Gray wolves follow white-tailed deer across Wisconsin (2018-2025), rising briefly after the 2021 wolf harvest

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Abstract

Earlier analyses of county-level extracts of the Snapshot Wisconsin camera network suggested that gray wolves (*Canis lupus*) arrive at cameras shortly after white-tailed deer (*Odocoileus virginianus*), select antlered bucks, and displace deer, but their wolf samples were too small to settle whether following rose after the February 2021 wolf harvest, whether displacement weakens near development, and how wolves respond to people. I tested these with a statewide extract (7,791,771 detections, 5,371 cameras, 2018–2025; 461 sequential wolf–deer encounters) and ran the same measures for coyote, black bear, bobcat, and wild turkey, the last as a non-predator control. Wolves arrived after deer in 74% of encounters against 50% under a permutation null ($P = 0.002$), in every zone with wolves and at every level of local wolf activity, a median 5.9 min behind; in the hard-antler months the wolf's nearest deer was a buck 1.40× more often than availability predicted ($P = 0.004$). The harvest produced a pulse: following rose from 0.63 (2019–2020) to 0.83 (2022–2023; odds ratio 2.75, $P = 0.002$) and returned to 0.68 by 2024–2025, with no change in any other species. Deer returned 2.19× more slowly after a wolf than their baseline, and 2.5× more slowly than a random-instant null expects; the delay was larger in forest than farmland and declined with development, but did not vary across a 12-fold

range of wolf activity. Against the same null, deer avoided people everywhere (2.1× the null), coyote, bear, and turkey modestly (1.1–1.15×), and wolf and bobcat not at all: the wolf's raw delay after a person is what sparse, clustered visits produce by chance. Following is the wolf's normal behavior, briefly intensified by the harvest; displacement is mediated by the landscape.

Keywords: camera trap, *Canis lupus*, human disturbance, landscape of fear, *Odocoileus virginianus*, predator–prey, Snapshot Wisconsin, wolf harvest

Teaser text

Across Wisconsin's wolf range, trail cameras show wolves arriving a few minutes behind deer. The 2021 wolf hunt briefly made that more common, then it faded. Deer stay away longer after a wolf in forest than in farmland; wolves show no measurable avoidance of people.

Two earlier analyses of this camera record, by the author, of a one-county and then a five-county extract, left three specific questions open. First, following appeared to be almost entirely a post-wolf-harvest behavior: wolves arrived after deer in 55% of encounters before February 2021, no different from chance, and in 85% after, but the pre-harvest sample held only 40 encounters. Second, deer displacement by wolves appeared strongest in undeveloped country and weakest near towns, but splitting the record by period, place, and deer class left only a few dozen wolf encounters in each cell. Third, the wolf's own delay in returning after a person, the largest response measured, was stronger in the southern counties, and the five-county record could not distinguish among three possible causes: latitude, the history of wolf recolonization (Wydeven et al. 2009), and the amount of human development. All three questions required more wolf encounters over a wider area.

This report used such a record. The Wisconsin Department of Natural Resources (DNR) Office of Applied Science produced a statewide extract with the same extraction script as the

prior two, with the county filter removed. The statewide extract contained 12 times the detections of the five-county extract and four times its wolf–deer encounters, and it covered the full occupied wolf range.

The wider record also allowed a cleaner test of the wolf harvest question. The February 2021 wolf hunt was short and intense: roughly 218 wolves were killed in under three days, the state quota was exceeded, and hunters and hounds were active in wolf country in the weeks before and after the season (Treves and Louchouarn 2022). Because the disturbance was not confined to the three days of the hunt, I treated all of 2021 as affected. The main comparison was therefore the two years before the hunt (2019–2020) against the two years after (2022–2023). The later years (2024–2025) were first set aside, under the hypothesis that wolf behavior returns toward its earlier state as time passes, and that hypothesis was then tested directly.

The larger record allowed two further checks. The extract included coyote (*Canis latrans*), black bear (*Ursus americanus*), bobcat (*Lynx rufus*), and wild turkey (*Meleagris gallopavo*). If the wolf harvest changed wolf behavior specifically, the change should appear in wolves and in no other species using the same trails over the same years. And if the return-delay measure reflects danger, that measure should find little when it is applied to the turkey, which poses no danger to deer.

Finally, the statewide extract changed how the landscape was measured. Wisconsin's four Deer Management Zones (Northern Forest, Central Forest, Central Farmland, and Southern Farmland) divide the state from remote forest to settled farmland. Two established ideas helped make predictions along this gradient: prey avoid the places a predator makes dangerous (the "landscape of fear"; Laundré et al. 2001), and prey gain protection near people because predators avoid people (the "human shield"; Berger 2007). Human activity is also known to shift wildlife

activity patterns at this state's scale (Gaynor et al. 2018; Gilbert et al. 2022; Clare et al. 2023). An index of local wolf activity at each camera added a test the five-county record could not support: whether the deer's response to a wolf depends on how often wolves are present. The risk allocation hypothesis predicts that it should; an animal facing frequent danger cannot afford a strong response to every instance of it (Lima and Bednekoff 1999).

Methods

Dataset and validation.

The data are a statewide extract of the Snapshot Wisconsin citizen-science camera network (Wisconsin DNR Office of Applied Science), built from the same extraction script as the two prior wolf-enriched extracts with the county filter removed. The extract has the same three tables as before (detections, survey effort, and a human-modification covariate) joined on a shared camera identifier. It held 7,791,771 detections on 5,371 cameras (5,395 cameras of effort; 103,375 camera-months; each camera-month carried its days active and a 1-mi² Public Land Survey System section location), from January 2018 through December 2025. Wolves appeared on 810 cameras, with 7,742 wolf detections against the five-county record's 1,856. The extract also carried 190,596 coyote, 33,243 black bear, 18,516 bobcat, and 452,275 wild turkey detections. Deer data arrived already resolved to antlered, antlerless, and fawn classes; this report pooled all deer classes for the main analyses. Two class-resolved results that require no landscape covariate, buck selection in the hard-antler months and the bear's following of fawns, are reported here, and the full class-resolved analysis is left to a companion analysis (in preparation). The extract was checked against the five-county record directly: sampled five-county wolf records appeared identically in the statewide file, all three tables joined with no unmatched records, and effort was complete for every camera-month. No animal was captured or

handled for this study; the data are volunteer camera-trap photographs, and the work is consistent with the American Society of Mammalogists' guidelines for the use of wild mammals in research (Sikes et al. 2016).

