the study area are more commonly observed hunting subnivean rodents by pouncing through the snowpack during the winter (D. Stahler *pers.comm.*). Therefore, the facilitative relationship between apex and mesocarnivores through carcass scavenging might not be even between coyotes and foxes, nor as strong for both in the summer/spring when rodent availability increases, as well as ungulate neonates, vegetation, and insects (Jensen et al., 2022). Also, the presence of grizzly and black bears that emerge in the summer after winter-long hibernations can complicate these relationships because bears often limit carrion consumption for other scavengers (Allen et al., 2014). Collectively, these factors demonstrate how multi-carnivore interactions often depend on both the availability and necessity of scavenging opportunities.

Notably, while our study highlights the positive aspects of apex and mesocarnivore interactions, we did not explore variations in red fox and coyote population trends. In fact, previous research documented a 39% decline in coyote abundance following wolf reintroduction in the Lamar Valley of Yellowstone, an area adjacent to the study area (Berger & Gese, 2007). Additionally, Merkle et al. (2009) showed a decrease in wolf-coyote interactions over time (between 1997 and 2007) in our study area, indicative of changes to coyote density and/or behavior (e.g., wolf avoidance). In NE Oregon, coyotes balanced high scavenging rates from cougar's kills with high predation rates, as cougars were responsible for 23% of coyote mortalities (Ruprecht et al., 2021). Despite benefiting from carrion made available by wolves and cougars, red fox and coyote populations may experience top-down regulation via direct killing that maintain their populations at low densities (Sinclair, 2003). Long-term studies that estimate

population trends of mesocarnivores with respect to apex carnivore densities are required to test such effects.

The magnitude and impact of trophic-mediated responses related to large carnivore recoveries have become a contentious issue, perhaps nowhere more so than in Yellowstone National Park (Brice et al., 2022; Hobbs et al., 2024; Ripple & Beschta, 2012). The reintroduction of wolves and recolonization of cougars to this area likely changed mesocarnivore distributions and abundance, yet the resulting populations of red foxes and coyotes may have also benefited from living with their dominant counterparts. Overall, red foxes and coyotes in our study area exhibited more attraction than avoidance to apex carnivores during winter months, when small prey and alternative food resources are scant. Such attraction, possibly a consequence of desperate foraging decisions in winter, can also prove fatal. However, risks to mesocarnivores are uneven across dominant-subordinate carnivore pairings, with apex carnivore behavior adding nuance to the *landscape of fear* for mesocarnivores, a novel insight from our study. Mesocarnivores appear to walk a thin line between the risks and rewards of associating with their dominant counterparts, which in turn is governed by the spatiotemporal dispersion of resources and inter-carnivore relationships. Our results showcase the complexity of interspecific relationships within a rich carnivore guild, and highlight key trophic links that can promote community resilience in the wake of rapidly changing ecological conditions in the Anthropocene.

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Figure 1 | Locations of camera stations, gradient of habitat covariates, and photo-capture rates of mesocarnivores (red fox = red, coyote = blue) and apex carnivores (wolf = green, cougar = pink) in northern Yellowstone National Park, USA.

