# Wolf–Deer Camera-trap Detections Across Wisconsin's Statewide Wolf Range (2018–2025): A Temporary Increase in Wolves Following Deer After the 2021 Wolf Harvest, Displacement Effects by Habitat Zone, and Avoidance of People Across Co-occurring Species

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## Abstract

Two prior analyses of wolf-enriched extracts of the Snapshot Wisconsin camera network — one county, then five northwestern counties — showed that gray wolves (Canis lupus) tended to arrive at cameras shortly after white-tailed deer (Odocoileus virginianus), that they arrived after antlered bucks more often than the bucks' numbers would predict, and that deer returned to a site more slowly after a wolf has passed than after a person (Vraniak 2026b, 2026c). Those analyses also reported three patterns their wolf sample was too small to settle: a rise in following after the February 2021 wolf harvest, weaker displacement of deer by wolves near towns, and a long delay before a wolf returns to a site after a person has passed. Here I tested all three with an extract built by the same data pipeline, but statewide: 7,791,771 detections on 5,371 cameras (2018–2025), including 7,742 wolf detections on 810 cameras and 461 sequential wolf–deer encounters — four times the five-county count. I also ran the same measures for coyote, black bear, bobcat, and wild turkey. The turkey, which poses no danger to deer, served as a control. Before the new analyses, the statewide extract reproduced every published five-county value exactly. The statewide analyses produced four results: (1) Wolves arrived after deer in 74% of encounters, against 50% expected by chance (P = 0.002). This held in every Deer Management Zone that had wolves and at every level of local wolf activity. The median gap between deer and wolf detection stayed near 5.9 minutes in every subset. In the hard-antler months (September–December), an antlered deer is reliably a buck. In those months, the wolf's nearest deer was a buck 1.40× more often than the bucks' share of deer at the same cameras would predict (P = 0.004). During the October–November rut the selection rose to 1.48×. The same test run across the whole year found almost nothing (1.10×), because for most of the year antlers cannot separate the sexes. (2) The hunting harvest of wolves produced a temporary increase in wolves following deer, a pulse, not a lasting change. Setting aside the hunting year 2021 itself and comparing the two years before the wolf harvest (2019–20) with the two years after (2022–23), the following rose from 0.63 to 0.83 (Fisher's exact P = 0.0019; odds 2.77× with zone held constant). By 2024–25 the fraction (0.68) had returned to the pre-harvest level (P = 0.43). No other species changed across the same years: the coyote's following deer fractions in the same two windows were 0.61 and 0.62 (13,461 encounters), and bear and turkey were also unchanged. (3) Deer returned 2.19× more slowly after a wolf than their own usual return interval. The delay was larger in forest zones than in farmland (2.38× vs 1.71×, P = 0.020). It also declined steadily as development increased, on the corrected 1-km human-modification index: 2.53× on the wilder half of the cameras, 1.86× on the more-developed half (P = 0.009). The delay did not change across a twelve-fold range of

local wolf density (P = 0.22); that is, deer used wolf-rich and wolf-poor cameras equally (r = −0.005). Deer also returned 1.53× more slowly after a turkey. That value estimates the part of any such delay that has nothing to do with danger; the wolf's delay stands well above it, while the bear's (1.56×) does not. That pooled bear value carries a caveat. Compared in season (June–November) and by deer class, against class-specific turkey references on the same cameras, the bear's delay stood above the reference for every deer class. (4) Wolves returned 2.42× more slowly after a person — the largest value among the deer–wolf–human comparisons — and the delay differed by zone: 3.06× at farmland cameras, 1.35× in the Central Forest. The deer's delay after a person was nearly the same everywhere (1.82–1.92×). Ranked across species, the return delay after a person ran: turkey 5.03×, bear 3.91×, coyote 2.50×, wolf 2.42×, bobcat 1.85×. The most heavily hunted species showed the longest delays. I interpret the wolf hunting harvest effect as a pulse, a temporary change in wolf behavior that faded as the population began to recover. The displacement results were a response set off by each passage, sized by the surrounding landscape – larger in forests than farms - and unaffected by how often wolves are present.

