Recreation shifts North American mammals in time more than in space

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Abstract

When people walk, ride and run along a trail, do the animals that live nearby leave, or do they simply wait until dark? Evidence on how much trail traffic wildlife tolerates comes mostly from single sites and from contrasts between trails that are open and closed or cameras on and off trails. Such contrasts cannot say how the response grows with the amount of use. We estimated continuous dose-response relationships between recreation traffic and mammal activity from 12,806 camera deployments at 8,603 locations in 326 arrays across the United States (SNAPSHOT USA, 2019–2024), in which the same cameras recorded both people and wildlife. Across 49 species, detection rates showed no general decline with traffic (pooled rate ratio 1.01, 95% CI 0.95–1.08, per tenfold increase in traffic). Three species declined and four carnivores increased. In contrast, the share of detections made at night rose with traffic across 27 species (pooled odds ratio 1.23, 1.14–1.32). Six species shifted robustly toward the night, and none shifted toward the day. For some species the shift came from fewer daytime detections, for others from more night-time ones. Where the traffic of nearby trails mattered, its effect was local: raccoon detections fell only within about 35 m of busy trails, and the night shifts of deer and coyote weakened away from trails. Other species responded to people recorded at the camera, whether on or off the mapped trail network. Only raccoon showed a traffic threshold: its detections fell beyond about 30 recreation events per 100 trap nights (95% CI 7–75). Apparent effects of body mass were not robust to modelling shared ancestry and between-species variation, and no conclusion depended on the COVID-19 pandemic years. At the traffic levels recorded on North American trails, recreation is associated more consistently with when mammals are active than with where they occur. Managers should therefore consider the timing of use alongside the density of trails.

1 Introduction

Outdoor recreation is one of the most extensive ways in which people use land, and it is growing. In the United States, the outdoor recreation economy added $639.5 billion to gross domestic product in 2023, 2.3% of the total, and grew faster than the economy as a whole (U.S. Bureau of Economic Analysis, 2024). A record 175.8 million Americans took part in outdoor recreation that year, with hiking the most popular activity (Outdoor Industry Association, 2024), and the national parks received 331.9 million visits in 2024, more than in any previous year (National Park Service, 2025).

Worldwide, protected areas receive some 8 billion visits a year (Balmford et al., 2015). Demand rose further during the COVID-19 pandemic: in Oslo, for example, recreational activity in green space nearly quadrupled during the 2020 lockdown (Venter et al., 2020). These visits carry real benefits. Contact with nature is associated with better mental health (Bratman et al., 2019), and wildlife is part of what people come to see: about 148 million US residents watched wildlife in 2022 (U.S. Fish and Wildlife Service, 2023).

The same trails that deliver these benefits carry people into habitat that roads and buildings do not reach. Recreation is permitted in most of the world's protected areas, and a global review of 274 studies found at least one effect of recreation on animals in 93% of them, 59% of those effects negative (Larson et al., 2016). Even quiet, non-motorized use matters: in northern California, protected areas open to such use had one-fifth the density of native carnivores of neighbouring areas closed to it (Reed and Merenlender, 2008). Land managers are therefore asked to provide for public enjoyment while conserving the wildlife that makes it worthwhile, and the decisions they face are about quantities: how many people a trail can carry, how close to sensitive habitat it may run, and at which hours or seasons it should close. The evidence available to them is mostly categorical. Studies typically compare trails open or closed, cameras on or off trail, or periods before and after a change in access. A review of 38 years of research found that only 53 of 330 studies reported any quantitative threshold, most of them as distances to people or trails rather than amounts of use, and called for studies that measure recreation as a continuous variable (Dertien et al., 2021). A contrast between two states says that something changed, but not how the change scales with the number of people passing.

An animal faced with people on a trail has at least two options. It can avoid the places people use, which would appear as fewer detections where traffic is high. Or it can keep using those places but shift its activity to the hours when people are absent, which would appear as a larger share of detections at night. Evidence for the first response is mixed. Across 32 protected forests in the eastern United States, hiking had measurable effects on some species, but these were minor compared with those of habitat, and most species did not avoid trails (Kays et al., 2017). Across North America, a third of 24 mammal species responded negatively to human presence or footprint, whereas 58% were positively associated with it (Suraci et al., 2021), and in western Alberta the response depended on landscape context (Marion et al., 2024). Evidence for the second is more consistent. A global meta-analysis found that mammals increased the nocturnal share of their activity by a factor of 1.36 near people (Gaynor et al., 2018), and when human activity changed abruptly during the pandemic, mammals became more nocturnal where human activity was higher, carnivores most of all (Burton et al., 2024). How far either response extends from a trail is less clear. Field studies have reported effects reaching about 100 m from a trail (Taylor and Knight, 2003; Marion et al., 2021), and in the Canadian Rocky Mountains the effect of trail use on grizzly bears and wolves fell by half only at 267 and 576 m (Thompson et al., 2025).

Recent studies have begun to measure recreation as a continuous variable, using counts of hikers (Marion et al., 2021), fitness-app data (Lacour et al., 2025; Marion et al., 2024) or people recorded

by the cameras themselves (Procko et al., 2023; Gump and Thornton, 2023; Peters et al., 2025; Lamb and Chow, 2026). Several examined both where and when animals were active (Gump and Thornton, 2023; Lamb and Chow, 2026). The closest to a synthesis sampled four Italian protected areas with a standard protocol and found that body mass shaped how mammals responded to people (Salvatori et al., 2024). These studies cover one region each, or a few protected areas, and none tests for a threshold in the amount of use. To our knowledge, no study has combined a continuous measure of trail traffic with both spatial and temporal responses, tests for thresholds and a test of species traits, across a national network.

This study began with a simple question: as a trail gets busier, do the mammals around it disappear, or do they become creatures of the night? SNAPSHOT USA, a coordinated national camera-trap survey, offers an unusual chance to answer it. Its cameras record people as well as wildlife, so the same instrument measures both the dose and the response, at thousands of locations spanning a wide range of traffic. From the initial question we derived six hypotheses, each with a prediction that the data could contradict.

If people displace wildlife in space, detection rates should fall as traffic rises (H1). If wildlife instead avoid people in time, the share of detections made at night should rise with traffic (H2). When we found evidence for H2, we asked a further, exploratory question: does the night share rise because animals are detected less often by day, or more often by night (H3)? The answer distinguishes animals that withdraw during busy hours from those that compensate after dark. If tolerance has limits, responses should be non-linear and steepen beyond some traffic level (H4). If sensitivity depends on how a species lives, the strength of its response should vary with body mass and diet (H5). Finally, if the effect of traffic is local, it should be strongest close to the trail and fade with distance (H6). We tested each hypothesis with species-level models, required effects to survive both a correction for multiple testing and a permutation test that respects the clustering of cameras, and then asked how the effects scaled across species.

2 Methods

2.1 Camera-trap surveys

We used the SNAPSHOT USA releases for 2019–2023 (Rooney et al., 2025) and for 2024 (`https://doi.org/10.5061/dryad.bnzs7h4qf`), both released under a CC0 licence. Each autumn, co-operating teams deploy arrays of unbaited camera traps in a coordinated survey window, using a common protocol. The combined data comprise 12,806 deployments at 8,603 locations in 326 arrays, in all 50 states and the District of Columbia, totalling 509,452 trap nights (Table 1; Fig. 1a). The cameras recorded 721,346 independent mammal events of 131 species.

The two releases differ in format, so we harmonized them to a single schema. Timestamps are recorded in local camera time. We assigned each camera a time zone from its coordinates and converted all times to UTC. Detections falling outside a deployment's start and end dates were removed. Consecutive detections of the same label at the same camera within 30 min were merged

into one independent event, the convention for camera-trap data.

Table 1: Survey effort, recreation and wildlife by SNAPSHOT USA year. States are assigned from camera coordinates and include the District of Columbia. Recreation events are independent detections of people on foot, bicycle or horseback.