The human-modification covariate in the initially delivered extract was built from a different source layer (the 2022 static Global Human Modification snapshot at 90 m resolution) than the 1-km native-resolution layer used in the prior extracts (Kennedy et al. 2019). On the 527 cameras shared with the five-county extract, the two versions correlated at only $r = 0.44$. That delivery was set aside, and the covariate was re-pulled at the native 1-km scale (Google Earth Engine, Global Human Modification collection, 1,000-m scale, no resampling). The re-pull was verified before use. On the 526 shared five-county cameras with values in both extracts, it correlated with the parent layer at $r = 0.97$. The medians were identical (0.203 in both), and the median difference was zero. The accompanying raster agreed with the per-camera table when sampled independently. All but six cameras received values, and none of those six ever recorded a wolf. Development analyses in this report use the verified 1-km values. The Deer Management Zones carried the broader landscape context. Before any statewide analysis was run, the full analysis pipeline was rebuilt from the raw five-county files and required to reproduce the earlier values exactly. It did: 116 sequential encounters (4 co-occurrences), follow fraction 0.75, median lag 5.8 min, before and after fractions 0.55 ($n = 40$) and 0.85 ($n = 76$), 559 pre-harvest wolf detections, and return-delay ratios of 2.24× (110 cameras), 1.83× (432), and 2.78× (89). The identical code produced everything reported here. Analyses were run in Python 3 (numpy, scipy, statsmodels).

Zones, coordinates, and the wolf-activity index.

Each camera was assigned to a Deer Management Zone by point-in-polygon against the DNR's published zone boundaries (Wisconsin DNR 2026). The camera's location was the center of its PLSS section, converted to coordinates accurate to about 1.6 km, sufficient at zone scale, uncertain only for cameras within about 1.6 km of a zone boundary. The camera locations were distributed as follows: Central Farmland 2,066, Southern Farmland 1,643, Northern Forest 1,520, Central Forest 166. Cameras carrying wolf detections followed the distribution of packs: 528 in the Northern Forest, 203 in the Central Farmland, 69 in the Central Forest, and 10 in the Southern Farmland. The Southern Farmland is an area wolves cross but where no packs are established; its values are shown in tables but excluded from tests. Local wolf activity at each camera was indexed as independent wolf detections (30-min independence) per 100 camera-days. The 810 wolf cameras were split into thirds of 270 cameras each, with median activity 0.12, 0.40, and 1.49 per 100 camera-days, a 12-fold range.

Measures.

All measures are unchanged from the earlier analyses. For each detection of a focal species, the nearest deer at the same camera within 30 min on either side was scored as *co-occurrence* (within 30 s; excluded from the directional test), *follow* (the deer came first), or *precede* (the deer came after). The follow fraction is FOLLOW / (FOLLOW + PRECEDE); 0.50 means no consistent order. Significance was assessed with a permutation test: in each of 500 iterations, every detection of the focal species was moved to a random date on which its camera was active in the same season, keeping its time of day, and the classification was recomputed. This comparison holds camera, season, time of day, and deer availability fixed, so it shows what follow fraction would arise with no temporal association. The encounter window was also varied

(15, 30, and 60 min) as a sensitivity check. Displacement was measured per camera as a ratio: the median time for a responder to return after a disturber has passed, divided by the responder's own median interval between independent detections. A camera qualified if it had at least three baseline intervals and three post-disturber returns. A ratio above 1.0 means the animal returned more slowly than usual. A Wilcoxon signed-rank test on the log ratio tests whether the delay exceeds 1.0. Group comparisons used Fisher's exact test for proportions, Mann–Whitney *U* and Kruskal–Wallis *H* tests for ratio distributions, Spearman rank correlations for continuous gradients, and logistic or ordinary-least-squares models when several influences were held constant at once.

A null expectation for the return-delay index.

A ratio of 1.0 is not the right reference for the index when a responder's visits are sparse and clustered, because the time from an arbitrary instant to the next visit is then longer than the typical gap between visits. I therefore built a null expectation for each camera and pair: every passer detection was moved to 20 random days on which the camera was active, keeping its time of day, and the delay to the responder's next detection was measured from those instants exactly as from the real ones. The null ratio is the median of those delays divided by the same baseline. The quantity of interest is the observed ratio relative to the null ratio, paired within camera and tested with the Wilcoxon signed-rank test on the log difference; a value of 1.0 means the responder returned no later after the passer than after a random instant at the same hour. Raw ratios are reported alongside, because they are what the earlier analyses reported and what other camera studies will compare against.

Analyses of the other species, and the turkey control.

Every measure was then run, unchanged, for four other species: coyote, black bear, and bobcat (the other mammalian predators the cameras record in numbers) and wild turkey. The turkey served as the control. It is not a predator of deer, so its follow fraction in relation to a deer shows what the directional measure reports when no predator–prey relationship exists, and the deer's return delay after a turkey estimates the part of any passage-keyed delay that does not come from danger. The wolf-harvest window comparison was applied to every species in the same way. This made the other species a specificity check: an effect of the wolf harvest should appear in the harvested species and in no other.

Deer classes and seasonal windows.

Volunteers resolved deer to antlered, antlerless, and fawn classes, but the classes are only readable in season. In September–December, the hard-antler months, an antlered deer is reliably a buck and an antlerless deer reliably a doe. For most of the rest of the year antlers are absent or in velvet, and the classes blur. Fawns are reliably classifiable while they carry spots, from May through August. By fall, many fawns are recorded as antlerless, so fall fawn results are read with that loss in mind. The class-selection test asked whether the class of the wolf's nearest deer departed from what the cameras showed. The expected share is the class composition of deer detections at the same cameras within the same window. Significance comes from 10,000 draws in which each encounter's class is drawn from its own camera's shares.

Design of the wolf harvest comparison.

The primary comparison excluded 2021 entirely, because hunter activity preceded the February season and continued after it. It compares 2019–2020 (101 wolf–deer encounters, from 1,611 wolf detections) against 2022–2023 (115 encounters, from 2,504). The years 2024–2025 were

held out and then used to test whether behavior returned to its earlier state. The simple split of all years at 22 February 2021 is reported as a robustness check. Two controls address wolf numbers: post-harvest wolf detections were subsampled to the pre-harvest count (300 draws), and the wolf-activity index was carried as a covariate. The other species provide the third, specificity control.

Results

Wolves arrive after deer throughout the statewide record; the other species sort by their relationship to deer.

Across the occupied range, 461 sequential wolf–deer encounters (51 co-occurrences within 30 s excluded) gave a follow fraction of 0.74, against the permutation value of 0.50 ($P = 0.002$; Table 1). The result does not depend on any one place or any one level of wolf density. It is significant separately in the Northern Forest (0.73, $n = 251$, $P = 0.002$), the Central Forest (0.84, $n = 25$, $P = 0.006$), and the Central Farmland (0.74, $n = 182$, $P = 0.002$), and in each third of the wolf-activity range (0.69, 0.68, 0.75; $P = 0.068$, 0.034, 0.002). In a joint model, the odds that a wolf arrived after a deer rose 1.29× per standard deviation of log wolf activity ($P = 0.023$). The median gap between the deer's passage and the wolf's arrival was 5.9 min overall and stayed between 3.8 and 6.3 min in every subset, matching the five-county value of 5.8. Widening the encounter window lowered the follow fraction (0.79, 0.74, and 0.71 at 15, 30, and 60 min) and left the permutation value at 0.50 and P at its floor at every width. As in the earlier analyses, what varies across time and place is *how often the wolf arrives after a deer, not how closely*.