*Keywords: camera trap; gray wolf; Canis lupus; white-tailed deer; Odocoileus virginianus; wolf harvest; predation risk allocation; landscape of fear; human shield; deer management zones; mesopredator; wild turkey; Snapshot Wisconsin.*

## Introduction

The two prior studies of this camera record left three specific questions open (Vraniak 2026b, 2026c). 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 forty 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 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 twelve 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 record allowed two further checks. The extract included coyote, black bear, bobcat, and wild turkey. 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 (Gilbert et al. 2022; Clare et al. 2023; Gaynor et al. 2018). 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).

## Materials and 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 PLSS 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 deferred to a companion re-analysis (below). 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.

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 published values exactly. It did: 116 sequential encounters (4 co-occurrences), follow fraction 0.75, median lag 5.8 minutes, before/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 one mile — sufficient at zone scale, uncertain only for cameras within about a mile of a zone boundary. The camera locations fell: Central Farmland 2,066, Southern Farmland 1,643, Northern Forest 1,520, Central Forest 166. Wolf cameras 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-minute 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 twelve-fold range.

***Measures***

All measures are unchanged from the parent studies. For each detection of a focal species, the nearest deer at the same camera within 30 minutes on either side was scored as *co-occurrence* (within 30 seconds; 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. 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 has 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 and $\chi^2$ tests for proportions, Mann–Whitney and Kruskal–Wallis 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.

### *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 against 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 wolf 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 offered. 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. Where class-resolved return delays are compared against the turkey reference, the comparison is paired within camera: each class's delay after the focal species is set against that same class's delay after a turkey on the same cameras, within June–November.

### *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 February 22, 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 ($P = 0.002$). 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 minutes overall and stayed between 3.8 and 6.3 minutes in every subset, matching the five-county value of 5.8. As in the prior studies, what varies across time and place is how often the wolf arrives after a deer, not how closely (Table 1).

The hard-antler months gave the parent studies' 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, Figure 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 minutes 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 bookkeeping, 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 = 0.75). The measure therefore reported no following where no following existed, and the ordering it returned — a chasing hunter first, two generalists next, an ambush hunter and a non-predator 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 2019–20 and 0.83 in 2022–23 (Fisher's exact P = 0.0019; odds 2.77×, P = 0.0018 with zone held constant). The all-years split gives 0.67 against 0.76 (P = 0.042; odds 1.63×) (Figure 2). The by-year record explains the difference (Figure 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 February 22) 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: 2024–25 (0.68, n = 167) is indistinguishable from the pre-harvest years (P = 0.43) and significantly below 2022–23 (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 measurement year windows, the coyote did not change (0.61 to 0.62 to 0.60 across the three windows; Fisher P = 0.35), although its encounter sample is thirty 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 wolf 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 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.