Year	Deployments	Arrays	Locations	States	Trap nights	% with recreation	Recreation events	Mammal events
2019	1,484	106	1,481	51	51,596	30.2	4,806	65,239
2020	1,483	98	1,454	43	52,097	34.9	9,281	73,101
2021	1,801	107	1,648	46	65,877	30.1	4,129	91,179
2022	2,381	132	2,129	46	94,176	47.9	6,658	129,490
2023	2,529	147	2,211	50	108,114	53.7	11,363	161,534
2024	3,128	185	2,694	50	137,592	67.3	15,559	200,803
All years	12,806	326	8,603	51	509,452	47.7	51,796	721,346

2.2 Measuring recreation traffic

We measured traffic with the same cameras that recorded wildlife. Recreation events were independent detections of people on foot, bicycle or horseback. Hunters, motorized vehicles, park staff and domestic animals were kept as separate classes. Motorized traffic entered the models as a covariate. Researchers and camera technicians were never counted as traffic. The dose for each deployment was $\log(r + 1)$, where r is recreation events per 100 trap nights. Traffic varied over more than three orders of magnitude: 47.7% of deployments recorded at least one recreation event, and the busiest recorded more than 1,000 events per 100 trap nights (Fig. 1b). We report effects per tenfold increase in traffic, calculated as $\exp(\beta \ln 10)$ from the slope β on the dose scale. Because the dose is $\log(r + 1)$, this closely approximates a tenfold change wherever traffic exceeds about one event per 100 trap nights. Camera events are an index of traffic rather than a count of visitors, a point we return to in the Discussion.

2.3 Trail placement and habitat

A camera on a busy trail records many people, but it may also record many animals simply because animals travel along trails. To separate this placement effect from a response to people, we described each camera's position in the trail network. We used OpenStreetMap paths from Overture Maps, which include the informal and local paths that official layers often miss. From these we computed the distance to the nearest trail and the trail density within 1 km. We also recorded whether the camera was placed on a hiking trail or a road, and computed the distance to the nearest road from the USGS National Map transportation layer. Habitat was described by the shares of forest and developed land within 500 m (NLCD 2021), mean elevation and terrain ruggedness (the standard deviation of elevation; USGS 3DEP, 30 m), and the habitat and development level recorded by survey teams. Land cover is not available outside the conterminous United States, so we flagged these locations with an indicator. All spatial layers were fetched only within 2 km of cameras.

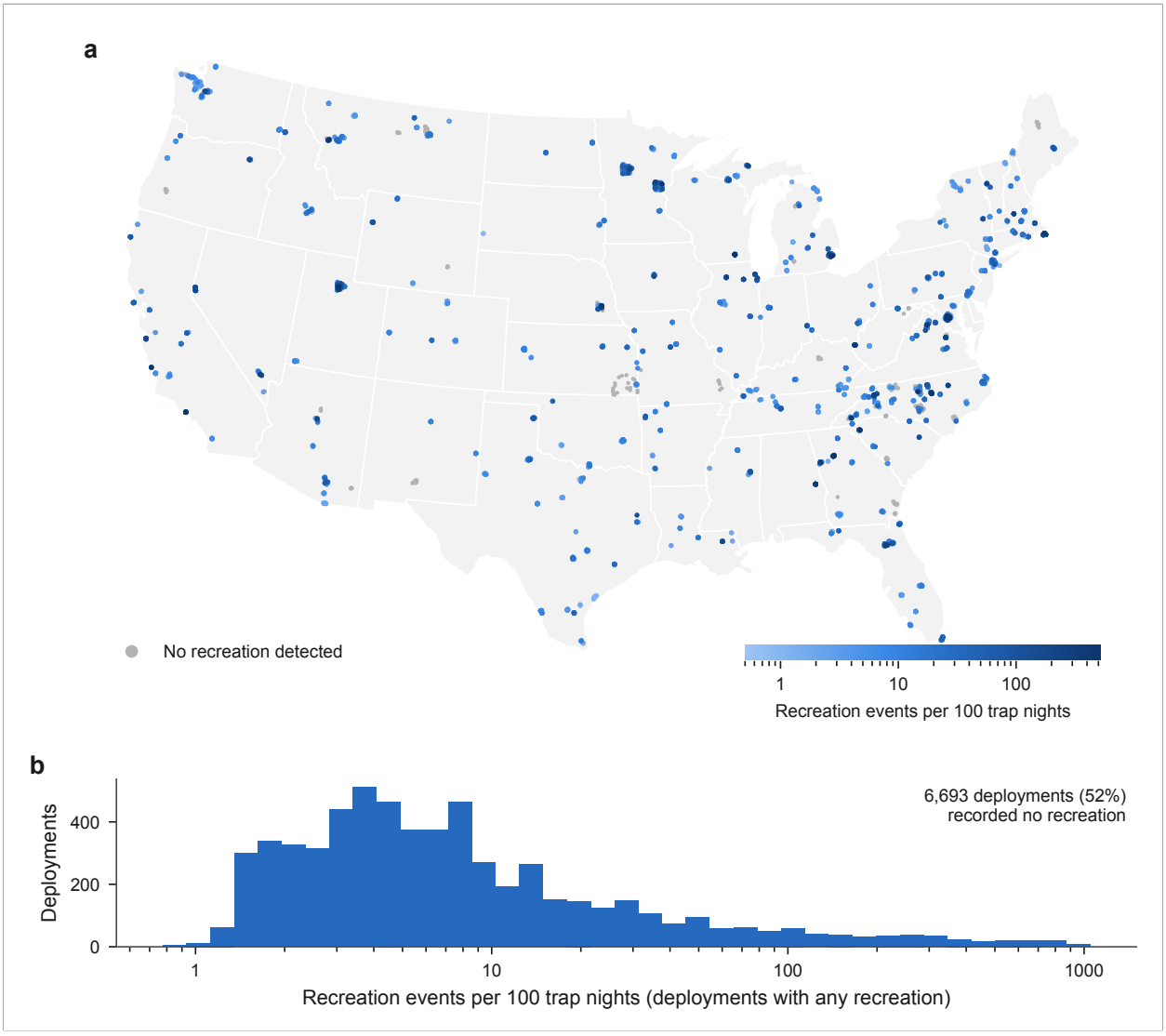


Figure 1: Where the cameras were and how much recreation they recorded. (a) The 8,487 SNAPSHOT USA camera locations in the conterminous United States, 2019–2024. Colour shows the recreation traffic recorded by each camera (people on foot, bicycle or horseback per 100 trap nights, averaged over a location's deployments; log scale). Grey points recorded no recreation. A further 116 locations in Alaska, Hawaii and Puerto Rico are analysed but not shown. (b) The spread of traffic among the deployments that recorded any recreation (log scale). The 6,693 deployments (52%) that recorded none form the zero end of the traffic gradient.

2.4 Species models

For each species we fitted two generalized additive mixed models in mgcv (Wood, 2017), one for each kind of response. Both included random intercepts for array and survey year, a smooth of log distance to trail ($k = 4$), and the placement and habitat covariates above.

To test spatial avoidance (H1), we modelled the number of independent events per deployment with a negative binomial distribution and an offset of log trap nights. We included only deployments in arrays where the species was detected at least once. Zeros from outside a species' range would otherwise dilute the estimate.

To test temporal avoidance (H2), we modelled the number of night events against the number of day events at each deployment. Night was defined as the sun below civil twilight ($-6°$) and day as the sun above the horizon, both computed from the solar position at each camera. Twilight events were left out. A binomial model proved too confident: night and day counts varied between cameras more than a binomial distribution allows, with an estimated dispersion of up to 4.0 in white-tailed deer. Under that model, permutation null distributions were 1.8–2.9 times wider than nominal. We therefore used a quasi-binomial family, which estimates the dispersion and widens the standard errors to match. The traffic effect in this model is an odds ratio. A value above one means that a larger share of a species' detections occur at night where traffic is higher.

Traffic entered each model twice. A smooth term ($k = 6$) described the shape of the relationship (H4), and a separate fit with a linear term gave one slope per species for comparison across species. Models were fitted by fast restricted maximum likelihood (`bam`). Any fit that produced convergence warnings was refitted with full restricted maximum likelihood (`gam`).

A species' estimate was reported only if it passed four quality rules. It needed data from at least ten arrays. For night share, between 3% and 97% of its detections had to fall at night, because outside that range the model approaches separation. The slope's standard error had to be at most one on the log scale, and no fit could produce convergence warnings. Of the 87 taxa with at least 30 events, 82 could be fitted for detection rate and 49 passed the rules; 60 could be fitted for night share and 27 passed.

To ask how the night shift arises (H3), we refitted the detection-rate model separately to night counts and to day counts for each species with a night-share estimate. We framed this question after seeing the night-share results, and we treat it as exploratory.