The hard-antler months gave the earlier buck-selection finding its statewide test, and it passed. The window held 151 wolf–deer encounters. Following was at its strongest there (0.79, permutation $P = 0.004$). Among the 125 encounters whose nearest deer was a classed adult,

43.2% were bucks. Only 30.9% of the classed adult deer at the same cameras in the same months were bucks. The wolf's nearest deer was therefore a buck 1.40× more often than chance (P = 0.004). The rut sharpened the selection: in October–November, 52.2% observed against 35.2% available (1.48×, P = 0.004). The same test run across the whole year found almost nothing (1.10×, P = 0.37). The selection was not absent in the other months; it could not be seen, because without hard antlers the classes cannot be read. An all-year analysis dilutes a real seasonal signal.

The other species order themselves by their relationship to deer (Table 3; Fig. 5A). Coyote and bear also arrived after deer more often than chance, 0.61 over 13,461 encounters and 0.63 over 1,953 (both P = 0.002), respectively, but with longer gaps: 9.6 and 10.9 min against the wolf's 5.9. The bear's following resolved to a target. In May–August, when the nearest deer was a fawn, the bear was the second-comer in 82% of encounters (78 of 95). When the nearest deer was a doe, the bear was second in 59% (Fisher's exact P = 0.00001). Here the follow measure detects a target within a species, not merely a species. Bear–fawn encounters all but vanish from the fall record: 7 statewide in September–November. Part of that is real, as fawns grow and travel with doe groups. Part is hidden, because a September fawn without spots is recorded as antlerless. The bobcat, which hunts from ambush and does not trail adult deer, showed no consistent order (0.52, n = 1,086, P = 0.19). The turkey landed at chance: across 30,323 turkey–deer encounters the follow fraction was 0.49, against a permutation value of 0.50 (P = 0.87). The measure therefore reported no following where no following existed, and the ordering it returned, a chasing hunter first (wolf), two generalists next (bear and coyote), an ambush hunter (bobcat) and a non-predator (turkey) at chance, matched each species' hunting relationship to deer.

The wolf harvest effect was temporary, and it appeared only in the wolf.

The clean comparison shows *the wolf harvest effect at nearly three times the strength* of the simple split. Following ran 0.63 in 2019–2020 (64 of 101) and 0.83 in 2022–2023 (95 of 115; Fisher's exact test, odds ratio 2.75, $P = 0.002$; odds 2.77×, $P = 0.002$ with zone held constant in a logistic model). The all-years split gives 0.67 (82 of 123) against 0.76 (258 of 338; odds ratio 1.61, $P = 0.042$; Fig. 2). The by-year record explains the difference (Fig. 1). The follow fraction ran 0.61–0.65 through 2019–2020; rose with the wolf harvest to 0.87 in 2021 (0.88 in the months after 22 February) and 0.91 in 2022; stood at 0.77 in 2023; and was 0.65 in 2024. The years held out under the return-to-baseline hypothesis confirm it: 2024–2025 (0.68, $n = 167$) is indistinguishable from the pre-harvest years (odds ratio 1.24, $P = 0.43$) and significantly below 2022–2023 (odds ratio 0.45, $P = 0.008$). The simple split is weaker because it averages the temporary rise with its own decline.

The other species provide the specificity check. Run through the same year windows, the coyote did not change (0.61 to 0.62 to 0.60 across the three windows; Fisher's exact $P = 0.35$), although its encounter sample is 30 times the wolf's and it uses the same trails. The bear did not change (0.64, 0.64, 0.63; $P = 0.95$), and neither did the turkey (0.49, 0.50, 0.49; $P = 0.26$). *Whatever changed in 2021–2023 changed only in the harvested species*. Weather, deer behavior, camera effort, and other landscape-wide influences were excluded, because those would have moved the other species as well. (The bobcat's windows drift downward, 0.60, 0.51, 0.46, nominal $P = 0.037$, but bobcat following is indistinguishable from chance overall, this is one contrast among many run here, and it was not analyzed further.)

The change was also localized to zone. Within the clean year windows, *the Northern Forest accounts for nearly all of it* (0.56 to 0.80, Fisher's exact $P = 0.004$), while the Central

Farmland was already at 0.71 before the wolf harvest and did not change significantly (to 0.84, $P = 0.18$). Neither remaining control altered the result. Subsampling the 5,655 post-harvest wolf detections to the 2,087 pre-harvest count left the post-harvest fraction at 0.76 (95% band 0.70–0.83; 1 draw in 300 reached the pre-harvest value), and the wolf harvest term was unchanged when the wolf-activity index was added as a covariate.

Deer displacement: larger in forest zones, unchanged across wolf density.

Deer returned 2.19× more slowly after a wolf than their own usual interval (383 cameras; Wilcoxon $W = 9{,}196$, $P < 10^{-36}$). *In hours, the median interval was about 16 h at baseline and 35 h after a wolf.* Against the random-instant null the response is larger still, because a random instant at the same hour is followed by a deer sooner than the baseline gap (null ratio 0.88): the observed delay was 2.55× the null expectation ($W = 7{,}253$, $P < 10^{-41}$), and 83% of cameras lay above their own null (Table 4). The size of the delay follows the landscape: 2.38× in the Northern Forest against 1.71× in the Central Farmland (Mann–Whitney $U = 11{,}526$, $n = 266$ and 73, $P = 0.014$; across the three zones with packs, Kruskal–Wallis $H_2 = 6.32$, $P = 0.042$). Referenced to the null the zone contrast sharpens (excess 2.71× in the Northern Forest, 2.53× in the Central Forest, 1.76× in the Central Farmland; $H_2 = 10.9$, $P = 0.004$). This reproduces, on official habitat boundaries and without any satellite index, the five-county finding that *displacement of deer by wolves is strongest in undeveloped country and weakest near development* (Fig. 3).

The corrected human-modification index carried the same result onto a continuous gradient. Across the 383 qualifying cameras, the *deer's delay after a wolf declined as development increased* (Spearman $r = -0.134$, $P = 0.008$). On the wilder half of the cameras the delay was 2.53×. On the more-developed half it was 1.86× (Mann–Whitney $U = 21{,}178$, $n = 192$

and 191, $P = 0.009$). Across thirds of the index it fell steadily: 2.58×, 2.13×, 1.84×. Referenced to the null the gradient holds ($r = -0.165$, $P = 0.001$; wilder half 2.80×, developed half 2.27× the null, $P = 0.004$). The five-county gradient, deer displacement by wolves strongest in wild country and weakest near development, is therefore confirmed statewide, on the same covariate the earlier analyses used, at four times their wolf sample. By deer class, the gradient is thinner. Within the seasonal class windows, only the doe's delay runs in the gradient's direction (wilder half 1.88×, developed half 1.63×; not significant at 219 cameras). *The buck's delay does not ease near development at all*. This is consistent with the five-county reading that the near-town easing is carried by does, but it is not yet significant class-by-class at statewide sample sizes.