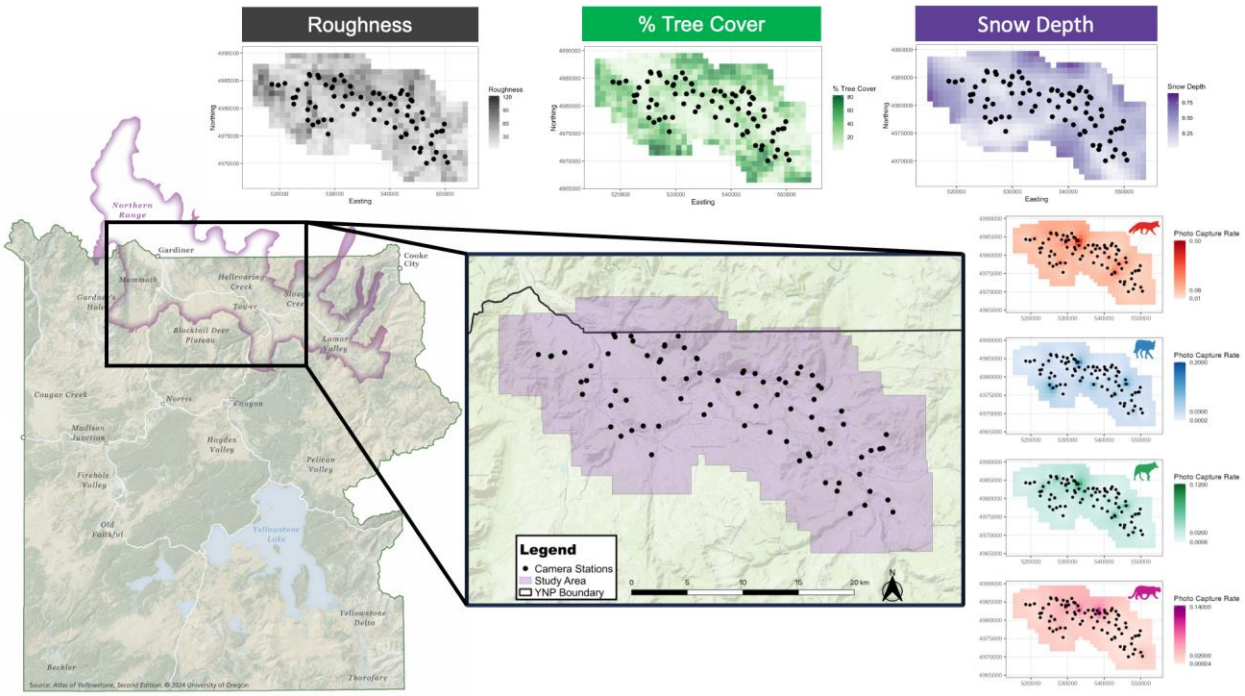


Figure 2 | Pairwise comparisons of Pianka's spatial index overlap for study species, computed from detections at camera stations. Estimates are yearly means and 95% CIs.

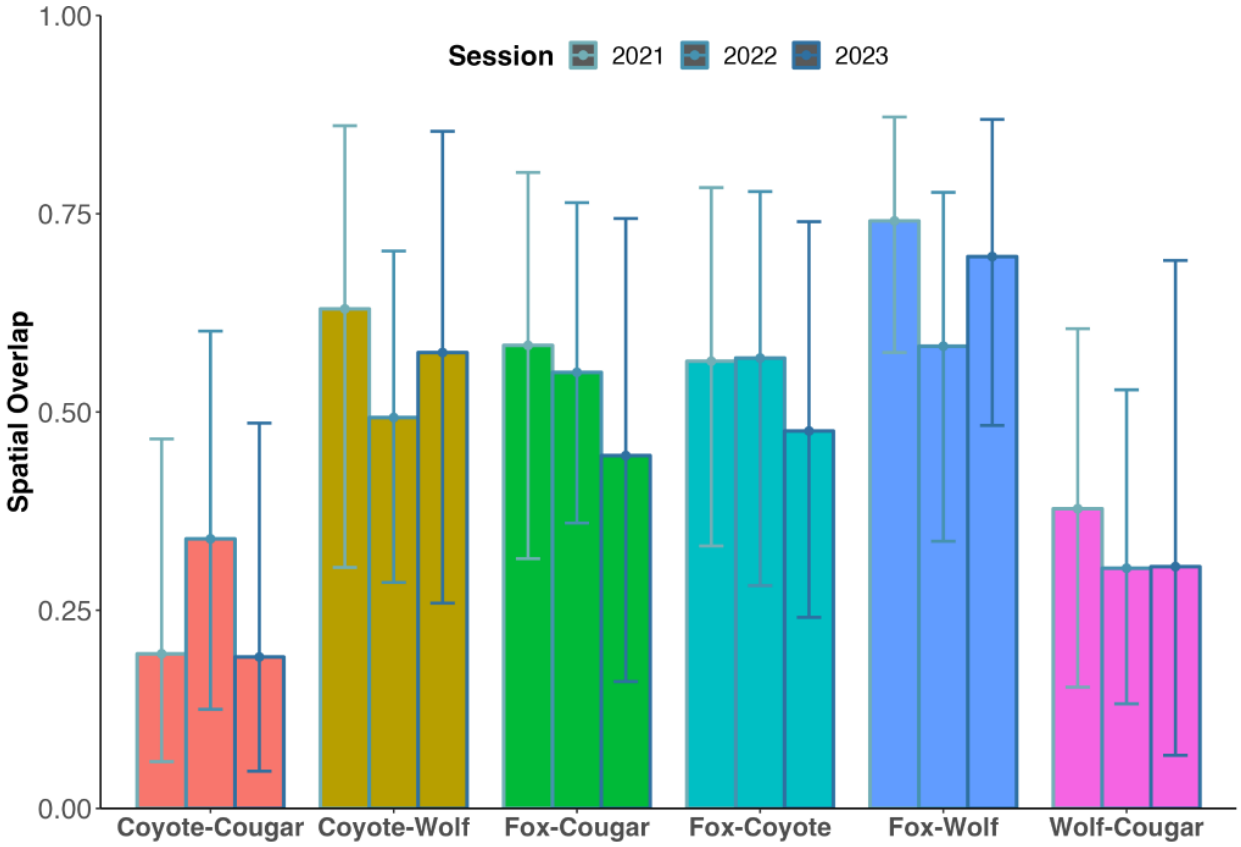


Figure 3 | (a) Apex and mesocarnivore naive occupancy probabilities estimated from camera trapping surveys between 2021–2023. **(b)** Coyote occupancy probability for 2021–2023, conditional on wolf presence-absence. Conditional occupancy was based on the best-supported, second-order multi-species occupancy model for each session.