2.5 Thresholds and zone of influence

The last two hypotheses concern the shape of the response, and we tested both for the robust effects. A smooth curve can show that a response bends, but not where. To ask whether responses steepen beyond a particular level of traffic (H4), we therefore fitted a hinge model. In it, the traffic slope is allowed to change at a breakpoint c, through the term $\max(\text{dose} - c, 0)$ added to the linear traffic term. We located c by profiling the model deviance over a grid of traffic levels from 1 to 300 events per 100 trap nights. The grid was restricted to lie between the 10th and 95th percentiles of non-zero traffic, so that both segments had data. To obtain confidence intervals that account for

the search over c, we used an array-level bootstrap. In each of 1,000 draws, arrays were resampled with replacement, the breakpoint was located again, and both slopes were re-estimated. We judged that a threshold was present when the bootstrap interval of the change in slope excluded zero and fewer than half of the draws placed the breakpoint at the edge of the grid. These fits used the discretized `bam` algorithm, and the negative binomial dispersion was held at its value in the linear model.

To ask whether the effect of traffic fades away from trails (H6), we needed a measure of the traffic on the trail itself, not of the people recorded at a camera away from it. Off-trail cameras also record people: 40% of cameras more than 1 km from a mapped trail detected at least one recreation event. For each camera, we therefore took as its dose the mean traffic recorded by the other cameras of the same array and year that stood on a hiking trail. Leaving the camera's own count out means that a camera on a trail never contributes to its own dose. This restricted the analysis to arrays with at least one other camera on a trail: 3,527 deployments in 113 arrays, of which 2,943 were off trail. We then replaced the single traffic slope with a slope that varies smoothly with distance to the nearest trail. This is a varying-coefficient term, $f(\text{distance}) \times \text{dose}$ ($k = 5$). It gives the effect of trail traffic as a continuous function of distance, from the trail itself to 2 km. We tested whether the slope varied with distance by comparing this model with the constant-slope model, using a χ^2 test for detection rate and an F test for the quasi-binomial night share. Where the effect at the trail differed from one, we defined the zone of influence as the distance at which its 95% confidence interval first included one. We report this analysis only for effects with detections in at least 20 of the arrays. For comparison, we also fitted the same model with the traffic recorded at each camera as the dose (Fig. S2). That model asks a different question: whether people met at a camera have a different effect close to a mapped trail than far from one.

2.6 Inference and robustness

With dozens of species and two responses, some apparent effects will arise by chance. Within each response we adjusted p-values across species to control the false discovery rate (Benjamini and Hochberg, 1995). Cameras within an array share a landscape, a survey team and often a trail system, so model-based standard errors may still understate uncertainty. We therefore added an array-level permutation test. In each of 199 permutations, every array received traffic values resampled from a randomly chosen donor array. This preserves the way traffic is clustered within arrays but breaks its link to wildlife. We compared the observed Wald statistic for the traffic slope with its permutation distribution. We call an effect robust only if it has $q < 0.05$ and a permutation $p < 0.05$, and only robust effects are named in the main text.

For detection rate, we also fitted each model by maximum likelihood without traffic, with a linear traffic term and with a smooth one, and compared them by likelihood-ratio tests. These asked whether traffic had any effect and whether that effect was non-linear. The quasi-binomial night-share model has no likelihood, so these tests were not possible there. We assessed residual spatial autocorrelation with Moran's I of location-mean deviance residuals, using row-standardized

weights on the eight nearest neighbours and 199 permutations.

Finally, we refitted every model under five alternative choices that might plausibly alter the results. First, we excluded 2020 and 2021, when the COVID-19 pandemic changed visitation. Second, we restricted the data to cameras not on hiking trails. Third, we removed possible camera-setup events, meaning generic human detections on a deployment's first or last day. Fourth and fifth, we shortened the independence window to 15 min and lengthened it to 60 min.

The pandemic years deserved a direct test, not only a refit without them. In 2020 the mean traffic recorded per camera was 30 events per 100 trap nights, two to five times that of any other year, and the share of cameras placed on hiking trails was three times as high. Animals may also have responded differently to people while visitation was unusual. For each robust effect, we therefore added terms that let the traffic slope differ in 2020 and in 2021, and tested them jointly against a single slope (χ^2 or F test, as above). We also re-estimated the breakpoint of the one threshold we found (H4) without 2020, and without 2020 and 2021, each with 200 bootstrap draws.

2.7 Exploratory tests of path type and dispersed use

The distance results (H6) suggested that several species respond to people wherever they are recorded, including away from mapped trails. This raised two questions that were not among our hypotheses, and we treat the analyses that address them as exploratory. The first is whether it matters which kind of path people use. We divided the Overture paths within 1 km of each camera into official paths, those within 25 m of a USGS National Map trail, and unofficial paths, the rest. The tolerance absorbs offsets between the two sources. Unofficial paths include paths made by users, but also local and park trails that the federal layer does not map, so their density is an upper bound on the density of informal paths. They made up 80% of the path length near the average camera, and 78% of camera locations had no official trail within 1 km. The second question is whether it matters how far use spreads from the path network. For each camera we computed a dispersed-use index: among the other cameras of its array and year that lay more than 100 m from any mapped path, the share that recorded at least one recreation event. The index was computed only where at least three such cameras were available (11,152 deployments in 293 arrays).

For each robust effect, we added the moderator, either the logarithm of one plus unofficial path density or the index, to the species model, first as a main term and then together with its interaction with traffic. In the path models, the single trail-density covariate was replaced by the densities of official and unofficial paths. Because unofficial paths are most common where official ones are absent, a result for unofficial paths could reflect path density in general, so we repeated the test with official path density as the moderator. We report the main term as the ratio between cameras at the 90th and 10th percentiles of the moderator at equal traffic, and the interaction as the effect of traffic per tenfold increase in traffic at these two percentiles. P-values were adjusted for the false discovery rate across the 13 effects within each test. We did not run the permutation test for these models, so their inference rests on model-based standard errors, which for night share were anticonservative in the main analysis.

2.8 Trait synthesis

To ask whether sensitivity depends on how a species lives (H5), we related the species slopes to $\log_{10}$ body mass and diet guild by random-effects meta-regression. Each slope was weighted by $1/(\mathrm{SE}^2 + \tau^2)$, with the between-species variance τ^2 estimated by the DerSimonian–Laird method (DerSimonian and Laird, 1986). Body mass and diet came from EltonTraits 1.0 (Wilman et al., 2014). A species was classed as a carnivore, insectivore or herbivore when at least 60% of its diet came from that source, and as an omnivore otherwise. We had no prior expectation for the direction of these effects, so all tests were two-sided.

Related species may respond alike because they share ancestry rather than traits, which would make a trait effect appear stronger than it is. We therefore refitted the meta-regression with random effects for family as well as species, estimated by restricted maximum likelihood. The residual covariance was $\mathrm{diag}(\mathrm{SE}^2 + \tau^2_{\mathrm{species}}) + \tau^2_{\mathrm{family}} Z Z^\top$, where Z assigns species to families (EltonTraits, following Wilman et al., 2014). A trait effect that survives this model is not simply the signature of one or two families.

2.9 Software and data availability

Data processing used Python 3.11 (pandas, geopandas, statsmodels), and models were fitted in R with mgcv. All input data are openly licensed (CC0 or public domain). [Code repository and archived release DOI.]

3 Results

3.1 Do mammals avoid busy places?

If recreation displaced mammals, detection rates would fall as traffic rose. Across the 49 species with reliable estimates they did not: the pooled rate ratio was 1.01 (95% CI 0.95–1.08) per tenfold increase in traffic (Fig. 2a). H1 is therefore not supported as a general rule. Individual species, however, responded in both directions (Table 2). Three declined robustly: red squirrel (rate ratio 0.51, 0.38–0.68), eastern chipmunk (0.71, 0.58–0.86) and northern raccoon (0.90, 0.85–0.97). Four were detected more often where traffic was higher: North American river otter (3.13, 1.61–6.09), red fox (1.38, 1.22–1.56), grey fox (1.32, 1.10–1.58) and bobcat (1.31, 1.16–1.49). These associations hold after distance to trail, trail density and camera placement are taken into account. All seven kept their direction, with confidence intervals excluding one, under each of the five sensitivity analyses (Table S2). For most species the likelihood-ratio tests found no traffic effect at all: AIC favoured the model without traffic for 28 of 49 species, a smooth term for 15 and a linear term for 6.