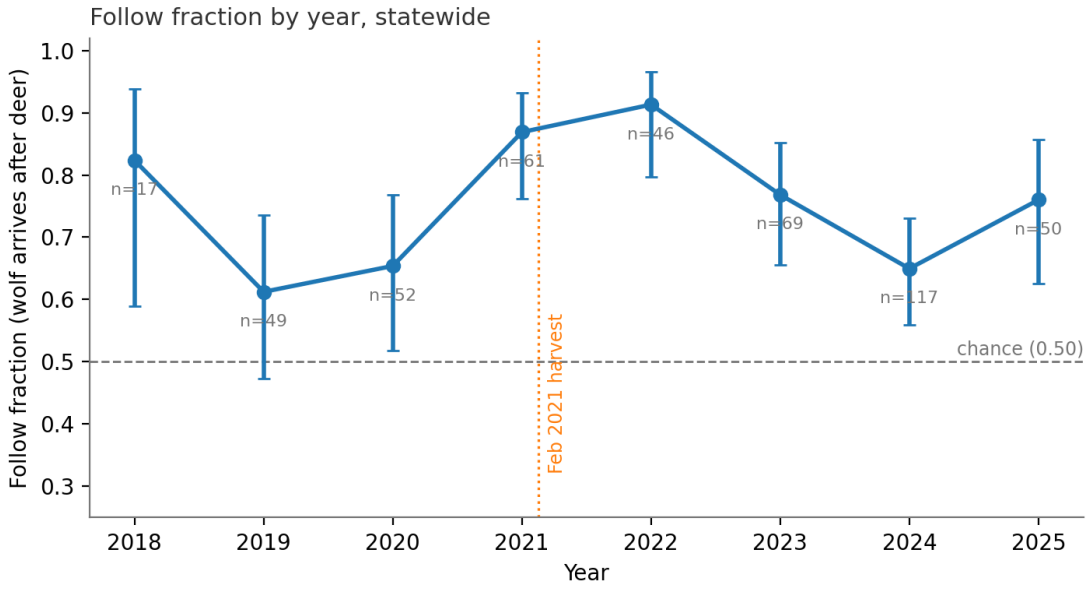


*Figure 1. Follow fraction by year with 95% Wilson intervals, against the permutation value (0.50). The February 2021 wolf harvest is marked. The fraction rises with the wolf harvest, peaks in 2021–22, and returns to pre-harvest levels by 2024. Data: statewide Snapshot Wisconsin extract, 2018–2025.*

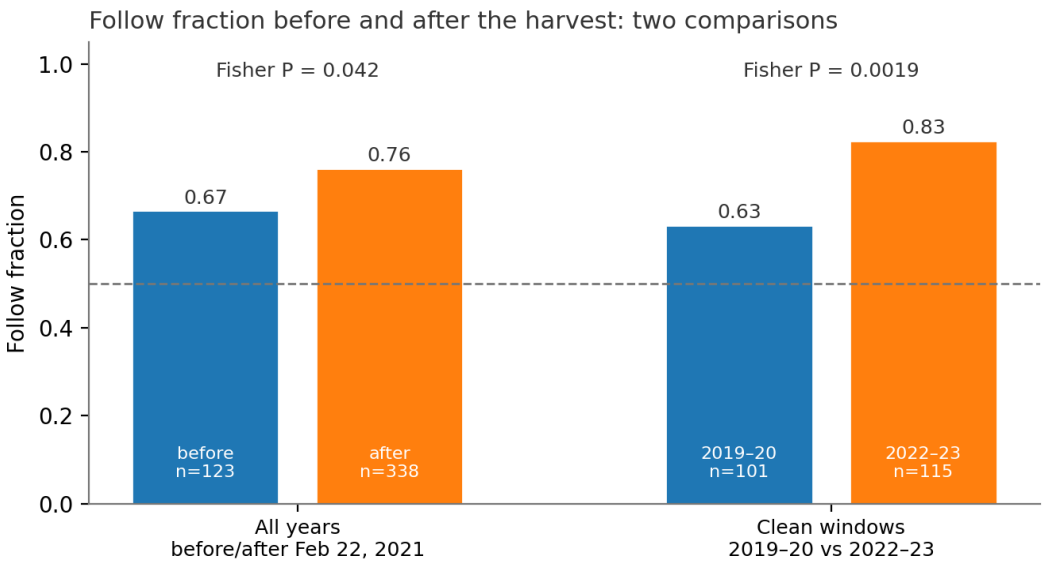


*Figure 2. The wolf harvest comparison two ways: all years split at February 22, 2021 (left), and the two clean windows with 2021 and 2024–25 excluded (right). Bars show follow fraction; the dashed line is chance.*