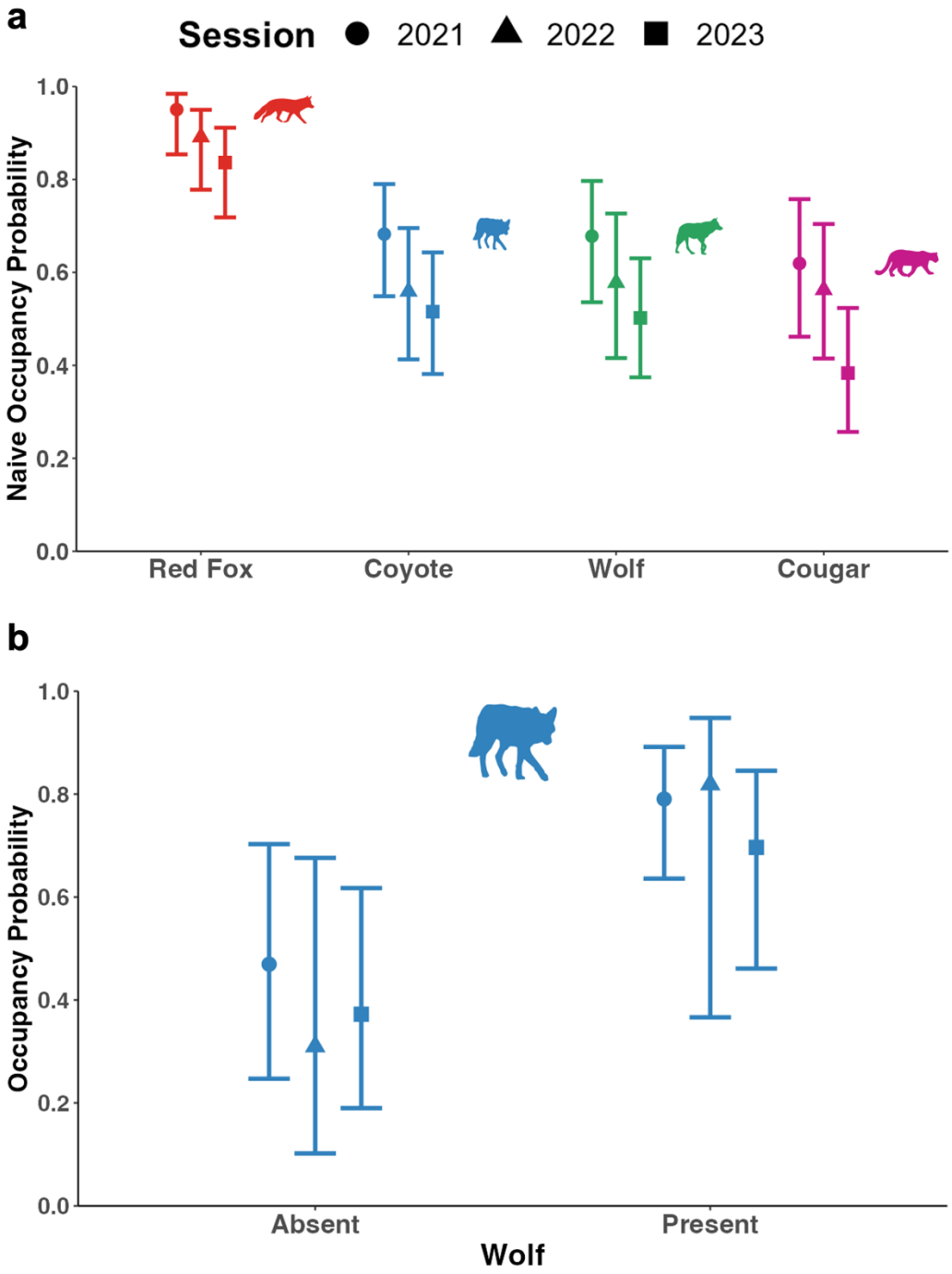


Figure 4 | Diel activity patterns with 95% bootstrapped CIs for study carnivores. Mean activity overlap **(a)** between apex and mesocarnivores, and **(b)** between apex carnivores and between mesocarnivores.