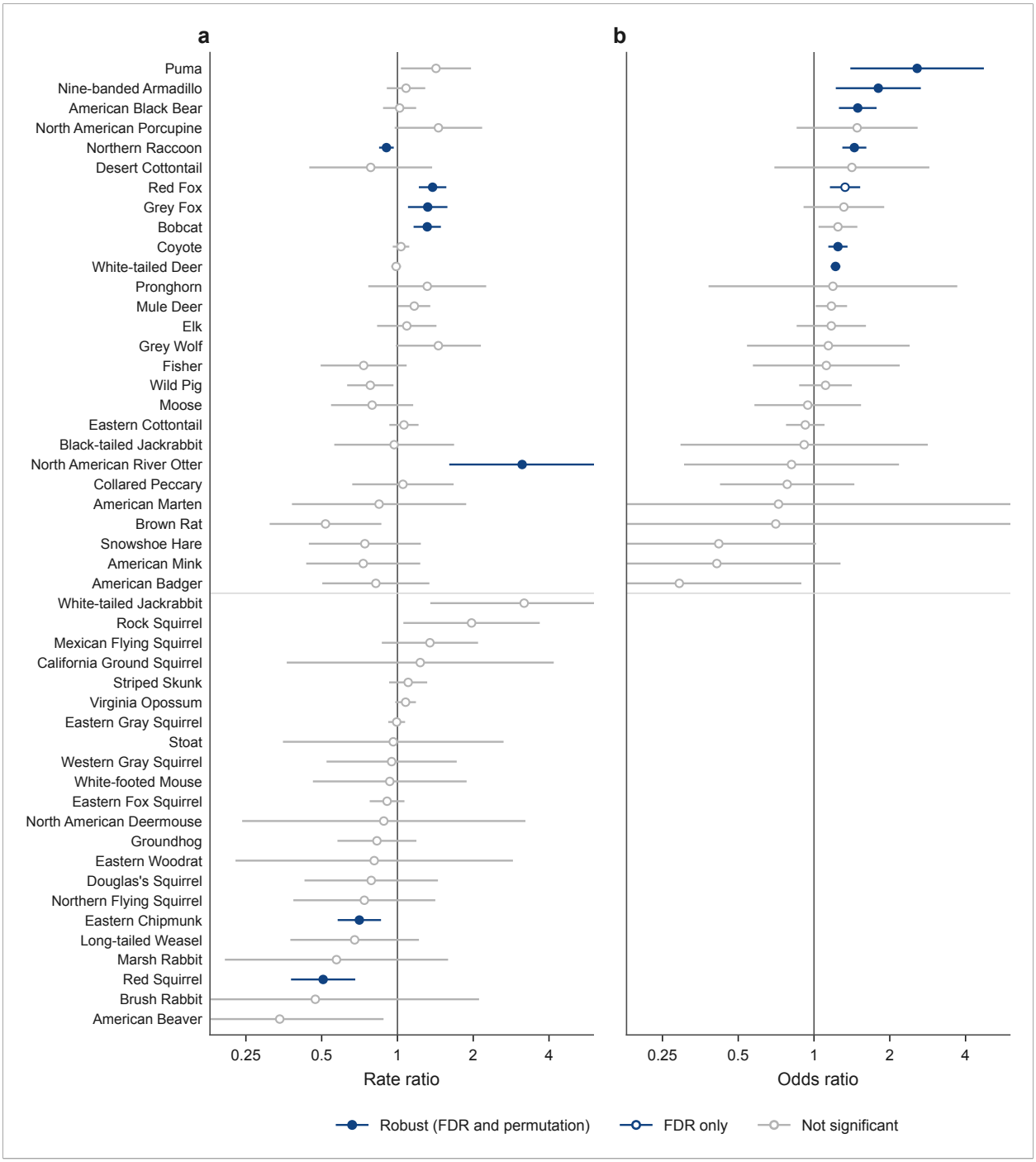


Figure 2: Few species were detected less often where traffic was high, but many were more active at night. Each row is one species, with its effect per tenfold increase in traffic on (a) detection rate (rate ratio) and (b) the share of detections at night (odds ratio). Values above one mean more detections, or a larger night share, at busier cameras. Points are estimates from the linear traffic term and lines are 95% confidence intervals, cut at the axis limits. Filled points are robust effects (false discovery rate $q < 0.05$ and array-permutation $p < 0.05$); open blue points pass the false-discovery-rate correction only; grey points are not significant. Species below the horizontal line have no night-share estimate, usually because they are almost entirely nocturnal.

Table 2: Robust traffic effects per tenfold increase in traffic, with 95% confidence intervals. Robust effects have a false discovery rate $q < 0.05$ and an array-permutation $p < 0.05$. Detection-rate effects are rate ratios; night-share effects are odds ratios.

Response	Species	Effect (95% CI)
Detection rate	Red squirrel	0.51 (0.38–0.68)
	Eastern chipmunk	0.71 (0.58–0.86)
	Northern raccoon	0.90 (0.85–0.97)
	Bobcat	1.31 (1.16–1.49)
	Grey fox	1.32 (1.10–1.58)
	Red fox	1.38 (1.22–1.56)
	North American river otter	3.13 (1.61–6.09)
Night share	White-tailed deer	1.22 (1.17–1.27)
	Coyote	1.24 (1.14–1.36)
	Northern raccoon	1.45 (1.30–1.61)
	American black bear	1.49 (1.26–1.77)
	Nine-banded armadillo	1.80 (1.22–2.66)
	Puma	2.57 (1.39–4.73)

3.2 Do mammals avoid busy times?

If mammals avoided people in time, a larger share of their detections would fall at night where traffic was high. This is what we found. Across 27 species the pooled odds ratio was 1.23 (1.14–1.32) per tenfold increase in traffic (Fig. 2b), supporting H2. Six species shifted robustly toward the night: white-tailed deer (odds ratio 1.22, 1.17–1.27), coyote (1.24, 1.14–1.36), northern raccoon (1.45, 1.30–1.61), American black bear (1.49, 1.26–1.77), nine-banded armadillo (1.80, 1.22–2.66) and puma (2.57, 1.39–4.73). No species shifted toward the day. Two further species fell just short of our criterion. Red fox passed the false-discovery-rate correction ($q < 0.001$) but not the permutation test ($p = 0.055$), and bobcat narrowly missed the correction ($q = 0.053$). The night-share effects kept their direction in every sensitivity analysis. In two of the five, excluding 2020–2021 and removing possible setup events, one of the seven significant effects had a confidence interval that included one (Table S2).

The diel activity curves show what these odds ratios mean (Fig. 3a). People were active almost entirely between dawn and dusk. At cameras with high traffic, coyote, black bear and puma were detected less in the middle of the day and more after dark than at cameras that recorded no people. White-tailed deer kept their dawn and dusk peaks but were detected less around midday.

3.3 Do animals withdraw by day or compensate by night?

A higher night share can arise in two ways: an animal may be detected less often during the day, or more often at night. Modelling the two counts separately showed that both routes occur (Fig. 3b). White-tailed deer were detected less often by day as traffic rose (0.92, 0.87–0.96), while their night detections changed little (1.05, 1.00–1.11). Raccoons declined in both periods, but more by day (0.80, 0.70–0.92) than by night (0.91, 0.85–0.98). Coyote and puma, in contrast, were detected

more often at night where traffic was high (coyote 1.09, 1.01–1.19; puma 1.82, 1.28–2.59), with no clear change by day. For black bear and armadillo, neither rate on its own differed clearly from one. Their shift is apparent only in the ratio of the two, which is estimated more precisely than either count. Because we formed this question after seeing the night-share results, we regard these patterns as hypotheses for further work rather than tests.