Wolf density does not change the delay. Across thirds of the wolf-activity range spanning a 12-fold difference, the ratio stayed near 2× (1.85×, 2.39×, 2.05× on 33, 139, and 211 qualifying cameras; Kruskal–Wallis $H_2 = 3.00$, $P = 0.22$; Spearman correlation with the continuous index $r = 0.02$, $P = 0.65$). The deer's baseline interval was also unrelated to wolf activity ($r = -0.005$, $P = 0.93$): deer used wolf-rich cameras as often as wolf-poor ones (Fig. 4). The risk allocation hypothesis predicts weaker responses where danger is frequent (Lima and Bednekoff 1999); the record shows no such weakening. The deer's delay after a wolf behaves as a response set off by the passage itself, near a doubling of the return interval wherever it occurs, rather than a response adjusted to local conditions.

The turkey provides a same-trail reference for this measure. Deer returned 1.53× more slowly even after a turkey (3,499 cameras; $W = 1{,}269{,}770$, $P < 10^{-196}$), and 1.66× the random-instant null. That delay cannot be fear of turkeys, so it estimates the part of any passage-keyed delay that comes from shared trail use and the timing of visits rather than from danger. Read against that reference, the species separate. The wolf stands well above it (2.19× raw; 2.55× the

null). The bobcat and coyote stand modestly above it (1.81× on 1,125 cameras and 1.75× on 3,479; 1.78× and 1.82× the null). The bear is only slightly above it (1.56× on 1,269; 1.60× the null): deer delayed about as long after a bear as after a turkey. The danger-specific part of the wolf's effect, the difference above the turkey value, is roughly four times the bear's (Table 3; Fig. 5B). These pooled values carry a caveat. They mix seasons and deer classes, and they compare across different sets of cameras. A companion analysis (in preparation) makes the comparison a second way, pairing each deer class's delay after a species against that same class's delay after a turkey on the same cameras within June–November; read that way the bear stands above its reference for every class, and the coyote's apparent margin disappears, so the pooled comparison understates the bear and overstates the coyote.

Avoidance of people: strong and landscape-based in deer, modest in coyote, bear, and turkey, absent in wolf and bobcat.

Deer returned 1.86× more slowly after a person (4,317 cameras; $W = 1{,}498{,}330$, $P < 10^{-300}$), 2.12× the random-instant null. The raw value was nearly the same in all four zones (1.82–1.92×; Kruskal–Wallis $H_3 = 5.75$, $P = 0.12$), but referenced to the null it was not: *the deer's response to a person was larger in the Northern Forest* (2.47× the null) and Central Forest (2.38×) than in the Central Farmland (1.97×) and Southern Farmland (1.94×; $H_3 = 39.6$, $P < 10^{-7}$), and it declined with the development index ($r = -0.087$, $P < 10^{-7}$). The deer's response to people therefore follows the same landscape gradient as its response to wolves, a gradient the raw ratio hid because the null expectation itself differs by zone.

The wolf's raw delay after a person was the largest of the three main relationships, 2.42× its own interval (278 cameras; $W = 6{,}149$, $P < 10^{-22}$; the median interval was about 28 days at baseline and 99 days after a person), and the raw value differed by zone (3.06× at 47 farmland

cameras, 2.45× at 195 Northern Forest cameras, 1.35× at 35 Central Forest cameras; $H_2 = 6.46$, $P = 0.039$). Against the random-instant null, however, none of this survives. The null expectation for a wolf's return after an arbitrary instant is 2.39× its baseline, because wolf visits are sparse and clustered, and the observed delay was 1.02× that expectation ($W = 17{,}369$, $P = 0.13$), with 54% of cameras above their null. The zone differences were differences in the null, not in the response (excess 1.09× in the farmland, 1.03× in the Northern Forest, 0.91× in the Central Forest; $H_2 = 4.85$, $P = 0.089$), and the excess was flat across the development index ($r = -0.003$, $P = 0.96$). The wolf's delay after a turkey was likewise at its null (1.03×, $P = 0.47$), and paired within camera the wolf returned no later after a person than after a turkey (1.06×, $n = 232$, $P = 0.18$). On this measure, at this record's resolution, the wolf shows no detectable avoidance of people. The wolf harvest windows showed no change in the raw measure either (2.06× in 2019–2020, 2.54× in 2022–2023, 2.30× in 2024–2025; $H_2 = 0.63$, $P = 0.73$; Table 2).

Across the five species, the raw delay after a person forms a ranking (Table 3; Fig. 5B): turkey 5.03× (2,847 cameras), bear 3.91× (992), coyote 2.50× (2,969), wolf 2.42× (278), deer 1.86× (4,317), bobcat 1.85× (901), every one above its own baseline (all Wilcoxon $P < 10^{-50}$). That ranking, however, is a ranking of how sparsely and how clustered each species visits a camera, because it follows the null expectations (turkey 4.02×, bear 3.27×, coyote 2.02×, wolf 2.39×, bobcat 1.79×, deer 0.84×) almost exactly. Referenced to the null, the order is different and the differences are small outside the deer: deer 2.12× the null, coyote 1.15× ($P < 10^{-33}$), turkey 1.12× ($P < 10^{-16}$), bear 1.11× ($P < 10^{-5}$), and wolf (1.02×, $P = 0.13$) and bobcat (1.02×, $P = 0.40$) at their null (Table 4). Paired against each species' own delay after a turkey, the bear (1.30×, $n = 821$, $P < 10^{-12}$) and coyote (1.28×, $n = 2{,}551$, $P < 10^{-35}$) returned later after a person than after a turkey, the deer did (1.17×, $n = 3{,}206$), the bobcat barely (1.08×, $P = 0.017$), and the wolf did

not. Coyotes and bobcats returned after a wolf passed at 1.57× (326 cameras) and 1.43× (232) their baselines, but both values lie below their null expectations (0.91× and 0.89× the null; P = 0.004 and 0.010): on this measure the two smaller predators returned sooner after a wolf than after a random instant, not later.