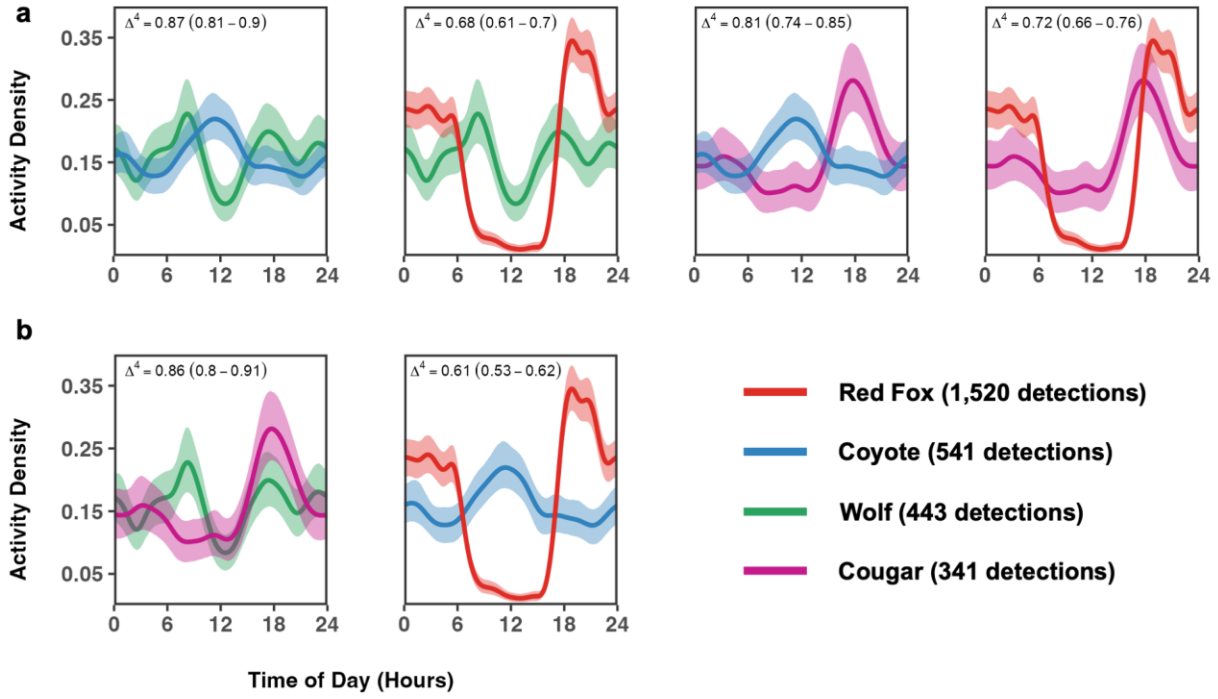
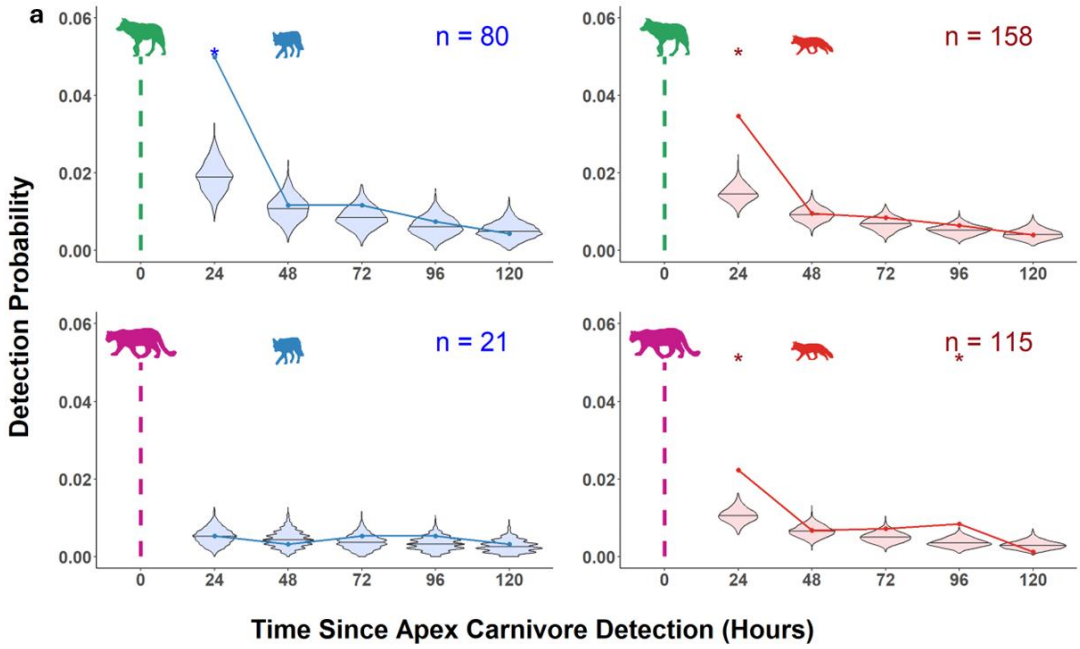


Figure 5 | (a) Daily binned temporal attraction-avoidance of mesocarnivores in response to apex carnivore detections at camera stations. Apex-mesocarnivore pairs include wolf-coyote (top-left), wolf-red fox (top-right), cougar-coyote (bottom-left), and cougar-red fox (bottom-right). Points and lines represent observed mesocarnivore detection probabilities, while violin plots show the distribution of expected mesocarnivore detection probabilities based on random movements (i.e., no attraction or avoidance). *denotes significant differences between observed and expected detection probabilities. **(b)** Median time differences of mesocarnivore detections following apex carnivore detections.