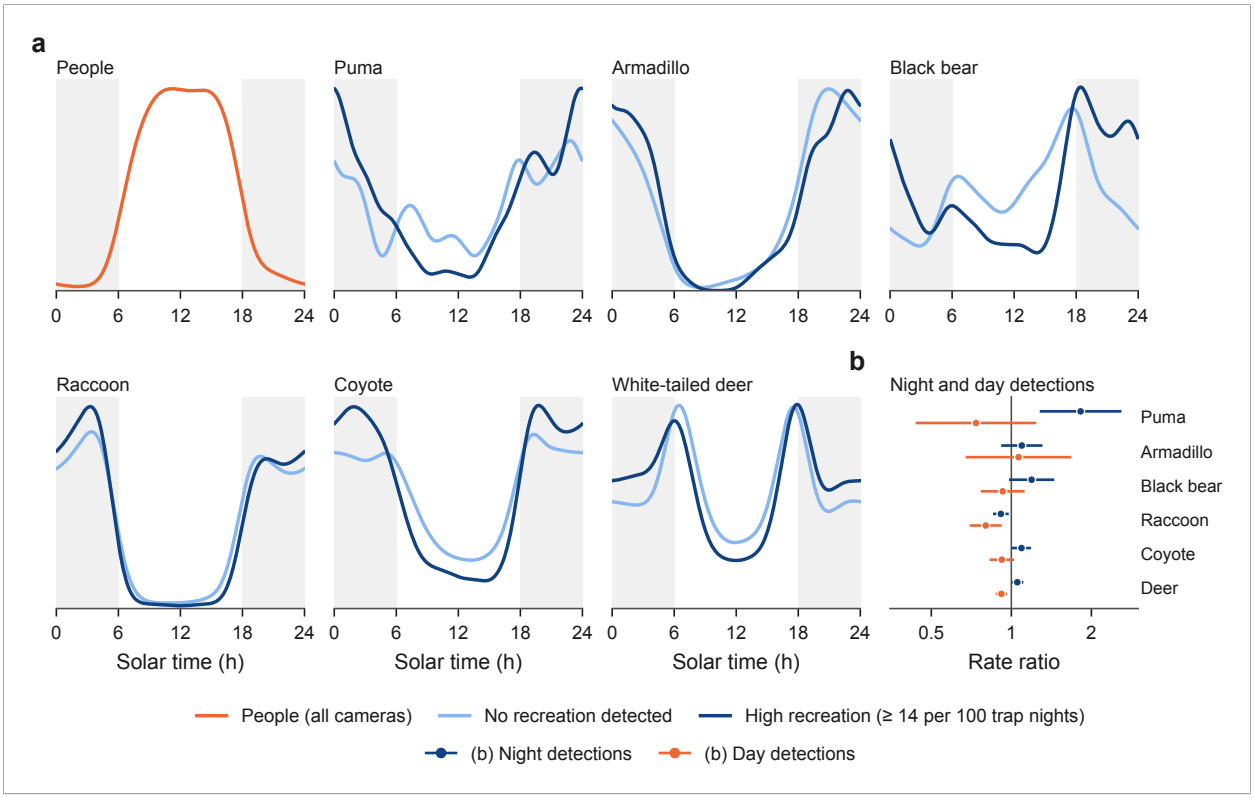


Figure 3: At busy cameras, the six species with a robust night shift moved activity out of the day, into the night, or both. (a) Activity over the 24-h day at cameras that recorded no recreation (light blue) and at cameras with high recreation (dark blue: the top quarter of non-zero traffic, at least 14 events per 100 trap nights). The first panel shows when people were recorded, at all cameras (orange). Time is solar time (UTC plus longitude/15), so cameras in different time zones align, and grey shading marks approximate autumn night. Curves are kernel densities (wrapped Gaussian, 1-h standard deviation), are descriptive, and are not adjusted for covariates. (b) Effect of traffic on night (blue) and day (orange) detection rates, from separate negative binomial models, as rate ratios per tenfold increase in traffic with 95% confidence intervals. A night shift can come from fewer day detections (deer, raccoon) or more night detections (puma, coyote).

3.4 Is there a level of traffic beyond which responses steepen?

If tolerance has limits, responses should be non-linear. Among species with robust detection-rate effects, the likelihood-ratio test favoured a curve over a straight line for raccoon, grey fox and river otter, and marginally for red squirrel ($p = 0.047$) (Fig. 4a). The forms differed. Raccoon detections were stable up to roughly 10–20 recreation events per 100 trap nights and declined beyond that. Grey fox detections rose to a peak at intermediate traffic and fell again at the highest levels. Red

fox, bobcat and eastern chipmunk changed steadily across the whole range. The night-share curves rose monotonically for most species (Fig. 4b). Armadillo was an exception: its night share peaked at low traffic, with wide uncertainty at higher levels.

A curve that bends does not by itself locate a threshold, so we asked whether a breakpoint could be identified with confidence. For raccoon detections it could. Below about 30 recreation events per 100 trap nights (bootstrap 95% CI 7–75), detection rate did not change with traffic (rate ratio 1.04, 0.93–1.22, per tenfold increase in traffic). Above it, detections fell steeply (0.41, 0.19–0.71). The change in slope was clearly supported (bootstrap $p = 0.002$), and only 2% of draws placed the breakpoint at the edge of the search range. Armadillo's night share also met the criterion, but with the opposite shape. It rose steeply at the lowest traffic levels (odds ratio 3.85, 1.44–14.5) and stopped rising above about 5 events per 100 trap nights (CI 2–20; above the breakpoint 0.27, 0.03–1.16; $p = 0.036$). The response therefore saturates rather than steepens, and the lower limit of its interval lies at the edge of the range we searched. Coyote night share showed a steepening that fell just short of the criterion ($p = 0.052$), as did the rise and fall of grey fox detections ($p = 0.076$). For the remaining nine effects, either the change in slope was not supported or the breakpoint could not be located: in up to 73% of draws it fell at the edge of the range. H4 is thus supported for raccoon detections only. For most species, a smooth or steady response describes the data as well as a threshold does.

3.5 Do species traits predict the response?

If sensitivity depends on how a species lives, the species' slopes should vary with body size and diet. Both responses varied with body mass (Fig. 5). For detection rate, the slope increased by 0.033 per tenfold increase in body mass (SE 0.015, $p = 0.031$; 49 species), so larger species were less likely to decline with traffic. Herbivores had lower slopes than carnivores (-0.073, SE 0.032, $p = 0.024$). For night share, the slope also increased with body mass (0.057, SE 0.028, $p = 0.046$; 27 species), so larger species were more likely to shift toward the night, and no diet guild differed from carnivores. Taken at face value, small species tended to be detected less where traffic was high, whereas large species tended to stay and change their timing.

These trait effects did not survive the check for shared ancestry. With random effects for family and species, the body-mass effect on night share fell to 0.043 (SE 0.032, $p = 0.18$; 13 families). The family variance ($\tau^2 = 0.0030$) absorbed most of the between-species variation, which indicates that the pattern rests largely on a few families: bears and cats shifted strongly, whereas hares and rabbits did not. For detection rate, the family variance was estimated at zero, but the body-mass effect weakened to 0.035 (SE 0.019, $p = 0.065$; 18 families). This weakening reflects the estimator of between-species variance rather than relatedness: restricted maximum likelihood estimated twice the variance that the DerSimonian–Laird method did. H5 is therefore not supported. The direction of the trait effects is consistent across models, but their strength depends on how relatedness and between-species variance are modelled.

