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ORIGINAL RESEARCH

Mesocarnivores vary in their spatiotemporal avoidance strategies at communications hubs of an apex carnivore

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Abstract
Mesocarnivores face interspecific competition and risk intraguild predation when sharing resources with apex carnivores. Within a landscape, carnivores across trophic levels may use the same communication hubs, which provide a mix of risks (injury/death) and rewards (gaining information) for subordinate species. We predicted that mesocarnivores would employ different strategies to avoid apex carnivores at shared communication hubs, depending on their trophic position. To test our prediction, we examined how different subordinate carnivore species in the Santa Cruz Mountains of California, USA, manage spatial overlap with pumas (*Puma concolor*), both at communication hubs and across a landscape-level camera trap array. We estimated species-specific occurrence, visitation rates, temporal overlap, and Avoidance–Attraction Ratios from camera traps and tested for differences between the two types of sites. We found that mesocarnivores generally avoided pumas at communication hubs, and this became more pronounced when pumas scent-marked during their most recent visit. Coyotes (*Canis latrans*), the pumas' closest subordinate competitor in our system, exhibited the strongest avoidance at communication hubs. Gray foxes (*Urocyon cinereoargenteus*) avoided pumas the least, which may suggest possible benefits from pumas suppressing coyotes. Overall, mesocarnivores exhibited various spatiotemporal avoidance strategies at communication hubs rather than outright avoidance, likely because they benefit from information gained while 'eavesdropping' on puma activity. Variability in avoidance strategies may be due to differential predation risks, as apex carnivores often interact more aggressively with their closest competitors. Combined, our results show how apex carnivores trigger complex species interactions across the entire carnivore guild and how trophic position determines behavioral responses and subsequent space use of subordinate mesocarnivores across the landscape.

Keywords Avoidance · Competition · *Puma concolor* · Scent-marking · Trophic interactions

Introduction

Apex carnivores usually occur at low population densities but often have disproportionate effects on their ecological communities (Estes et al. 2011; Ripple et al. 2014). As keystone species (species upon which other species depend and whose removal would lead to drastic changes in the ecosystem), apex carnivores structure ecosystems directly through predation and indirectly by causing behavioral changes in both prey and competitors (Brown et al. 1999; Ripple et al. 2014; Davis et al. 2018). Despite the risk of predation and antagonistic interactions with apex carnivores, smaller carnivores (hereafter 'mesocarnivores') are often attracted to apex carnivore activity. For example, mesocarnivores frequently scavenge from kills provided by apex carnivores (Allen et al. 2015a; Prugh and Sivy 2020) as the nutritional benefits apparently outweigh the risk of injury or death. While

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the effect of apex carnivores on specific species have been relatively well studied, their guild-wide impacts in a given system often remain unclear. Specifically, it is unknown whether mesocarnivore responses to apex carnivores can be best predicted simply by trophic position versus species-specific characteristics based on distinct foraging strategies and other traits.

Animals provide and receive information (i.e., communication) to help them assess their relationships with both other animals and their environment (Smith et al. 1989; Harmsen et al. 2010; Apps et al. 2019). Many carnivores communicate with conspecifics via scent marking, often at communication hubs that are used by multiple species (Allen et al. 2017; Apps et al. 2019). Carnivores use scent marking to assess and attract mates, as well as delineate territorial boundaries and resource use (Smith et al. 1989; Krofel et al. 2017; Cornhill and Kerley 2020a; Rafiq et al. 2020). Solitary carnivores often use scent marking as their primary means of communication due to their relatively low frequency of direct interactions with conspecifics (Harmsen et al. 2010; Allen et al. 2014; Cornhill and Kerley 2020a), highlighting the importance of communication hubs in structuring populations.