Discussion

The statewide record revised the wolf harvest story it tested, and the revised version makes better biological sense. In the five counties, following appeared to begin with the wolf harvest. Statewide, following is the wolf's normal behavior, present in every zone that holds wolves, at every density, with the wolf arriving a stable few minutes behind the deer, and the wolf harvest produced a temporary increase of two to three years that then subsided. A temporary change of this shape is what a behavioral response to a sudden population loss should look like. The February 2021 season removed roughly a third of the population within days, which disrupted pack structure directly, and the population and its social organization rebuilt over the following years (Treves and Louchouarn 2022). Temporary changes in wildlife behavior under acute human disturbance, which subside when the disturbance passes, have been documented in camera records from wartime Ukraine (Kudrenko et al. 2026). The other species added a check that single-species records could not provide: the coyote, bear, and turkey, recorded at the same cameras through the same years, the coyote at 30 times the wolf's sample, did not change across the wolf-harvest windows. Only the harvested species changed. The location of the change also aided interpretation: farmland-edge wolves already followed deer at the elevated rate before the harvest, and the change occurred among the deep-forest wolves, where the wolf population and the wolf harvest's disruption of it were concentrated. The camera record could not identify the mechanism; disrupted packs hunting less efficiently and trailing prey longer, younger pack

composition, and redistribution of surviving wolves are all possible. It can establish that the change was real, large, localized, temporary, and confined to the wolf.

The species comparison also tested the following measure itself. Coyote and bear trail deer beyond chance but less tightly than the wolf; the bobcat, an ambush hunter, shows no order; and the turkey lands at chance across 30,000 encounters. Together these results indicated that the follow fraction measures a real ordering of arrivals shaped by each species' hunting relationship to deer, and not an artifact of shared trails or clustered activity, the influences the permutation test was built to remove (see Gable et al. 2024 for direct observation of wolf–deer predation).

The displacement results separate two influences that the five-county record could not: landscape and density. Landscape changes the deer's response. *A deer in undeveloped forest stays away from a site for about two days after a wolf passes; a deer in farmland returns in under one.* This is consistent with the landscape-of-fear expectation that a predator dominates prey decisions where human presence is light (Laundré et al. 2001), and with the human-shield expectation that development blunts the predator's effect (Berger 2007; Gaynor et al. 2018). Density does not change the response. Across a 12-fold range of local wolf activity the delay neither weakened, as risk allocation predicts where danger is frequent (Lima and Bednekoff 1999), nor strengthened, and baseline deer site use was unrelated to wolf density. The response appears to be set off by the passage itself, sized by the surrounding landscape, and insensitive to how often it is set off. This is the kind of short-lived, reactive response that Clare et al. (2023) argued would be visible only at fine time scales, and it fits the framework in which predators impose costs on prey through behavior rather than through killing alone (Creel and Christianson 2008). The turkey result disciplines the measure's absolute size: about 1.5× of every such delay is unrelated to danger, and the danger-specific part is the amount above that value. On this reading,

the cost of wolves to deer accumulates with the number of encounters, not through any adjustment of the response per encounter.

The person-facing measures changed their frame once a null expectation was built for them. In the raw index the wolf appeared to be the most person-avoidant of the three main relationships, with an avoidance that varied by settlement; against the null, the wolf's delay after a person is what a sparse and clustered visitor produces after any instant, its zone differences are differences in that expectation, and the wolf shows no detectable avoidance of people at the resolution of this record. The same is true of the bobcat. The raw cross-species ranking, turkey, bear, coyote, wolf, deer, bobcat, which the earlier analyses and a first reading of this record took to follow hunting pressure, tracks the null expectations almost exactly and so measures visit sparseness, not fear. What survives is a smaller and more defensible set of statements. *Deer show the largest response to people in the record, about twice the null everywhere, and that response, like their response to wolves, is larger in the forest zones than in farmland.* Coyote, bear, and turkey show modest responses of a tenth to a seventh above the null, and the bear and coyote return later after a person than after a turkey on the same cameras. The predator-avoids-people mechanism assumed by the human-shield hypothesis (Berger 2007; Kuijper et al. 2016; Suraci et al. 2019) is therefore not measured in the wolf here, which does not mean it is absent: a wolf's return to a camera is a matter of days to weeks, and a response of hours would be invisible at that scale. The five-county north–south pattern in the wolf's raw delay is accordingly withdrawn as a finding about avoidance; what it reflected was the sparser visiting of wolves in the more settled south. The lesson for the measure is general. A return-delay ratio read against 1.0 understates the response of a frequent visitor such as deer and manufactures a response for a sparse one such as

the wolf, and camera studies that use passage-keyed return times should report the random-instant expectation beside the raw value.

The limits are of familiar kinds. These are camera detections of unmarked animals: "follow" and "return" describe the order and spacing of passages at a camera, not the movements of tracked individuals (compare the GPS-collar work of Gable et al. 2024). The zone assignment relies on section-center coordinates accurate to about 1.6 km. The permutation test's smallest attainable P at 500 iterations is 0.002. The 2018 value (0.82, $n = 17$) shows that single small years vary widely. Running five species through several partitions multiplies the number of comparisons; the species results relied on here are the strongly supported ones (the turkey's chance-level following, the coyote's unchanged windows, the hard-antler buck selection, the development gradient in deer displacement, and the null-referenced deer response to people), and the one nominal surprise (the bobcat's window drift) is reported and not pursued. The random-instant null answers one question, what a return looks like after an instant with no passage, and not another, whether the passer's and responder's shared use of a trail inflates the raw ratio; the turkey reference addresses the second, and the two together bound the response from both sides. Class-resolved analysis beyond the results reported here is left to the companion analysis. The Southern Farmland contributes almost no wolf encounters, because no packs are established there. Confidence in the remaining results rests on the exact reproduction of the earlier pipeline, on consistency of direction across independent partitions (zones, density thirds, clean and simple windows, encounter windows), on the specificity check across species, on the turkey reference and the random-instant null, and on agreement with prior work that predicted responses of this kind would be visible at fine time scales.

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Author contributions

D.A.V.: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing (original draft, review, and editing).

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Conflict of interest

The author declares no conflict of interest.

Data availability

The statewide extract is drawn from the Snapshot Wisconsin citizen-science camera network (Wisconsin DNR Office of Applied Science) and is available from the DNR by data request. The per-camera return-delay tables, the encounter tables, the camera covariates, and the analysis code

will be deposited in a public repository on acceptance by Dryad or Zenodo. Exact localities of sensitive species are withheld for conservation reasons.

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Table 1.—Directional following by wolves of white-tailed deer, by group: sequential encounters (n), follow fraction, and the one-sided permutation P for groups or Fisher's exact P for contrasts. Statewide Snapshot Wisconsin extract, 2018–2025.

Group	**n**	**Follow fraction**	**P**
Statewide overall	461	0.74	0.002
2019–2020 (before harvest)	101	0.63	—
2022–2023 (after harvest)	115	0.83	0.002 (vs. before)
2021 (hunt year, excluded)	61	0.87	—
2024–2025 (held-out years)	167	0.68	0.43 (vs. before); 0.008 (vs. after)
Northern Forest Zone	251	0.73	0.002
Central Forest Zone	25	0.84	0.006
Central Farmland Zone	182	0.74	0.002
Wolf activity: lowest third	26	0.69	0.068
Wolf activity: middle third	85	0.68	0.034
Wolf activity: highest third	350	0.75	0.002

Table 2.—Raw return-delay ratios for the three main relationships (median return after the disturber ÷ the responder's own baseline; qualifying cameras in parentheses), with the random-instant null expectation for the statewide rows. Statewide Snapshot Wisconsin extract, 2018–2025.