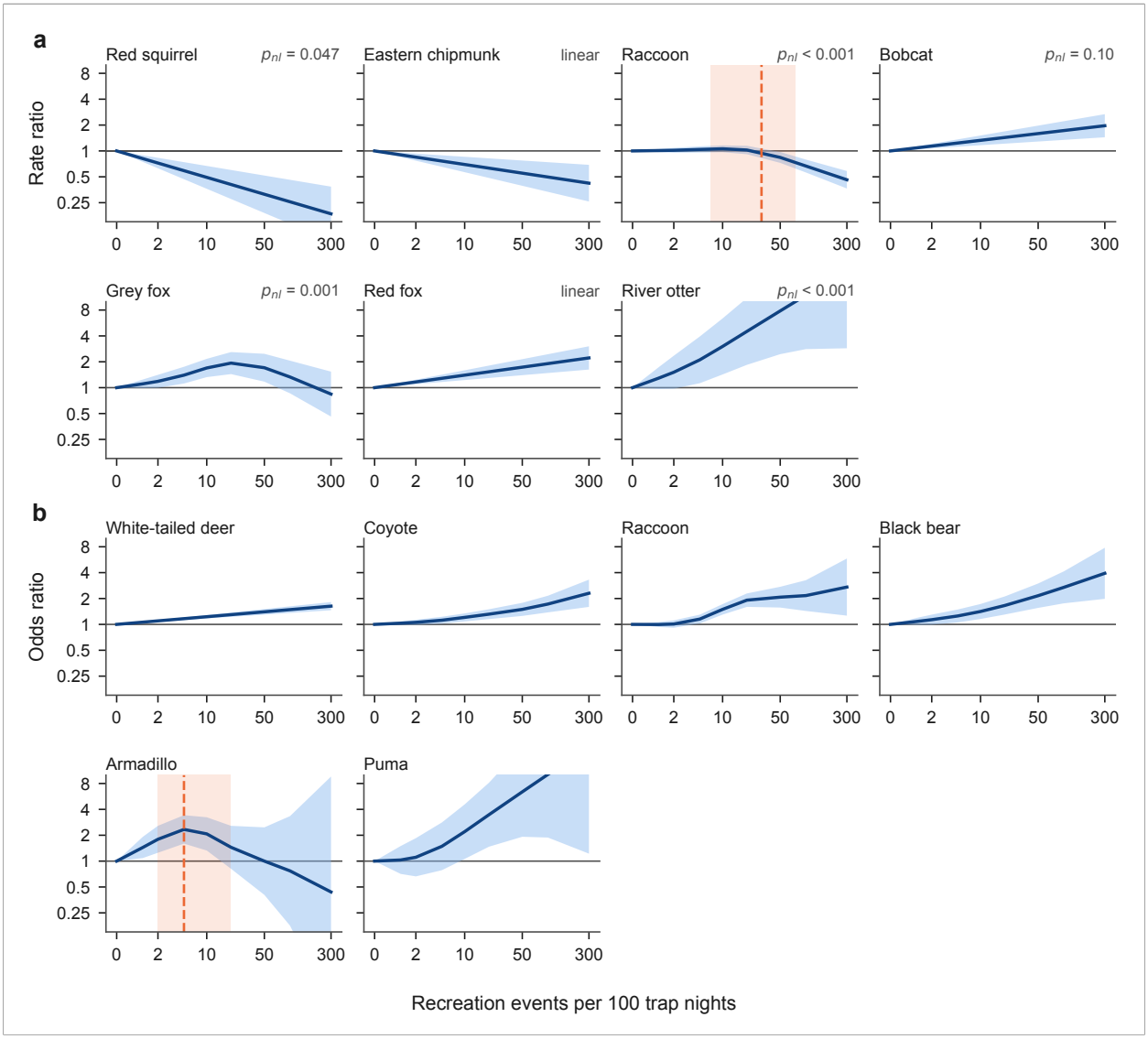


Figure 4: Most responses changed steadily with traffic; raccoon detections fell only beyond about 30 events per 100 trap nights. Curves show each robust effect relative to a camera with no traffic, with 95% confidence bands, for (a) detection rate and (b) night share. They come from the smooth traffic term of each species model, predicted at a reference camera off trails and roads with median habitat and distance to trail, without the random effects. In (a), the label gives the likelihood-ratio test of a curved against a straight-line traffic term (p_{nl}), and "linear" marks species whose curve reduced to a straight line. No such test is available for the quasi-binomial night-share models in (b). The dashed line and shaded band mark a breakpoint and its bootstrap 95% confidence interval (1,000 resamples of arrays), shown where the hinge model found one: raccoon detection rate and armadillo night share. Traffic is on a $\log(r + 1)$ scale, and curves are cut at the axis limits.

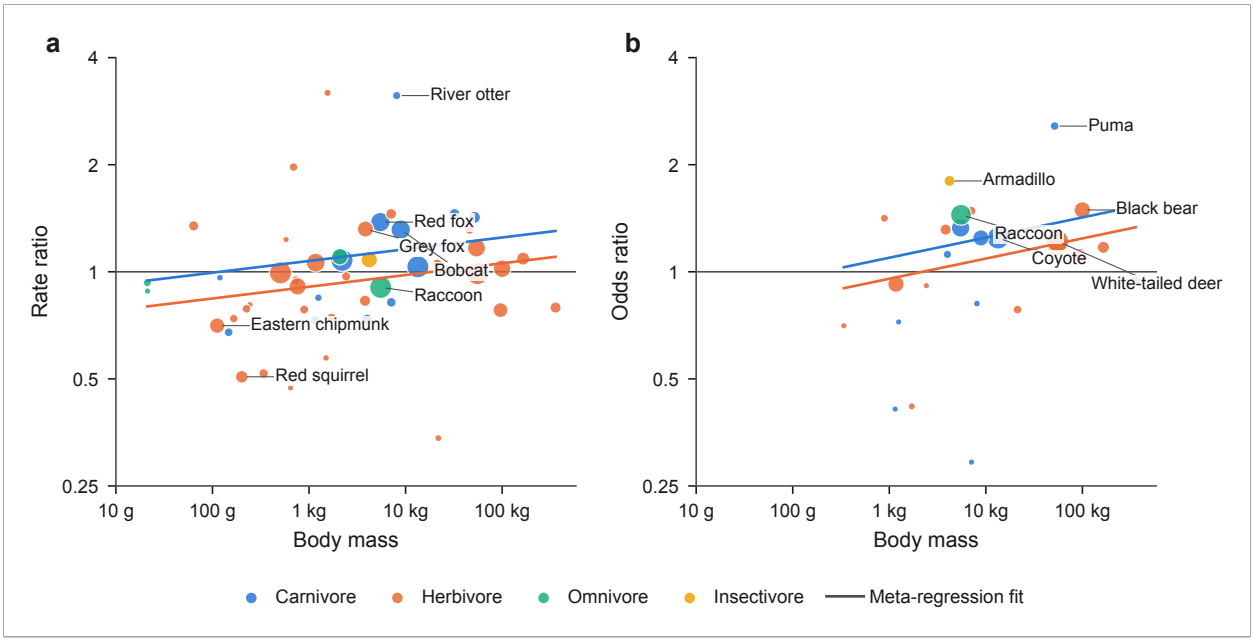


Figure 5: Body mass appeared to predict how species responded, but the pattern did not survive accounting for shared ancestry (see text). Each point is one species' effect per tenfold increase in traffic on (a) detection rate and (b) night share, plotted against its body mass and coloured by diet guild. Larger points are more precise (area proportional to 1/SE, capped at both ends). Lines are the meta-regression predictions for carnivores (blue) and herbivores (orange), the reference guild and the largest other guild. Species with robust effects are labelled.

3.6 How far from the trail does the effect reach?

If the effect of traffic were local, the effect of a trail's use would be strongest beside it and fade with distance. Using the traffic of each array's on-trail cameras as the dose, three effects varied with distance, and in each the effect weakened away from the trail (Fig. 6). Raccoon detections declined with trail traffic at the trail (rate ratio 0.62, 0.48–0.79, per tenfold increase in traffic) and at 10 m (0.73, 0.60–0.89). The confidence interval first included one at 35 m (0.88, 0.74–1.04), and from 100 m outward the effect was absent (1.00, 0.85–1.17; $p = 0.010$ for variation with distance). The night shift of white-tailed deer was largest at the trail (odds ratio 1.19, 0.99–1.42) and faded to 1.02 (0.92–1.14) at 300 m ($p = 0.037$), and that of coyote fell from 1.31 (0.96–1.80) at the trail to 1.04 (0.86–1.27) at 100 m ($p = 0.029$). For deer and coyote the gradient was supported, although no single distance had an interval clear of one. Raccoon night share also varied with distance ($p < 0.001$), but without a consistent gradient. For the remaining estimable effects, trail traffic was not associated with the response at any distance, and puma and river otter were detected in too few of these arrays to estimate. H6 is therefore supported for raccoon detections, with a zone of influence of about 35 m, and less firmly for the night shifts of deer and coyote.

This leaves a question: if trail traffic does not explain the fox, bobcat, squirrel and chipmunk effects, what does? These effects were estimated with the traffic recorded at each camera, and people were recorded far from mapped trails as well as on them. When we used that measure

in the distance model, 9 of the 13 effects did not vary with distance to a mapped trail (Fig. S2): people met at a camera 1 km from a trail were associated with the same response as people met on one. The red squirrel decline, for example, was 0.39 (0.23–0.66) on trails and 0.61 (0.39–0.94) at 1 km ($p = 0.64$). These species therefore appear to respond to people where people actually are, including off the mapped trail network, rather than to the use of the nearest trail. The analysis with trail traffic used 28% of the deployments, however, so weaker effects of trail traffic on these species cannot be excluded.