While scent marks may primarily function as signals to conspecifics, other species will also receive and use the information conveyed (Harmsen et al. 2010; Allen et al. 2017; Apps et al. 2019; Cornhill and Kerley 2020b). Mesocarnivores regularly visit and scent-mark at the same communication hubs as apex carnivores (Li et al. 2013; Allen et al. 2017; Apps et al. 2019; Cornhill and Kerley 2020b), despite the risk of encountering larger carnivores. By 'eavesdropping' on communication of larger carnivores, mesocarnivores likely benefit by acquiring information conveyed by intra- and interspecific scent marks, and by leaving their own scent marks in prominent areas for conspecifics and possibly other carnivores (Hughes et al. 2010; Garvey et al. 2016). Specifically, by visiting these communication hubs, mesocarnivores can gain valuable information on the location of food and other resources (Apps et al. 2019) as well as the proximity to specific individual apex carnivores (Garvey et al. 2016). By scent marking at the same sites as apex carnivores, mesocarnivores can signal their continued use of an area to conspecifics, or possibly cancel out the signals of conspecifics that they over-mark. The signals left by subordinate mesocarnivores may attract unwanted attention from dominant species, however, and increase the risk of an individual of getting injured or killed (Hughes et al. 2010; Moller et al. 2011). As such, scent marking at communication hubs likely entails attraction and avoidance among carnivore species, and the risks and rewards may vary for both the individuals and species involved. While this type of interspecific communication is likely common (e.g., Apps et al. 2019), we lack an understanding of the benefits gained by subordinate species and the behavioral strategies they use to limit risk from interactions with the rest of the carnivore guild at these sites.

Pumas (*Puma concolor*) are keystone apex carnivores that provide other species with carrion (Elbroch and Wittmer 2012; Allen et al. 2015a). Pumas are also solitary and primarily communicate with conspecifics via scent marking at communication hubs (often called 'community scrapes'; Allen et al. 2014), and these sites are regularly visited and used by subordinate carnivores (Allen et al. 2015b, 2017; Jackson et al. 2021). While mesocarnivores normally exhibit complex spatial and temporal avoidance of apex carnivores (e.g., Prugh et al. 2023), their willingness to visit communication hubs shared with pumas suggests the benefits of receiving information outweigh the risks. To date, however, it remains unknown if mesocarnivores are attracted specifically to the scent communication hubs or puma activity in general.

We examined how mesocarnivores respond to puma occurrence and visitation at known communication hubs and how this compared to their responses at landscape-level sites. We predicted that mesocarnivores would employ both spatial and temporal avoidance strategies to mitigate potentially lethal encounters at the landscape level, but that they would relax this avoidance at communication hubs to take advantage of information provided by pumas via scent marks. We also predicted that species with higher trophic positions (e.g.., coyotes [*Canis latrans*] and bobcats [*Lynx rufus*]), would better predict a greater avoidance of pumas than other species, both at communication hubs and landscape-level sites. Finally, we predicted that smaller carnivores would take advantage of the suppression of larger mesocarnivores and exhibit more attraction to pumas at both types of sites. To test our predictions, we deployed camera traps and documented multiple variables (occurrence, visitation, Avoidance–Attraction Ratios, and temporal overlap) by pumas and mesocarnivores at communication hubs and across our landscape-level array.

Materials and methods

Study area

We conducted our study in the Santa Cruz Mountains of California, USA (37° 10′ N, 122° 3′ W; Fig. 1). The study area (approximately 1700 km^2) is bounded by the Pacific Ocean to the west and California Highway 101 to the east, with elevation ranging from sea level to 1,155 m. The Santa Cruz Mountains encompass a spectrum of heavy human development and wild protected lands (managed by state, county, and city parks as well as private entities), creating a mosaic of land use where building density ranges from 0

Fig. 1 A map of the study area in the Santa Cruz Mountains, California, with the locations of camera traps at communication hubs shown as yellow stars and landscape-level camera traps across the study area shown as *blue squares*

to 9884 housing units per km^2 and 1/3 of the landscape falls within the wildland–urban interface (Yovovich et al. 2020). The major metropolitan areas of San Francisco and San Jose lie to the north and northwest, respectively, and the study area is divided by California Highway 17, which is a major cause of mortality for pumas (Wilmers et al. 2013) and other wildlife. The climate in the study area is characterized as Mediterranean with wet and dry seasons, with average daily high temperatures ranging from 15.5 to 24.4 °C, and most rainfall occurring between November and April (Wilmers et al. 2013).