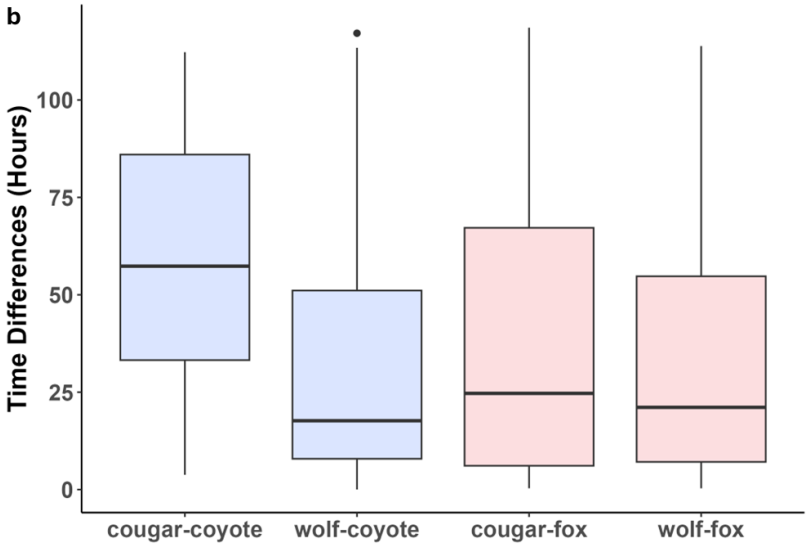
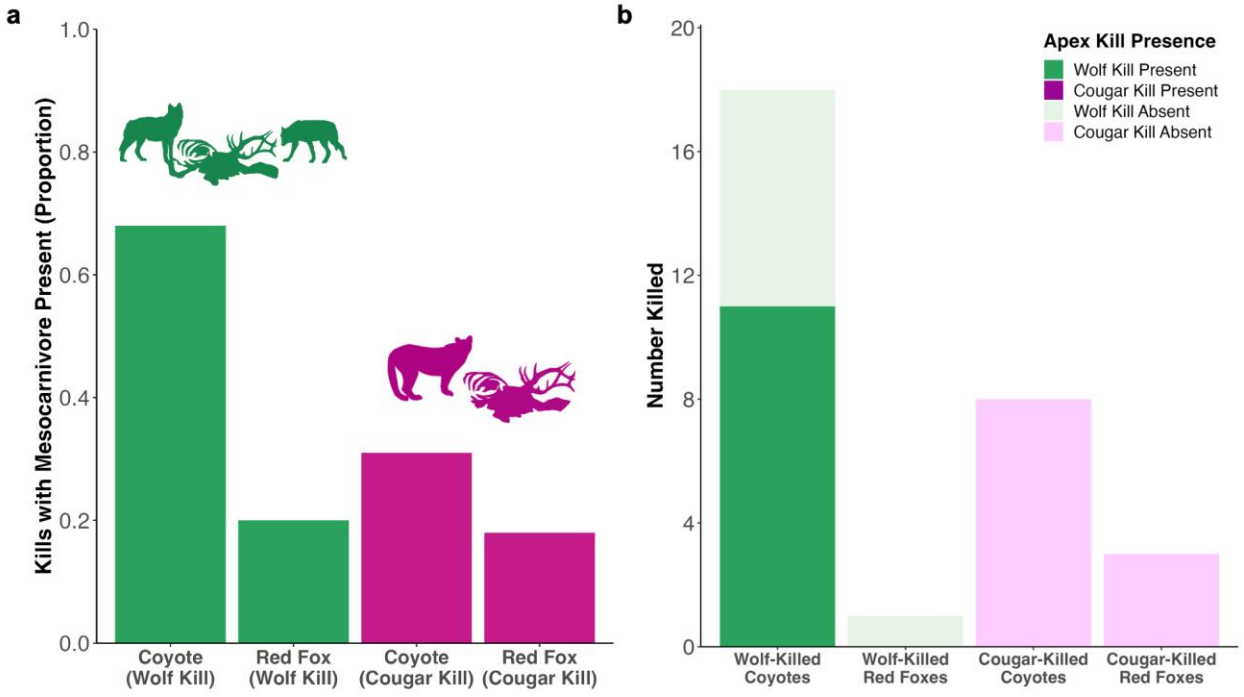


Figure 6 | Wolf (n = 327) and cougar (n = 257) kills, surveyed through GPS-cluster searches of collared wolves and cougars between 2016-2023, bearing **a)** presence of coyote and red fox scavenging expressed as a proportion, and **b**) counts of coyote and red fox killed. For methods see main text. Wolf and elk carcass graphics by Kira Cassidy.



SUPPLEMENTARY INFORMATION FOR:

Title: Species-specific interactions with apex carnivores yield unique benefits and burdens for mesocarnivores

Table S1: Covariate List for Detection and Occupancy Models & their Description and sources