Group	Deer after wolf	Deer after person	Wolf after person
Statewide overall	2.19× (383)	1.86× (4,317)	2.42× (278)
random-instant null	0.88×	0.84×	2.39×
observed ÷ null	2.55×	2.12×	1.02×
Northern Forest	2.38× (266)	1.87× (1,216)	2.45× (195)
Central Forest	1.80× (43)	1.90× (130)	1.35× (35)
Central Farmland	1.71× (73)	1.82× (1,662)	3.06× (47)
Southern Farmland	(1)	1.92× (1,309)	(1)
2019–2020 window	—	—	2.06× (68)
2022–2023 window	—	—	2.54× (98)
2024–2025 window	—	—	2.30× (97)

Table 3.—The five species under identical measures: following against deer (with permutation P and the two wolf-harvest windows), the deer's raw return delay after each species, and each species' raw return delay after a person. Statewide Snapshot Wisconsin extract, 2018–2025.

Species	Encounters	Follow fraction (permutation P)	2019–2020 / 2022–2023	Deer delay after (cameras)	Delay after person (cameras)
Wolf	461	0.74 (0.002)	0.63 / 0.83[a]	2.19× (383)	2.42× (278)
Coyote	13,461	0.61 (0.002)	0.61 / 0.62	1.75× (3,479)	2.50× (2,969)
Bear	1,953	0.63 (0.002)	0.64 / 0.64	1.56× (1,269)	3.91× (992)
Bobcat	1,086	0.52 (0.19)	0.60 / 0.51	1.81× (1,125)	1.85× (901)
Turkey (control)	30,323	0.49 (0.87)	0.49 / 0.50	1.53× (3,499)	5.03× (2,847)

[a] Fisher's exact P = 0.002; the window contrasts of all other species are not significant, except the bobcat's (P = 0.037, in the opposite direction; see text).

Table 4.—Return-delay ratios read against the random-instant null: the observed ratio, the null expectation (passer detections moved to 20 random active days of the same camera, time of day kept), their quotient paired within camera, and the Wilcoxon signed-rank test on the log quotient. Statewide Snapshot Wisconsin extract, 2018–2025.

Responder after passer	Cameras	Observed	Null	Observed ÷ null	W	P
Deer after wolf	383	2.19×	0.88×	2.55×	7,253	3×10^{-42}
Deer after coyote	3,479	1.75×	0.93×	1.82×	651,890	$< 10^{-300}$
Deer after bobcat	1,125	1.81×	0.98×	1.78×	93,485	6×10^{-93}
Deer after bear	1,269	1.56×	0.95×	1.60×	158,556	4×10^{-78}
Deer after turkey	3,499	1.53×	0.87×	1.66×	930,419	2×10^{-278}
Deer after person	4,317	1.86×	0.84×	2.12×	927,385	$< 10^{-300}$
Turkey after person	2,847	5.03×	4.02×	1.12×	1,655,377	3×10^{-17}
Bear after person	992	3.91×	3.27×	1.11×	202,866	2×10^{-6}
Coyote after person	2,969	2.50×	2.02×	1.15×	1,632,338	2×10^{-34}
Wolf after person	278	2.42×	2.39×	1.02×	17,369	0.13
Bobcat after person	901	1.85×	1.79×	1.02×	196,581	0.40
Coyote after wolf	326	1.57×	1.99×	0.91×	21,751	0.004
Bobcat after wolf	232	1.43×	1.60×	0.89×	10,873	0.010

Figure Legends

Fig. 1.—Follow fraction of wolves after white-tailed deer by year, with 95% Wilson intervals, against the permutation value of 0.50 (dashed). The February 2021 wolf harvest is marked. The fraction rises with the harvest, peaks in 2021–2022, and returns to pre-harvest levels by 2024. Statewide Snapshot Wisconsin extract, 2018–2025.

Alt text: Line chart of the yearly wolf-after-deer follow fraction from 2018 to 2025 with error bars; values near 0.6 before 2021 rise to about 0.9 in 2021 and 2022, then fall back to about 0.65 by 2024.

Fig. 2.—The wolf harvest comparison two ways: all years split at 22 February 2021 (left), and the two clean windows with 2021 and 2024–2025 excluded, with the held-out years beside them (right). Bars show the follow fraction with 95% Wilson intervals; the dashed line is chance.

Alt text: Two groups of bars. Left: before 0.67 and after 0.76. Right: 2019–2020 at 0.63, 2022–2023 at 0.83, 2024–2025 at 0.68. A dashed line marks 0.50.

Fig. 3.—Per-camera return-delay ratios (median return after the disturber ÷ the responder's own baseline) by Deer Management Zone for the three main relationships: bars are the observed median ratio, the short horizontal marks are the random-instant null expectation for the same cameras, and camera counts are at the base of each bar. The dashed line is the responder's baseline. Southern Farmland omitted for the wolf relationships (one qualifying camera).

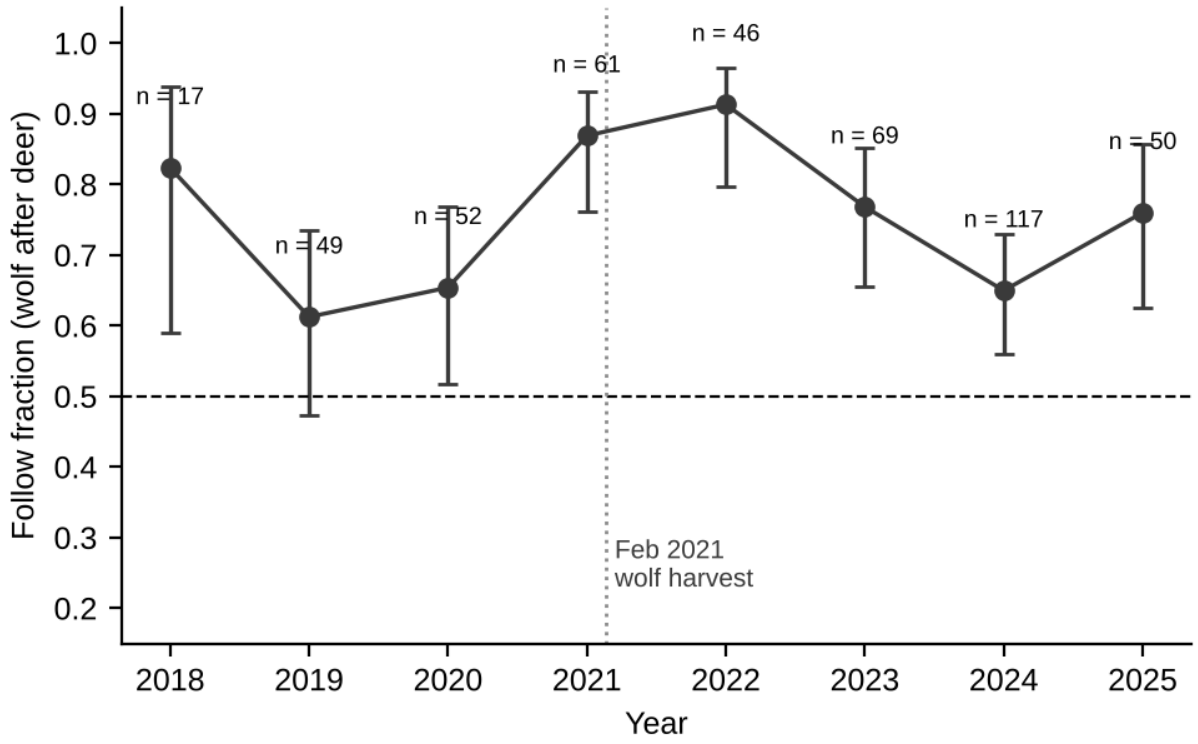
Alt text: Three panels of bars by zone. Deer after wolf: Northern Forest 2.38, Central Forest 1.80, Central Farmland 1.71, each far above a null mark near 0.9. Deer after person: about 1.8 to 1.9 in all four zones above null marks near 0.8 to 0.9. Wolf after person: 2.45, 1.35, and 3.06, each close to its null mark.