3.7 Does it matter whether people stay on official paths?

If people who leave the official network add to its effect, the same traffic should be associated with stronger responses where unofficial paths are dense. For six of the 13 robust effects, the effect of traffic differed with unofficial path density ($q < 0.05$; Table S5). In each of the six, the response was less favourable to wildlife where unofficial paths were dense (the 90th percentile) than where there were none. Red squirrel detections declined more steeply (0.29, 0.18–0.47, per tenfold increase in traffic, against 0.78, 0.52–1.15), and raccoon detections declined only where unofficial paths were dense (0.74, 0.68–0.80, against 1.18, 1.08–1.29). The night shift of deer was slightly stronger (1.29 against 1.16). The increases of red fox, grey fox and bobcat were present where there were no unofficial paths (1.95, 1.84 and 1.43) and absent where they were dense (1.03, 0.99 and 1.04). At equal traffic, red foxes were also detected less than half as often at cameras with dense unofficial paths (0.45, 0.30–0.68), and raccoon night share was higher (1.61, 1.18–2.21).

Only part of this pattern is specific to unofficial paths. Where official paths were dense, the raccoon decline was again steeper (0.84 against 0.96 per tenfold increase in traffic), the red fox increase was weaker (1.19 against 1.58) and the night shift of coyote was stronger (1.46 against 1.16; each $q < 0.01$). For raccoon and red fox, then, what matters may be the density of paths rather than their status. The steeper red squirrel decline, the loss of the grey fox and bobcat increases and the stronger deer night shift appeared only with unofficial paths.

The dispersed-use index gave no consistent pattern. Raccoon night share rose more steeply with traffic where use was dispersed (2.13 against 1.21 per tenfold increase in traffic), but the deer night shift weakened (1.05 against 1.36), and no other interaction passed the false discovery rate. The index varies only between arrays, so it is confounded with region and survey design, and it was correlated with traffic ($r = 0.49$). We therefore give it little weight.

3.8 How robust are these conclusions?

The night-share results were sensitive to how dispersion was modelled, which is why we adopted the quasi-binomial family. Under it, the standard deviation of the permuted test statistics was 1.2–2.0. This is much closer to the nominal value of one than under the binomial model (1.8–2.9), and the permutation test remains the more conservative check. Residual spatial autocorrelation in the detection-rate models was weak (median Moran's I 0.064, maximum 0.17). It was nevertheless

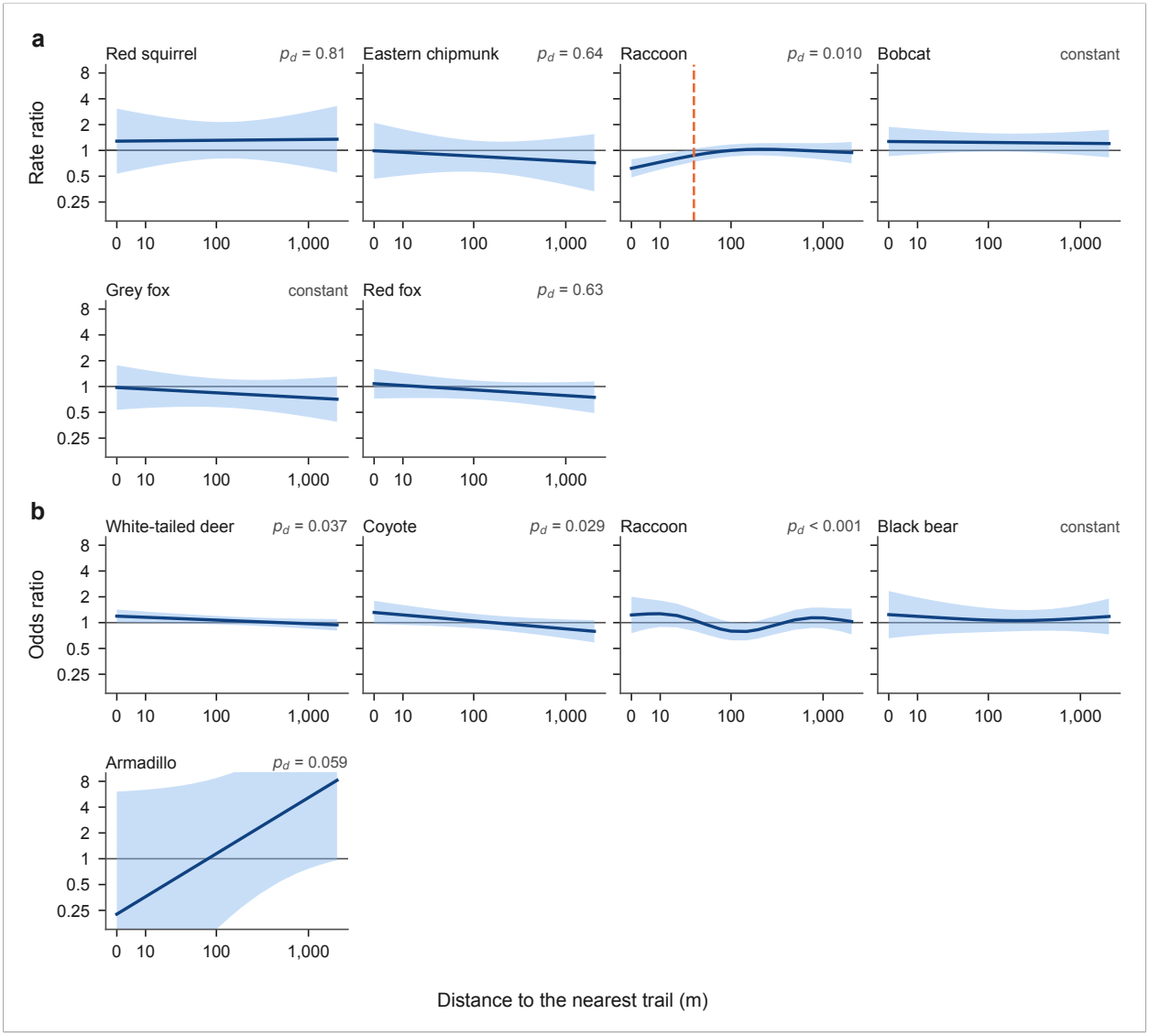


Figure 6: Where trail traffic mattered, its effect was confined to the first tens to hundreds of metres from the trail. Curves show the effect of trail traffic per tenfold increase in traffic at each distance from the nearest mapped trail, with 95% confidence bands, for the robust effects on (a) detection rate and (b) night share. Trail traffic for each camera is the mean traffic recorded by the other on-trail cameras of its array in that year (3,527 deployments in 113 arrays). p_d tests whether the effect changes with distance, against a model with one effect at all distances; "constant" marks effects for which the model chose a single effect. The dashed line marks the zone of influence, the distance at which the confidence interval first includes one. River otter detections and puma night share are not shown: these species were detected in fewer than 20 of the 113 arrays (11 and 9), too few to estimate. Distance is on a $\log(m + 10)$ scale, and curves are cut at the axis limits. Fig. S2 shows the same model with the traffic recorded at each camera.

detectable for 44 of 49 species, so the array random effect absorbs most, but not all, of the spatial structure (Text S1). No robust effect changed direction in any sensitivity analysis.

Because traffic in 2020 was unusually high, we asked whether the pandemic years drove the results. They did not. Fitted with separate slopes for 2020 and 2021, all 13 robust effects kept their direction in the other four years, and for 12 of them the confidence interval excluded one (Table S3). The exception was raccoon detection rate (0.94, 0.87–1.01), whose decline was steeper in 2020 (0.71, 0.62–0.81). This is what the breakpoint model predicts, since 2020 had more cameras above the threshold, and the threshold itself did not depend on the pandemic: without 2020 it lay at the same traffic level (30 events per 100 trap nights, 7–75), with a decline beyond it of 0.47 (0.18–0.75). The joint test found that the slope in the pandemic years differed from that in the other years for three of the 12 effects where it could be computed. Besides the steeper raccoon decline, the red fox increase was weaker in 2020 (1.05 against 1.54 in the other years), and the deer night shift was stronger in 2021 (1.43 against 1.19). The bobcat increase, for which the joint test failed, was also absent in 2021 (0.89, 0.65–1.22; $p = 0.009$ for the difference). The pandemic thus changed the strength of some responses, but none of the conclusions. Table 3 summarizes the evidence for each hypothesis.

Table 3: The six hypotheses, how each was tested and what the evidence shows.