The Santa Cruz Mountains provide habitat for a diverse carnivore community that differ in trophic position and body size. Pumas, the dominant carnivore species, co-occur with seven other mesocarnivores: coyotes, bobcats, American badgers (*Taxidea taxus*), non-native red foxes (*Vulpes vulpes*), gray foxes (*Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and Western spotted skunks (*Spilogale gracilis*). Many of these mesocarnivores are known to use and scent-mark at the communication hubs used by pumas (Allen et al. 2015b, 2017; Jackson et al. 2021).

Field methods

We primarily documented locations of communication hubs (e.g., community scrapes) in the Santa Cruz Mountains using GPS data from collared male pumas (see Wilmers et al. 2013). We also opportunistically documented additional communication hubs while performing other field work (Allen et al. 2014). We monitored visitation to 26 spatially independent (>1 km from each other) communication hubs (Fig. 1) by pumas and mesocarnivores using video camera traps with infrared flash (Bushnell TrophyCam, Overland Park, KS) from December 2010 to May 2016. We programmed camera traps to record a 60 s video when triggered with a 1 s delay before becoming active again. Camera traps were active for a mean of 991 (±83 SE) days.

We also established an array of 100 potential camera trap sites (Bushnell TrophyCam, Overland Park, KS) that encompassed the mosaic of habitats across the Santa Cruz Mountains from February 2015 to October 2020. The array had 4 km spacing between the center of each cell, and we placed camera traps within 400 m of the center of each cell along landscape features likely to maximize detection of carnivores (e.g., oriented along hiking trails, forest roads, or game trails used by wildlife). We were unable to place all camera traps each year due to land access or safety issues, leading to a continuous deployment of camera traps at 90 of the 100 potential sites. We deployed most camera traps for at least 4 years (mean = 4.2, range 1–5). As is standard procedure (e.g., O'Connell et al. 2011; Burton et al. 2015), we deployed camera traps at a height of 30–90 cm above the ground. We programmed camera traps to take three photos per detection event with a 1 min delay before becoming active again. Each year, we deployed camera traps in the spring and retrieved them on a rolling basis after a minimum of 3 months in the field, leading to a mean of 106.7 (±4.0) trap nights each year.

Statistical analyses

For each photo/video, we recorded the date, time, and species present. We also documented whether pumas had scent-marked (defined as either scraping, urine spraying, and/or defecation; Allen et al. 2014). We considered visits by the same species within 30 min of a previous visit at a given camera trap location to be the same individual and combined records to reduce pseudoreplication (Wang et al. 2015; Finnegan et al. 2021). For all tests, we considered alpha = 0.05 to determine statistical significance.

We defined occurrence as whether a species was detected or not at a site, and calculated visitation rates as the number of visits divided by number of trap nights. To test if pumas and mesocarnivores more frequently occurred at communication hubs or at the landscape level, we used a Fisher's exact test for each species. We validated the assumption of normality, and then used a *t* test to determine if pumas and mesocarnivore species more frequently visited communication hubs or landscape-level sites.