Fig. 4.—(A) Follow fraction of wolves after deer and (B) deer return delay after a wolf, across thirds of the wolf-activity range (independent wolf detections per 100 camera-days), with 95% Wilson intervals in A and camera counts in B. The follow fraction rises modestly with activity; the return delay does not change.

Alt text: Panel A, three points rising slightly from 0.69 to 0.75 across low, middle, and high wolf activity. Panel B, three bars near 2 (1.85, 2.39, 2.05) with no trend.

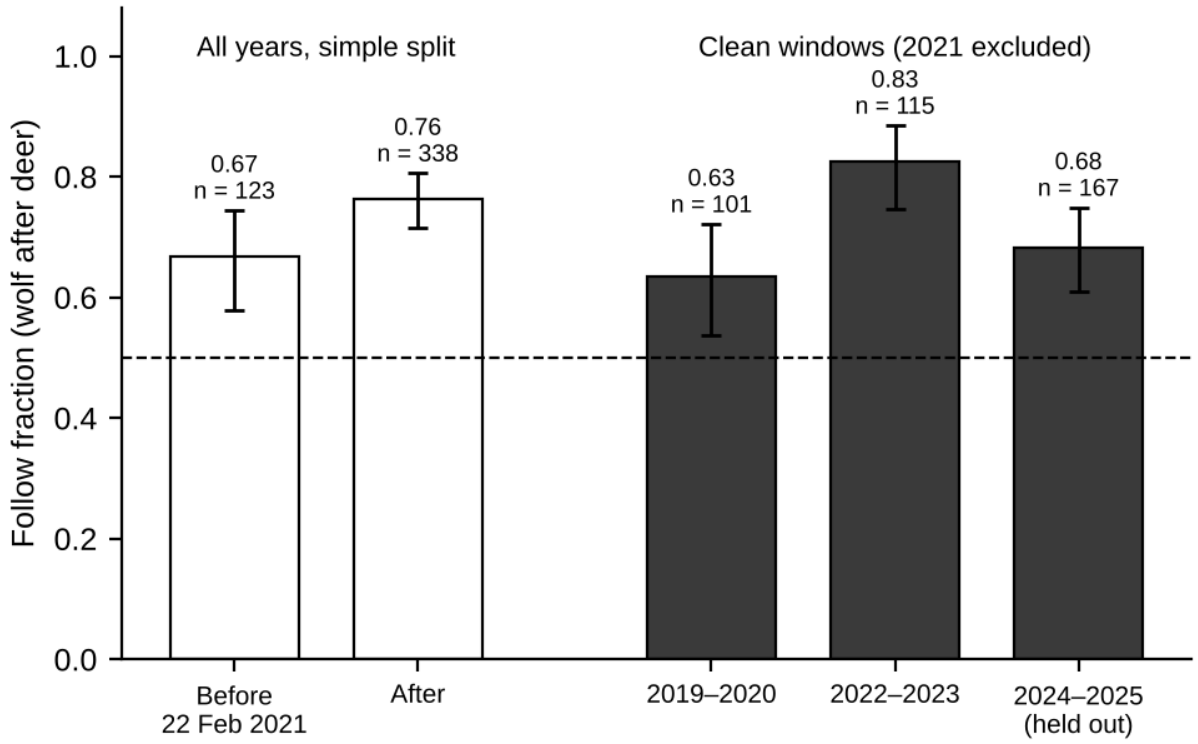
Fig. 5.—(A) Follow fraction against deer by species, with the permutation P above each bar; the turkey control sits at chance. (B) The deer's return delay after each species (left group) and each species' return delay after a person (right group): hollow bars are the raw ratio to baseline and filled bars the observed ÷ null quotient; the dashed line marks no response. Statewide Snapshot Wisconsin extract, 2018–2025.

Alt text: Panel A, bars for wolf 0.74, bear 0.63, coyote 0.61, bobcat 0.52, turkey 0.49 with a line at 0.50. Panel B, paired hollow and filled bars; the deer's filled bars are all above 1.5 with wolf highest at 2.55; among species after a person the filled bars are near 1.0 to 1.15 except deer at 2.12.


Follow fraction (wolf after deer)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
n = 17
n = 49
n = 52
n = 61
n = 46
n = 69
n = 117
n = 50
Feb 2021
wolf harvest
2018
2019
2020
2021
2022
2023
2024
2025
Year