	Hypothesis	Test	Evidence
H1	Detection rate declines with traffic	Per-species negative binomial GAMM; pooled slope	Not supported as a general rule; three species decline, four increase
H2	Night share rises with traffic	Per-species quasi-binomial GAMM; pooled slope	Supported; six species shift toward the night, none toward the day
H3*	The shift reflects fewer day detections	Separate night and day models	Varies by species: deer and raccoon withdraw by day; coyote and puma increase by night
H4	Responses steepen beyond a traffic level	Likelihood-ratio tests; hinge model with bootstrapped breakpoint	Largely not supported: raccoon detections fall beyond about 30 events per 100 trap nights; armadillo night share saturates at about 5; other responses smooth or steady
H5	Sensitivity depends on body mass and diet	Random-effects meta-regression, with family and species random effects	Not supported: mass effects in the expected direction lose support once family is included
H6	Effects fade with distance from trail	Trail traffic slope varying smoothly with distance	Supported for raccoon detections (zone of about 35 m); night shifts of deer and coyote fade within 100–300 m; other effects follow people recorded at the camera, not trail traffic

*Exploratory: formulated after the night-share results were known.

4 Discussion

We set out to ask whether busy trails empty the surrounding landscape of mammals or push them into the night. Across the United States the answer leans clearly toward the night. Detection rates showed no general decline with traffic. By contrast, the share of activity at night rose with traffic in the pooled estimate, robustly in six species and in the opposite direction in none. This is the pattern Gaynor et al. (2018) described from studies of human disturbance worldwide, here expressed as a continuous response to a measured dose of trail traffic within a single standardized survey. An earlier analysis of SNAPSHOT USA likewise found that coyotes were most active at night where human development was high (McTigue et al., 2024). For many species, then, a trail's cost may lie less in where animals can live than in when they can be active.

The species that did decline were small and largely diurnal: red squirrel and eastern chipmunk. For such species, a busy trail overlaps with most of their active hours, so a shift into the night may not be open to them, although we did not test this directly. Western grey squirrels and brush rabbits were likewise less frequent near trails in California (Lacour et al., 2025). At first sight this conflicts with the finding that human footprint favours smaller, faster-reproducing species (Suraci et al., 2021). However, that study separated footprint, the modification of land, from presence, the people themselves, and found that species could respond to the two differently. Our dose measures presence, and our models hold measures of footprint (development, land cover, roads and trail density) constant. Where presence was measured directly, in central California, larger predators avoided people in time rather than in space, whereas smaller ones were less active where people were present (Nickel et al., 2020). That is the same division between large and small species that we found.

Several carnivores showed the opposite pattern: red and grey foxes, bobcat and river otter were detected more often where traffic was higher. This contrasts with studies in which carnivores were the group most sensitive to people (Reed and Merenlender, 2008; Burton et al., 2024; Thompson et al., 2025). Part of the difference may lie in the species and part in the comparison. The wariest species, such as the wolves and grizzly bears of the Canadian Rockies (Thompson et al., 2025), are rare in our data, whereas the species that increased here are mesopredators. Reed and Merenlender (2008) compared protected areas with and without recreation, a contrast between places, whereas our estimates compare cameras within the same array. And during the pandemic, mammals in developed areas were more active, not less, where human activity was higher (Burton et al., 2024). One explanation for the increases is that people act as a shield, deterring larger predators or competitors and making busy areas safer for mesopredators (Berger, 2007; Muhly et al., 2011). Another is that carnivores use trails as travel routes: many predators selected trails in eastern US forests (Kays et al., 2017), and elusive carnivores in Italy were detected mainly on them (Greco et al., 2025). Two results argue against trail travel as the whole explanation. All four increases held when the analysis was restricted to cameras that were not on a hiking trail (Table S2), and none of the three that could be tested was associated with the traffic of nearby trails. The carnivores were detected more often where people were recorded, not where trails were busy.

The distance results sharpen this picture. Where trail traffic mattered, its effect was local. Raccoon detections fell only within about 35 m of a busy trail, and the night shifts of deer and coyote weakened within 100–300 m, although no single distance differed clearly from no effect. These distances are short compared with the several hundred metres over which grizzly bears and wolves avoid busy trails in the Rocky Mountains (Thompson et al., 2025), as might be expected of species that live close to people. In Washington, most responses to recreation extended away from trails and roads, but some disappeared a short distance from them (Gump and Thornton, 2023), a mixture much like ours. For the other species, the response followed the people recorded at the camera itself, whether that camera stood on a mapped trail or a kilometre from one. People were common away from the network: 30% of all recreation events were recorded more than 100 m from any mapped path. This suggests that how use spreads through a landscape, and not only how much of it the official trails carry, may matter to wildlife.

Our exploratory tests point the same way but do not settle the question. At equal traffic, several responses were less favourable to wildlife where paths were dense: declines were steeper, the deer night shift was stronger, and the increases of foxes and bobcat disappeared. Some of these differences appeared only with unofficial paths and others with official paths as well. Our measure of unofficial paths also mixes paths made by users with local trails that the federal layer does not map, and a direct index of dispersed use gave no consistent result. We therefore offer these results as a hypothesis rather than a finding: that the same number of people affects wildlife more when spread over a dense, partly informal network of paths than when kept to a few maintained trails.

That hypothesis can be tested more directly than our data allow. Where managers have mapped informal trails, the two networks can be separated on the ground rather than by subtraction from a federal layer. Where informal trails are closed or restored, cameras placed before and after closure, on the remaining trails and in the closed areas, would come closer to a test of cause. Trail counters on official trails, paired with cameras away from them, would show how much of the use in a landscape leaves the network, and tracking of visitors could show where it goes. The shape of our response curves suggests one further prediction. Responses were linear in the logarithm of traffic, so at a single camera a tenfold increase had the same effect whether traffic started low or high. If this holds, the first visitors to an undisturbed place matter more than further visitors to a busy trail, and a fixed amount of use would affect wildlife less in total when concentrated than when spread. Whether it does depends on how responses at single points add up across a landscape, which camera points alone cannot show.

We expected traits to explain why some species respond and others do not, and at first sight they did: larger species tended to shift toward the night rather than decline. This is the opposite of what was found across four Italian protected areas, where larger species avoided people and smaller ones were more opportunistic (Salvatori et al., 2024), but it matches the split between large and small predators in California (Nickel et al., 2020). In our data the pattern did not survive accounting for shared ancestry, however. Much of it rested on a few families, such as bears and cats that became more nocturnal and hares and rabbits that did not. This agrees with the finding

that, across North America, responses to human presence were unrelated to species traits, unlike responses to human footprint (Suraci et al., 2021). It is a useful negative result. A rule based on body size would be easy to apply in management, but with 27 to 49 species and strong family structure, the present data cannot separate the effect of size from the effect of lineage. A larger set of species, or surveys that sample several members of each family, would be needed to test it.

We also expected tolerance to have limits, with responses that steepen once traffic passes some level. Only raccoon behaved this way: its detections were unaffected up to about 30 recreation events per 100 trap nights and fell steeply beyond. Combined with the distance results, this describes a species that tolerates light use but withdraws from the immediate surroundings of busy trails, and the threshold was the same without the pandemic year 2020. For the other species, the responses were smooth or steady, and a single traffic limit would misrepresent them. Armadillo's night share even saturated at low traffic, so the first few people may matter more to it than any further increase.

Several limitations qualify these conclusions. The design is observational. Cameras were not placed at random with respect to traffic, and although trail placement, habitat and a permutation test address the most obvious confounders, they cannot establish cause. Camera events are an index of traffic, not a count of visitors, and relating them to trail-counter data is needed before the curves can be read as visitor numbers. SNAPSHOT USA surveys only in autumn, so seasonal responses, such as those during breeding, are outside its scope. Some spatial structure remains in the residuals. The test of distance from trails rests on the 113 arrays with cameras on trails, so it has less power than the main models. The tests of path type and dispersed use were exploratory, lacked the permutation test and rest on a measure of informal paths that includes unmapped official trails. Finally, detection depends on activity as well as presence, so a change in detection rate may reflect a change in movement rather than in numbers.

For managers, these results point to two levers, supported to different degrees. The first is timing. The shift into the night was the most consistent response to traffic, so limiting use at dawn, at dusk and at night would protect the hours into which many species move. A study in the Canadian Rockies reached a similar conclusion, recommending that use be concentrated in the middle of the day (Lamb and Chow, 2026). Such limits can be hard to apply, however, because recreation follows daylight and people's schedules. The second lever is space: keeping use on a limited number of maintained trails and closing informal ones. Our results are consistent with this lever, since several species responded to people away from the mapped network and some responses were less favourable where paths were dense, but they do not show that it works. It is the lever that the tests outlined above would evaluate. Because most responses lack a clear threshold, the response curves are better read as gradients of change than as limits that can be safely approached.

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