To determine if mesocarnivores were attracted to or avoided pumas at communication hubs and landscape-level sites, we calculated Avoidance–Attraction Ratios (Parsons et al. 2016). Avoidance–Attraction Ratios predict the likelihood of an event (the next visit of the mesocarnivore) based on the presence of a hazard (a visit by a larger carnivore in between). We measured the time between subsequent visits for each mesocarnivore species when a) no puma visited between (T1), and b) when a puma visited between visits of the mesocarnivore (T2). We only considered the two focal species when creating T1 and T2 and did not account for possible visits by a third species between our focal species. However, if a third species did visit, it is unlikely that it was always the same species (e.g., a skunk may visit between two coyote visits one time and a raccoon the next), diluting the possible effects this would have). We then compared values of T1 and T2 for each mesocarnivore at each type of site using Cox proportional hazard models, with an increase in time between visits of a mesocarnivore with a visit of a puma (T2) between indicating avoidance by the mesocarnivore. At both types of sites, we measured all visitation, but at communication hubs, we also considered visitation after visits where pumas scent-marked or not, to understand if scent marking behavior increased the perception of risk in mesocarnivores. We only included species with sufficient data for our analyses (coyote, bobcat, gray fox, and striped skunk) and removed those with too few detections (raccoons) or no detections (American badgers, red foxes, and Western spotted skunks) from the analyses. Note that due to small sample sizes for coyotes at communication hubs ($n = 23$ visits, $n = 10$ T2 "sandwiches" with pumas), results should be interpreted with caution.

We assessed habitat differences between communication hubs and landscape-level sites using a 500-m buffer around each camera trap. The main difference we found was that communication hubs were primarily in forest (range = 74–100% and mean = 92% forest), while the landscape-level sites varied more widely (range = 0.2–100% and mean = 78% forest). As we could not add covariates to the Avoidance–Attraction Ratios analysis, we decided to run the same analysis after removing all landscape-level sites with a smaller proportion of forest than the smallest value for communication hubs (removing 25 of 90 camera trap sites; new range = 74–100% and mean = 91% forest) to see if this affected our results. While this resulted in a decrease in sample size, especially for coyotes (going from $n = 385$ T2 "sandwiches" to $n = 36$), it did not change the magnitude or significance of our results for any mesocarnivore species. Because of this, we chose to use the analysis with all landscape-level sites due to the larger sample sizes and greater statistical power.

We used kernel density methods (Ridout and Linkie 2009) to estimate probability density distributions of activity levels for each carnivore species (pumas, coyotes, bobcats, gray foxes, and striped skunks; again excluding Northern raccoons and other rarely detected mesocarnivores due to low sample size) at communication hubs and the landscape-level sites using the *overlap* package (Meredith and Ridout 2014). We then compared the amount of temporal overlap (Δ, which ranges from 0 for no overlap to 1 for complete overlap) between pumas and each of the mesocarnivores at communication hubs and landscape-level sites. We used the Δ_1 estimator due to our low sample sizes for coyotes (Ridout and Linkie 2009), and the Δ_4 estimator for all other species. We calculated 95% confidence intervals for all overlap estimates from 500 bootstrapped samples, and estimated *p* values using the *activity* package (Rowcliffe 2021).

Results

We documented 961 visits by pumas and 2042 visits by mesocarnivores to communication hubs. We recorded 4 mesocarnivores regularly visiting communication hubs, including gray foxes ($n = 845$ total visits), striped skunks ($n = 687$), bobcats ($n = 476$), and coyotes ($n = 23$). At the landscape level, we documented 1,304 visits by pumas and 17,767 visits by mesocarnivores. We recorded 5 relatively common mesocarnivores, including gray foxes ($n = 8251$), striped skunks ($n = 3707$), bobcats ($n = 4646$), coyotes ($n = 895$), and raccoons ($n = 245$); while also confirming the presence of American badgers ($n = 11$), red foxes ($n = 6$), and western spotted skunks ($n = 6$).