***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 $P < 10^{-36}$). In hours, the median interval was about 16 hours at baseline and 35 hours after a wolf. The size of the delay follows the landscape: 2.38× in the Northern Forest against 1.71× in the Central Farmland (forest against farmland, Mann–Whitney P = 0.020; across zones, Kruskal–Wallis P = 0.043). 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 (Figure 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 = 0.0085). On the wilder half of the cameras the delay was 2.53×. On the more-developed half it was 1.86× (Mann–Whitney P = 0.009). Across thirds of the index it fell steadily: 2.58×, 2.14×, 1.82×. The five-county gradient — deer displacement by wolves strongest in wild country, weakest near development — is therefore confirmed statewide, on the same covariate the parent studies 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 twelve-fold difference, the ratio stayed near 2× (1.85×, 2.39×, 2.05×; Kruskal–Wallis 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 (Figure 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 the reference value for this measure. Deer returned 1.53× more slowly even after a turkey (3,499 cameras). That delay cannot be fear of turkeys, so it estimates the part of any passage-keyed delay that does not come from danger — likely shared trail use and chance timing. Read against that reference, the species separate. The wolf stands well above it (2.19×). The bobcat and coyote stand modestly above it (1.81× on 1,125 cameras; 1.75× on 3,479). The bear is only slightly above it (1.56× on 1,269): 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, Figure 5b). These pooled values carry a caveat. They mix seasons and deer classes, and they compare across different sets of cameras. The companion re-analysis therefore makes the comparison a second way: each deer class's delay after a species is measured against that same class's delay after a turkey, on the same cameras, within June–November, when bears are active. Read that way, the bear stood significantly above its reference for every class (bucks 1.55× over it, $P < 10^{-6}$; does 1.21×; fawns 1.22×). The buck's raw delay after a bear (4.29× on 1,074 cameras) is the largest return value in the record. The coyote's apparent margin disappeared (0.99–1.01× over the class references for all three classes). In short, the pooled comparison understates the bear and overstates the coyote. The full class-resolved analysis is taken up in the companion re-analysis.

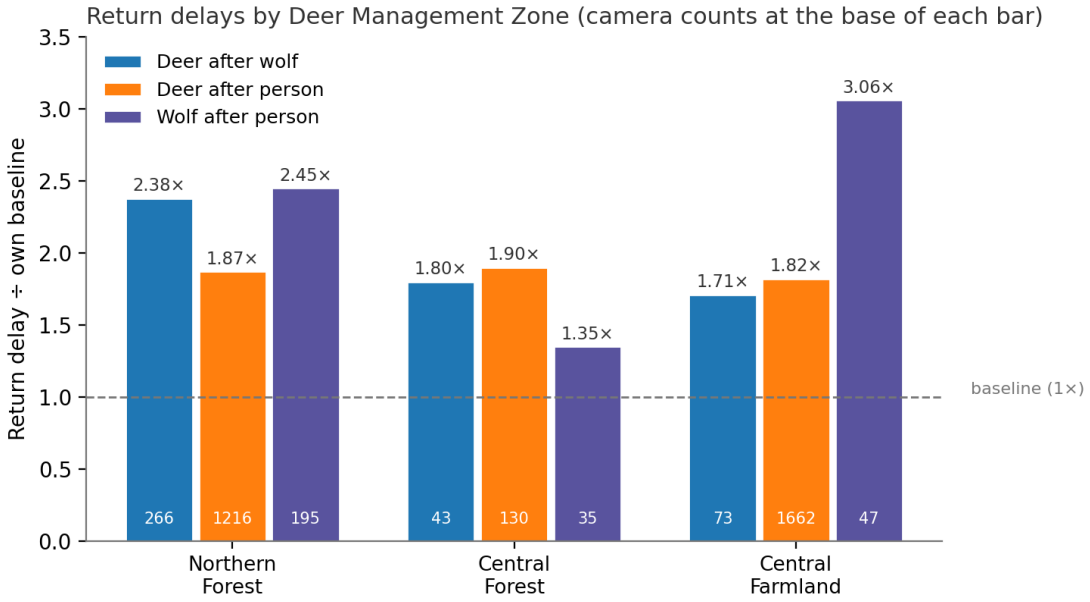


*Figure 3. Per-camera return-delay ratios (median return after the disturber ÷ the responder's own baseline) by Deer Management Zone, for the three main relationships. Camera counts at the base of each bar; the dashed line is baseline. Southern Farmland omitted: one qualifying wolf camera.*