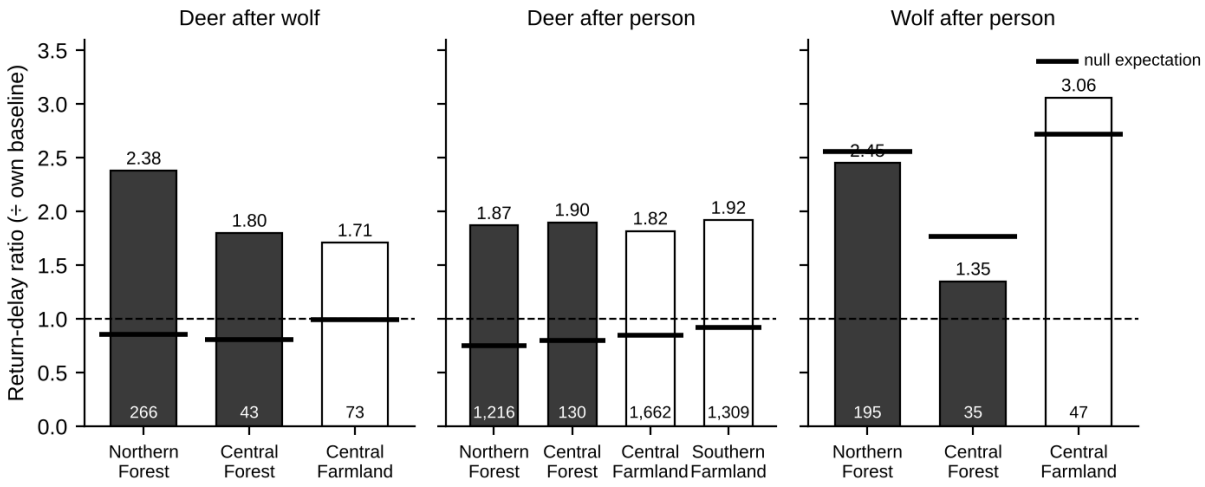
565

566


All years, simple split
Clean windows (2021 excluded)
Follow fraction (wolf after deer)
1.0
0.8
0.6
0.4
0.2
0.0
0.67
n = 123
0.76
n = 338
0.63
n = 101
0.83
n = 115
0.68
n = 167
Before
22 Feb 2021
After
2019–2020
2022–2023
2024–2025
(held out)

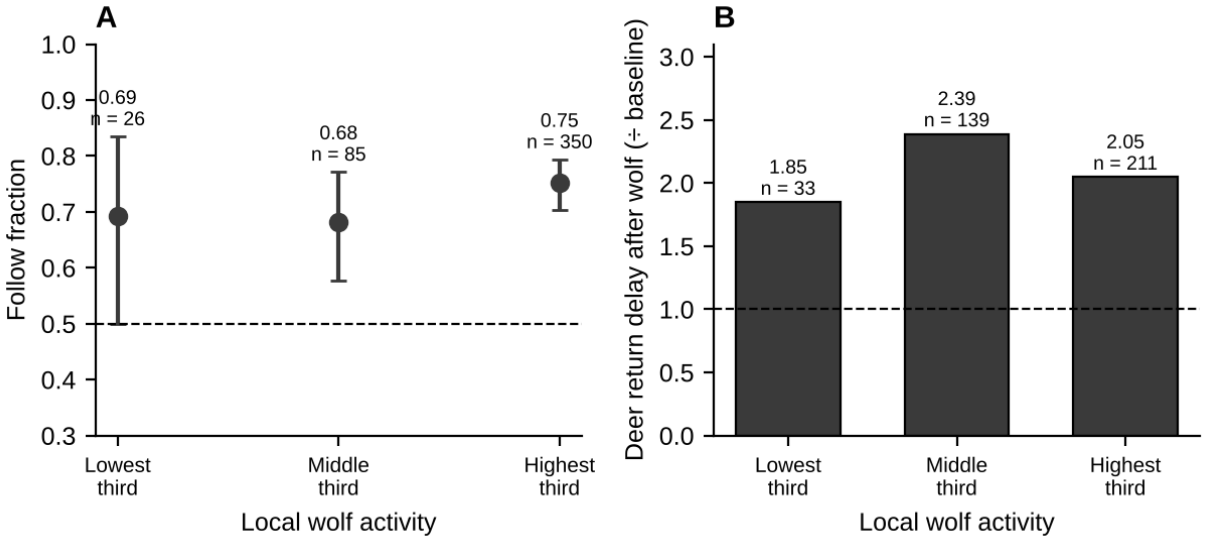
567

568


Deer after wolf
Deer after person
Wolf after person
null expectation
Return-delay ratio (÷ own baseline)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
2.38
1.80
1.71
1.87
1.90
1.82
1.92
2.45
1.35
3.06
266
43
73
1,216
130
1,662
1,309
195
35
47
Northern Forest
Central Forest
Central Farmland
Northern Forest
Central Forest
Central Farmland
Southern Farmland
Northern Forest
Central Forest
Central Farmland

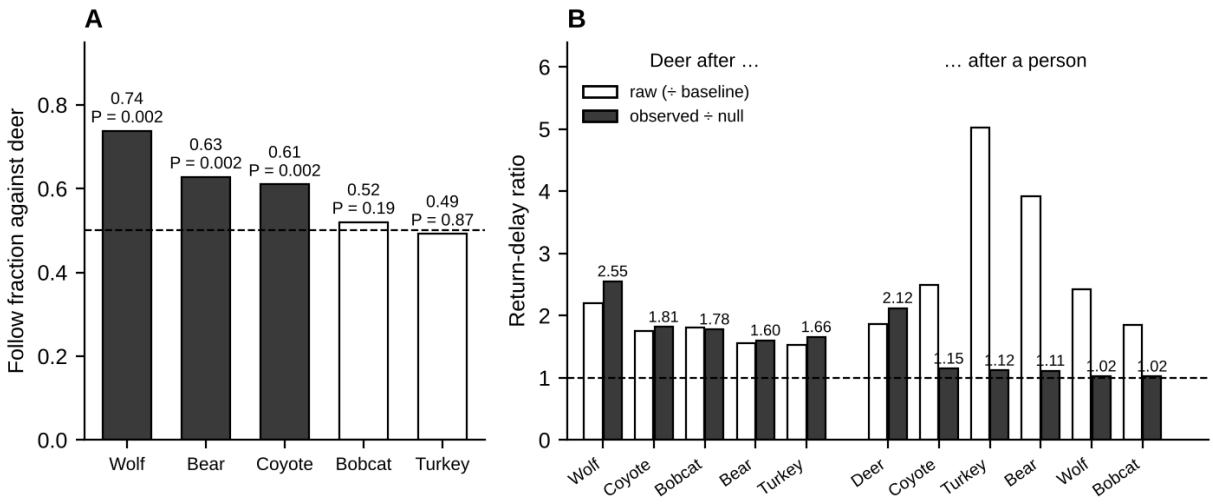
569

570


A
Follow fraction
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.69
n = 26
0.68
n = 85
0.75
n = 350
Lowest third
Middle third
Highest third
Local wolf activity
B
Deer return delay after wolf (÷ baseline)
3.0
2.5
2.0
1.5
1.0
0.5
0.0
1.85
n = 33
2.39
n = 139
2.05
n = 211
Lowest third
Middle third
Highest third
Local wolf activity

571

572


A
Follow fraction against deer
0.0
0.2
0.4
0.6
0.8
0.74
P = 0.002
0.63
P = 0.002
0.61
P = 0.002
0.52
P = 0.19
0.49
P = 0.87
Wolf
Bear
Coyote
Bobcat
Turkey
B
Return-delay ratio
0
1
2
3
4
5
6
Deer after …
… after a person
raw (÷ baseline)
observed ÷ null
2.55
1.81
1.78
1.60
1.66
2.12
1.15
1.12
1.11
1.02
1.02
Wolf
Coyote
Bobcat
Bear
Turkey
Deer
Coyote
Turkey
Bear
Wolf
Bobcat

573