We found little variation in occurrence between types of sites (Table 1), with the exception of coyotes, which

Table 1 Summary statistics for occurrence and visitation rates for carnivores at communication hubs and landscape-level sites

	Occurrence			Visitation rate			
	Landscape	Comm. hub	*p*	Landscape	Comm. hub	*t*	*p*
Puma	82 (91.1%)	26 (100.0%)	0.20	129.5 (21.5)	49.6 (11.3)	2.05	**0.04**
Coyote	46 (51.1%)	7 (26.9%)	**0.04**	276.5 (47.7)	774.6 (215.4)	3.38	**0.001**
Bobcat	88 (97.8%)	25 (96.2%)	1.00	50.6 (9.7)	181.6 (47.9)	4.21	**<0.0001**
Gray Fox	78 (86.7%)	26 (100.0%)	0.69	91.0 (21.4)	129.7 (59.3)	0.77	0.44
Striped Skunk	80 (88.9%)	25 (96.2%)	0.30	62.5 (12.4)	101.8 (26.6)	1.47	0.15
Raccoon	37 (41.1%)	9 (34.6%)	0.65	361.7 (52.7)	782.3 (153.9)	3.23	**0.002**

We defined occurrence as whether a species was detected at a site, and calculated visitation rates as the number of visits divided by number of trap nights (with SE noted in parentheses)

Bold values indicate statistically significant difference

occurred at significantly fewer communication hubs (26.9%) than at the landscape level (51.1%; $p = 0.04$). We documented pumas at all 26 communication hubs, and at 91% of the 90 camera traps at the landscape level. Occurrence rates of all other mesocarnivores did not vary significantly between types of sites (Table 1).

Visitation rates had greater variation between types of sites (Table 1). Pumas visited communication hubs more frequently (49.6 trap nights per visit) than across the landscape (129.5 trap nights per visit; $p = 0.04$). Conversely, we recorded coyotes and bobcats three times more frequently at the landscape level than at communication hubs, while we recorded racoons twice as frequently at the landscape level (Table 1). Gray foxes and striped skunks did not significantly vary in their visitation rates between types of sites (Table 1).

We observed that all mesocarnivores avoided pumas at communication hubs and the landscape level (Table 2) when using Avoidance–Attraction Ratios, but the magnitude of effect varied among species. Bobcats (66.7% decrease vs. 67.6% decrease) and gray foxes (64.2% decrease vs. 66.9% decrease) showed slightly less avoidance at communication hubs and striped skunks (72.6% decrease vs. 65.5% decrease) showed more avoidance at communication hubs. While coyotes lacked sufficient sample sizes to be certain of the statistical significance of avoidance effects at communication hubs, they showed a 99.9% decrease at communication hubs compared to only 68.6% decrease at the landscape level.

Scent-marking by pumas also affected avoidance behavior by mesocarnivores (Table 1). Bobcats (66.3% decrease vs. 52.7% decrease) and striped skunks (57.8% decrease vs. 50.6% decrease) exhibited greater avoidance after pumas' scent-marked than when they did not. We never documented coyotes visiting after pumas scent-marked (100% of their visits came directly after a visit by a puma that did not scent-mark). In contrast, gray foxes (51.9% decrease vs. 57.7% decrease) exhibited decreased avoidance after pumas scraped compared to when they did not.

We also found evidence that mesocarnivores had less temporal overlap with pumas at communication hubs than at the landscape level (Fig. 2). Coyotes had the largest change (16%, from $\Delta_1 = 0.69$ to $\Delta_1 = 0.85$), shifting from primarily nocturnal at the landscape level to a bimodal pattern at communication hubs (Fig. 2). Other species exhibited less shifts in temporal activity, but all had less temporal overlap with pumas at communication hubs than at the landscape level; striped skunks had a 10% decrease in overlap, gray foxes a 7% decrease, and bobcats a 5% decrease (Fig. 2).

Discussion

As an apex carnivore and keystone species, pumas create communication hubs that are visited and actively used by the rest of the carnivore community. We documented, however, that

Table 2 The Avoidance–Attraction Ratios of mesocarnivores to puma visits (where negative values indicate avoidance and positive values indicate attractance) at communication hubs and landscape-level sites