Occupancy Covariates		
Variable	**Type, Range**	**Description**
Cover	Continuous	Values accrued from the Rangeland Analysis Platform's (RAP) annual percent tree cover landsat satellite data (Robinson et al., 2019). Originally at 30-m spatial resolution but aggregated to 1 km. We used the cover value associated with the cell that a given camera station lies within.
Topographic Roughness	Continuous	Values represent the sum of the absolute value of the difference in elevation between each grid cell and its surrounding eight neighbors (3 x 3 window) (Kohl et al., 2019; Ruth et al., 2019). A value of 0 represents a flat surface while the maximum value represents the roughest terrain in the study area. Originally at 30-m spatial resolution but aggregated to 1 km. We used the roughness value associated with the cell that a given camera station lies within.
Photo Capture Rates	Continuous	Number of independent photographs of a species captured at a camera station divided by the total number of operational camera days. We used photo-captures for each species of interest segregated by sessions.
Snow Depth	Continuous	Daily snow depth data at 1-km grid cell accrued from SNODAS. We used the average value of all days within each session, so that snow depth values in a grid varied between but not within sessions.
Detection Covariates		
Cover Ratio	Continuous	Values accrued from the Rangeland Analysis Platform's (RAP) annual percent tree cover landsat satellite data (Robinson et al., 2019), originally at 30 m spatial resolution. We used the 30 m cover value at a given camera station and divided it by the mean cover within a 1-km buffer around that camera station. High values indicate a large difference between cover at the camera station relative to the surrounding landscape
Topographic Roughness Ratio	Continuous	We used the 30-m roughness value (Kohl et al., 2019) at a given camera station and divided it by the mean roughness within a 1-km buffer around that camera station. High values indicate a large difference between roughness at the camera station relative to the broader surrounding landscape and may be suggestive of a "pinch point" that funnels wildlife through it.
Number of Cameras	Continuous, Range: 0-2	Number of active/operational cameras at a given station.

Table S2 | Pianka's spatial overlap index for each species pairwise comparison during each session.

	2021			2022			2023		
Species Pair	**Mean**	**SE**	**95% CI**	**Mean**	**SE**	**95% CI**	**Mean**	**SE**	**95% CI**
Red Fox – Coyote	0.56	0.12	0.33 – 0.78	0.57	0.13	0.28 – 0.78	0.48	0.14	0.24 – 0.74
Red Fox – Wolf	0.74	0.08	0.58 – 0.87	0.58	0.11	0.34 – 0.78	0.7	0.1	0.48 – 0.87
Red Fox – Cougar	0.58	0.13	0.32 – 0.8	0.55	0.11	0.36 – 0.76	0.45	0.16	0.16 – 0.74
Coyote – Wolf	0.63	0.15	0.30 – 0.86	0.49	0.11	0.29 – 0.7	0.58	0.17	0.26 – 0.85
Coyote – Cougar	0.2	0.11	0.06 – 0.47	0.34	0.12	0.13 – 0.6	0.19	0.11	0.05 – 0.49
Wolf – Cougar	0.38	0.13	0.15 – 0.61	0.3	0.1	0.13 – 0.53	0.31	0.16	0.07 – 0.69

Table S3 | Detection and occupancy covariates in the best-supported first-order models for red fox, coyote, wolf, and cougar in each session.

Session-Species	Detection model (p)	Top occupancy model (Ψ)
2021		
Red Fox	*Cover ratio*	*Null*
Coyote	*Null*	*Null*
Wolf	*Null*	*Null*
Cougar	*Cover ratio*	*Roughness*
2022		
Red Fox	*Roughness ratio*	*Null*
Coyote	*Cover ratio*	*Null*
Wolf	*Null*	*Null*
Cougar	*Cover ratio*	*Snow depth + Roughness*
2023		
Red Fox	*Active cameras + Cover ratio*	*Null*
Coyote	*Cover ratio*	*Null*
Wolf	*Roughness ratio*	*Null*
Cougar	*Active cameras + Cover ratio*	*Cover + Roughness*

Table S4 | AIC model comparison for all candidate first- and second-order multi-species occupancy models considered during each session. Bolded rows indicate selected models that we reported results for. K = number of model parameters, AIC = Akaike Information Criterion, ΔAIC = difference in AIC from the top model.

Model	K	AIC	ΔAIC	AIC_{weight}
2021				
First-Order Detection + Occupancy	11	2870.8	0	0.54
Second-Order Detection Only	16	2871.5	0.7	0.39
Second-Order Detection + Occupancy (Penalized)	**17**	**2875**	**4.2**	**0.067**
First Order Detection Only	10	2885.7	14.9	0.0003
Second-Order Null	14	2889.3	18.5	5.2E-05
First-Order Null	8	2903.3	32.4	4.9E-08
2022				
Second-Order Detection + Occupancy	**19**	**2300**	**0**	**0.78**
First-Order Detection + Occupancy	13	2302.7	2.7	0.21
Second-Order Detection Only	17	2308.3	8.3	0.012
First Order Detection Only	11	2310.6	10.6	0.004
Second-Order Null	14	2314.8	14.8	0.0005
First-Order Null	8	2316.6	16.6	0.0002
2023				
Second-Order Detection + Occupancy	**22**	**2327.6**	**0**	**0.57**
First-Order Detection + Occupancy	16	2328.2	0.6	0.43
Second-Order Detection Only	20	2341.2	13.6	0.0007
First Order Detection Only	14	2344.3	16.7	0.0001
Second-Order Null	14	2376.4	48.7	1.5E-11
First-Order Null	8	2380.1	52.5	2.3E-12

Table S5 | Beta coefficient estimates for detection and occupancy covariates retained in the top second-order multi-species occupancy model for each session.