Species	Landscape		Comm. Hub		Marking		No Marking	
	$\beta \pm$ SE	*p*	$\beta \pm$ SE	*p*	$\beta \pm$ SE	*p*	$\beta \pm$ SE	*p*
Bobcat	−1.13 ± 0.05	<0.0001	−1.10 ± 0.12	<0.0001	−1.09 ± 0.15	<0.0001	−0.75 ± 0.18	<0.0001
Coyote	−1.16 ± 0.16	<0.0001	–	–	–	–	–	–
Gray Fox	−1.11 ± 0.05	<0.0001	−1.03 ± 0.09	<0.0001	−0.73 ± 0.12	<0.0001	−0.85 ± 0.13	<0.0001
Striped Skunk	−1.06 ± 0.06	<0.0001	−1.30 ± 0.10	<0.0001	−0.86 ± 0.14	<0.0001	−0.71 ± 0.14	<0.0001

At communication hubs we also considered the effects of if the puma in the previous visit scent-marked or not

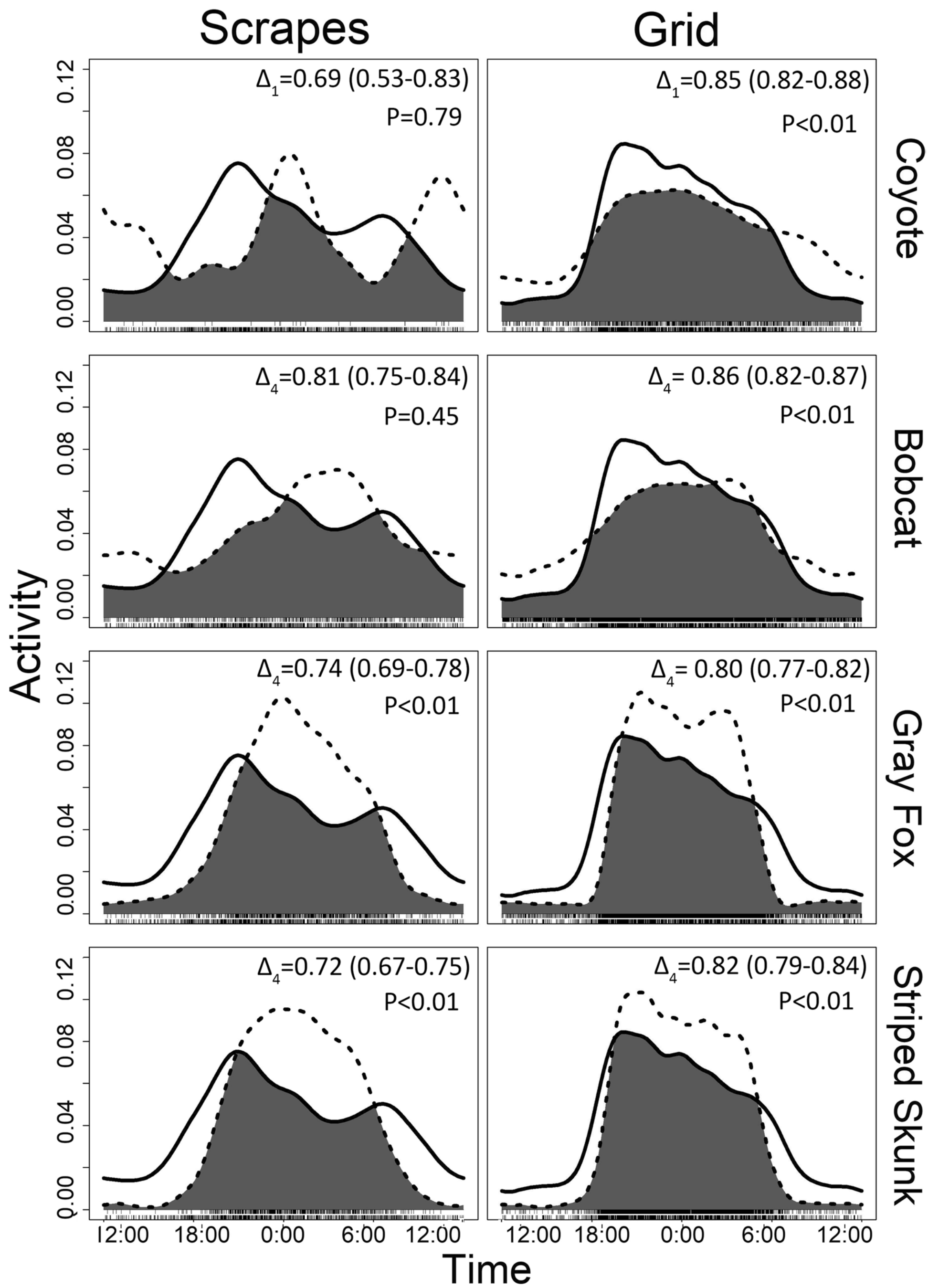

Fig. 2 Temporal overlap (in *gray*) between species (with species of interest shown as a *dotted line* and pumas shown as a *solid line*) visiting communication hubs and landscape-level sites across the study area. Temporal overlap values (Δ_1 or Δ_4) are listed along with 95% confidence intervals within parenthesis. The *lines under each graph* show individual detections of the mesocarnivore (*top*) and puma (*bottom*)

most mesocarnivores do not visit these communication hubs with the same frequency as they visit sites across the wider landscape, and this less frequent visitation of mesocarnivores to communication hubs reduces their overlap with pumas at communication hubs. This overall avoidance of communication hubs and recent puma activity is likely because mesocarnivores place themselves at considerable risk, including injury or death, by visiting the communication hubs of apex carnivores (Hughes et al. 2010; Moller et al. 2011; Donadio and Buskirk 2006). The opportunity to eavesdrop on communication by apex carnivores and gain information on their activity and resource use from communication hubs, however, seems to be a risk most mesocarnivores are willing to take to some extent as they visited these hubs at varying levels. Some species, such as coyotes, showed strong negative responses to puma visits, whereas others such as gray foxes showed positive responses. While various behavioral traits determine dominance within mesocarnivore guilds (e.g., Allen et al. 2016), differences in body size and trophic position likely contributed to the complex attraction and avoidance patterns we observed. Combined, our results show that scent marking by an apex carnivore at communication hubs affects the distribution and space use of subordinate mesocarnivores and thus contributes to the structure of carnivore communities.

Coyotes, which are the pumas' closest subordinate competitor in our study system, avoided communication hubs more than any other mesocarnivore; whereas gray foxes exhibited the least avoidance. Coyotes occurred at almost twice as many sites at the landscape level and visited sites across the landscape three times more frequently than communication hubs. This may partly be explained by habitat, as coyotes more frequently used grassland sites in the study area that were avoided by pumas, but coyotes also showed the same patterns when we analyzed only forest sites (see section "Statistical analyses"). Coyotes also showed the largest change in temporal overlap, with a substantial shift in activity at communication hubs, and the greatest degree of puma avoidance when comparing communication hubs to landscape-level sites. As the pumas' closest competitor, coyotes are often killed by pumas (Murphy and Ruth 2009) and likely avoid communication hubs to reduce the direct risk of puma aggression (sensu Allen et al. 2017). In contrast, gray foxes showed no variation in occurrence or visitation rates between types of sites and exhibited less avoidance of pumas at communication hubs than at the landscape level. Gray foxes are known to investigate and use puma scent marks by rubbing their bodies on puma scent (Allen et al. 2017). This benefit or the reduced risk of coyote predation using sites they avoid may be why gray foxes exhibited less avoidance of communication hubs than other mesocarnivores (e.g., Levi and Wilmers 2012; Newsome and Ripple 2015).