Detection model (p)					Occupancy model (Ψ)				
[Species] Covariate	***β***	**SE**	***z***	***P***	**[Species] Covariate**	***β***	**SE**	***z***	***P***
2021									
[redfox] (Intercept)	-0.29	0.26	-1.14	0.253	[redfox] (Intercept)	0.78	0.58	1.35	0.178
[redfox] cover ratio	-0.19	0.08	-2.27	0.023	[coyote] (Intercept)	-0.79	0.39	-2.01	0.045
[coyote] (Intercept)	-1.11	0.20	-5.52	3.3E-08	[wolf] (Intercept)	-1.09	0.39	-2.83	0.005
[wolf] (Intercept)	-1.56	0.18	-8.45	3.0E-17	[cougar] (Intercept)	0.45	0.57	0.78	0.433
[cougar] (Intercept)	-1.54	0.39	-3.91	9.2E-05	[cougar] scale(roughness)	1.71	0.52	3.32	0.001
[cougar] cover ratio	-0.16	0.17	-0.92	0.357	[redfox:coyote] (Intercept)	1.47	0.31	4.68	2.9E-06
					[redfox:wolf] (Intercept)	1.14	0.34	3.33	0.001
					[redfox:cougar] (Intercept)	1.20	0.40	2.96	0.003
					[coyote:wolf] (Intercept)	1.35	0.49	2.74	0.006
					[coyote:cougar] (Intercept)	-1.00	0.55	-1.81	0.071
					[wolf:cougar] (Intercept)	-0.10	0.51	-0.19	0.847
2022									
[redfox] (Intercept)	-0.67	0.20	-3.33	8.7E-04	[redfox] (Intercept)	0.51	0.88	0.58	0.561
[redfox] roughness ratio	-0.25	0.15	-1.71	0.088	[coyote] (Intercept)	-1.32	1.69	-0.79	0.432
[coyote] (Intercept)	-2.33	0.28	-8.20	2.3E-16	[wolf] (Intercept)	-1.39	1.71	-0.81	0.417
[coyote] cover ratio	0.14	0.06	2.44	0.015	[cougar] (Intercept)	-2.04	2.44	-0.84	0.402
[wolf] (Intercept)	-2.03	0.18	11.49	1.5E-30	[cougar] scale(snow depth)	-0.94	0.49	-1.92	0.055
[cougar] (Intercept)	-1.64	0.28	-5.92	3.2E-09	[cougar] scale(roughness)	1.16	0.57	2.04	0.042
[cougar] cover ratio	-0.11	0.12	-0.90	0.369	[redfox:coyote] (Intercept)	0.51	1.80	0.28	0.778
					[redfox:wolf] (Intercept)	0.78	1.78	0.44	0.660
					[redfox:cougar] (Intercept)	3.04	2.41	1.26	0.208
					[coyote:wolf] (Intercept)	2.30	1.06	2.16	0.031
					[coyote:cougar] (Intercept)	0.07	1.08	0.06	0.949
					[wolf:cougar] (Intercept)	-0.54	1.12	-0.48	0.629
2023									
[redfox] (Intercept)	-1.57	0.43	-3.69	2.2E-04	[redfox] (Intercept)	0.37	0.55	0.68	0.497
[redfox] active cameras	0.63	0.22	2.80	0.005	[coyote] (Intercept)	-1.16	0.78	-1.48	0.138
[redfox] cover ratio	-0.11	0.05	-2.20	0.028	[wolf] (Intercept)	-1.69	0.94	-1.81	0.070
[coyote] (Intercept)	-1.73	0.23	-7.38	1.6E-13	[cougar] (Intercept)	-2.27	1.19	-1.92	0.055
[coyote] cover ratio	0.16	0.06	2.69	0.007	[cougar] scale(roughness)	1.60	0.59	2.69	0.007
[wolf] (Intercept)	-0.52	0.27	-1.89	0.058	[cougar] scale(cover)	-1.10	0.59	-1.87	0.061
[wolf] roughness ratio	-0.78	0.26	-3.03	0.002	[redfox:coyote] (Intercept)	0.55	0.87	0.64	0.525
[cougar] (Intercept)	-6.06	2.46	-2.47	0.014	[redfox:wolf] (Intercept)	1.23	0.97	1.27	0.205
[cougar] active cameras	2.57	1.23	2.09	0.036	[redfox:cougar] (Intercept)	1.74	1.17	1.49	0.137
[cougar] cover ratio	-0.34	0.12	-2.74	0.006	[coyote:wolf] (Intercept)	1.23	0.67	1.84	0.066
					[coyote:cougar] (Intercept)	0.34	0.74	0.46	0.648
					[wolf:cougar] (Intercept)	0.36	0.77	0.47	0.637

Figure S1 | Detection probabilities for each species as a function of covariates retained in the top second-order multi-species occupancy model for each session. Shaded regions are 95% confidence intervals.