Spatiotemporal behavior also varied for other mesocarnivores between communication hubs and landscape-level sites. None of the other mesocarnivores (bobcats, raccoons, or striped skunks) showed variation in occurrence between sites, but all showed less temporal overlap with pumas at communication hubs (with most mesocarnivores showing 5–10% decreases in overlap). Bobcats and raccoons visited communication hubs less frequently than landscape-level sites, and bobcats showed increased avoidance at communication hubs (while raccoons visited communication hubs so infrequently that we were unable to calculate Avoidance–Attraction Ratios). Striped skunks did not vary in occurrence or visitation rates between types of sites but showed the most substantial changes in avoidance. It is possible these species use temporal avoidance and infrequent visits to balance the risk of predation with benefits of accessing communication hubs. For example, pumas often interact aggressively with bobcats, their closest felid competitor, and the other mesocarnivores are also regularly killed and eaten by pumas (Murphy and Ruth 2009). Mesocarnivores are known to spatially and temporally avoid humans and dominant carnivores (Sivy et al. 2017, Finnegan et al. 2021, but see Prugh et al. 2023), and our results highlight the behavioral diversity mesocarnivores use to assess and avoid intraguild predation and competition. While mesocarnivores can likely benefit from eavesdropping on puma scent marking and activity, we found that they exhibited a variety of spatiotemporal avoidance strategies at communication hubs rather than outright avoidance to potentially facilitate coexistence with pumas.

Our results support even stronger evidence of behavioral changes in mesocarnivores when considering avoidance after pumas scent-marked. Mesocarnivores generally avoided communication hubs more after a puma had scent-marked during its previous visit: bobcats and striped skunks showed greater avoidance after scent marking, while coyotes and raccoons never visited directly after a visit in which a puma scent-marked and rarely scent-marked at these communication hubs. This avoidance is likely a fear response by subordinate mesocarnivores to fresh puma activity and scent, and yet many mesocarnivores still regularly use these communication hubs, highlighting the temporal but not spatial avoidance of pumas. Communication hubs are usually at prominent locations that are likely to be found by other individuals (Krofel et al. 2017; Cornhill and Kerley 2020a), and it is possible that mesocarnivores are using these sites to communicate primarily with conspecifics, just in the same areas as the rest of the carnivore community. When considering the prevalence of overmarking and more complex interspecific communication that occurs between carnivores (Wikenros et al. 2017; Apps et al. 2019); however, this is unlikely. The exception to this pattern of stronger avoidance was gray foxes, which exhibited less avoidance after pumas scent-marked, likely again explained by gray foxes' use of puma scent marks for rubbing on their bodies (Allen et al. 2017). While the benefits gained by gray foxes are clearer, it raises the question of what benefits other mesocarnivores receive from visiting and using these locations.

Scent communication that is imperceptible to humans can be difficult to study, and our research provides foundational information on how mesocarnivores use the communication hubs of apex carnivores. While we explored multiple behavioral responses, we only touched on the complexity of marking and investigation in the carnivore community, and there are many avenues for future research. Scent-marking is not limited to interactions just with pumas; instead, mesocarnivores are likely reacting to communication with the entire carnivore community, and possibly more broadly with prey and even humans. Understanding differences between investigating and counter marking is key to understanding the interspecific carnivore competition and interactions. It also seems important to include trophic dynamics, as the effects of apex carnivores on the communication behaviors of their closest subordinate mesocarnivore competitors appear to be different than on smaller mesocarnivores. While we provide a mechanistic understanding of how the scent marking of an apex carnivore affects the distribution and space use of subordinate mesocarnivores, it is also important to understand how this communication influences other ecological interactions and the fitness of individuals that are adept at exploiting this information. With this understanding, what seems like simple communication may scale up to population level responses and affect ecosystem processes.

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Author contribution statement MLA and CCW conceived and designed the experiments. MLA performed the fieldwork and annotated images. ACA and MLA analyzed the data. MLA wrote the manuscript, and all other authors provided editorial advice.

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Data availability Data will be made available by authors for any reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All field experimental procedures were performed within the guidelines set by the Independent Animal Care and Use Committee at the University of California, Santa Cruz (Protocols Wilmc0709 and Wilmc1101) and the American Society of Mammalogists (Sikes et al. 2011).

Consent to participate Not applicable.

Consent for publication Not applicable.

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