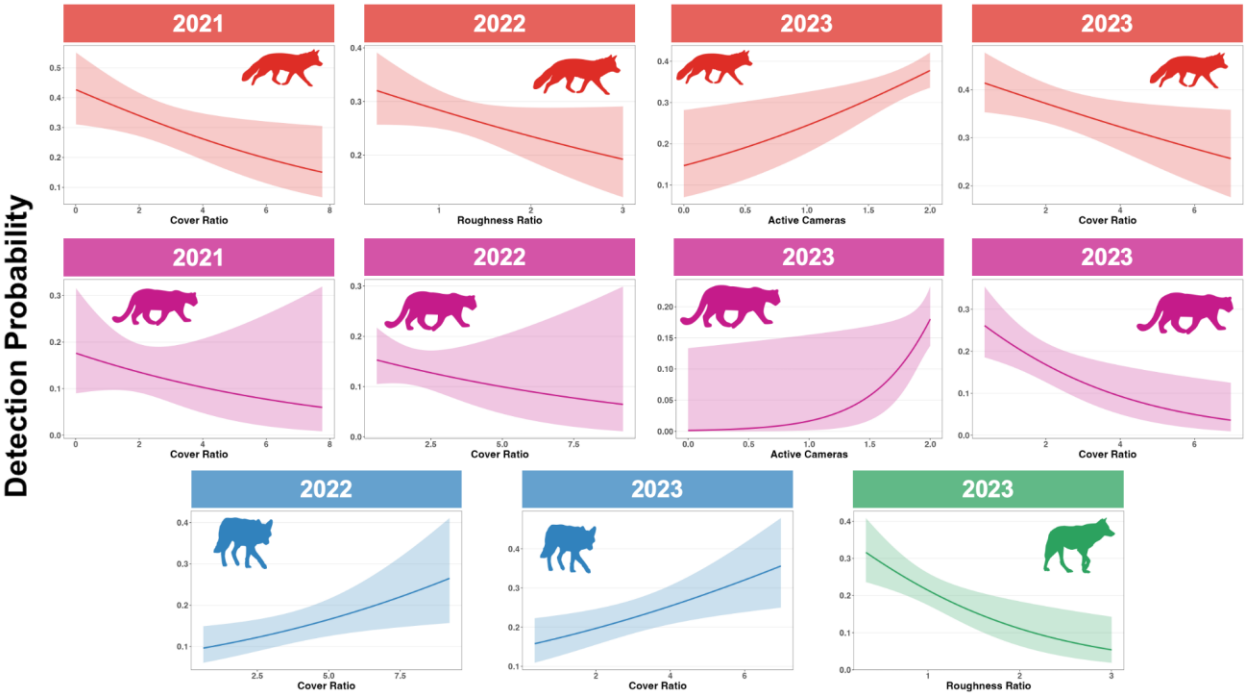
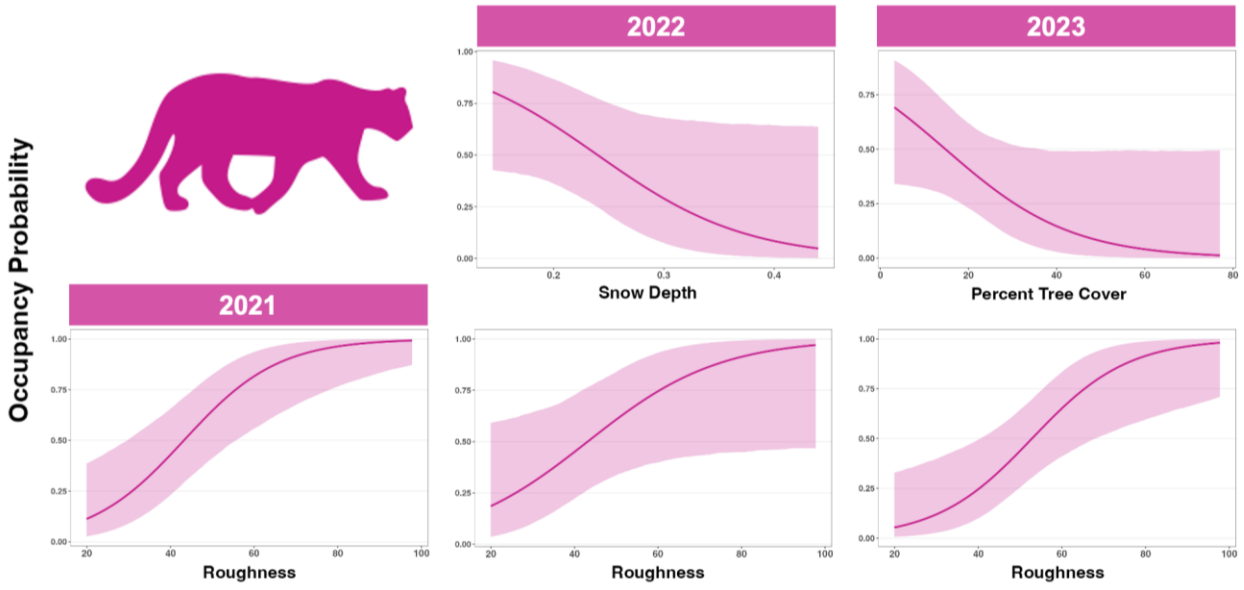


Figure S2 | Marginal occupancy probability for cougar as a function of habitat covariates retained in the top second-order multi-species occupancy model for each session. Shaded regions are 95% confidence intervals.



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