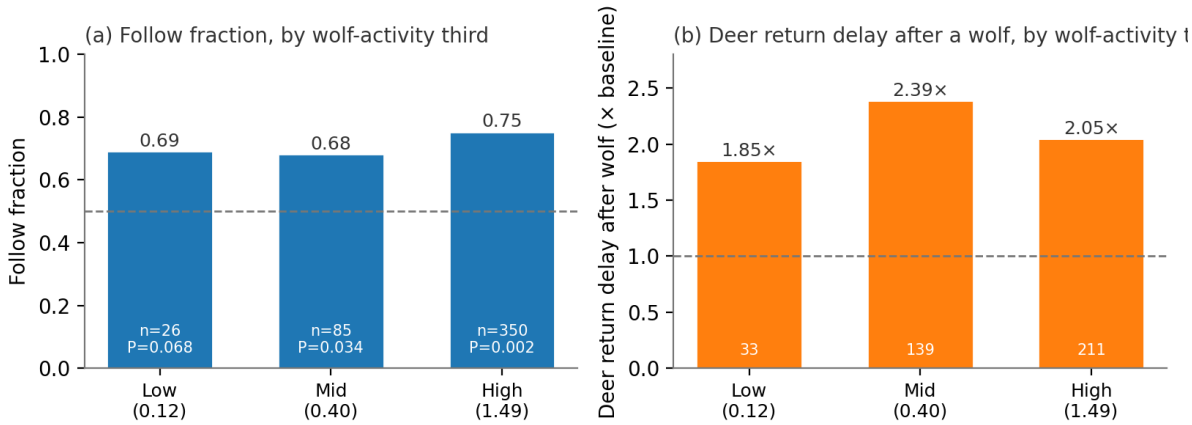


*Figure 4. (a) Follow fraction and (b) deer return delay after a wolf, across thirds of the wolf-activity range (independent wolf detections per 100 camera-days). The follow fraction rises modestly with activity; the return delay does not change.*

***Avoidance of people: nearly constant in deer, zone-dependent in the wolf, ordered by hunting pressure across species***

Deer returned 1.86× more slowly after a person (4,317 cameras, $P < 10^{-100}$), and the value was nearly the same in all four zones (1.82–1.92×; Kruskal–Wallis P = 0.12). The wolf's delay after a person was the largest of the three main relationships — 2.42× its own interval (278 cameras, Wilcoxon $P < 10^{-22}$; the median interval was about 28 days at baseline and 99 days after a person). Unlike the deer's, the wolf's delay differed by zone (Kruskal–Wallis P = 0.040): 3.06× at the farmland cameras (47 cameras), 2.45× in the Northern Forest (195), and 1.35× in the Central Forest (35 — only slightly above baseline, P = 0.04). The five-county pattern of stronger avoidance in the south reappears in direction (south 2.57× against north 1.93× at a township median split, P = 0.089) but not as an independent effect of latitude (Spearman across the full township range, P = 0.45). At state scale, the gradient follows the amount of settlement, not latitude. The corrected index sharpened where that settlement effect lives. Camera-level development does not carry it: Spearman r = 0.055 (P = 0.36) across the 278 cameras, and flat within the Northern Forest (P = 0.82). The Central Forest cameras are no less developed at the 1-km pixel than the Northern Forest cameras (median index 0.10 against 0.11). The wolf's avoidance of people is therefore tuned by the settlement character of the surrounding region — farmland against public-forest block. It is not tuned by the development of the camera's own square kilometer. The deer's delay after a person, uniform across zones, is uniform across the continuous index as well (r = −0.016, P = 0.28). The wolf harvest windows show no significant change in this measure (2.06× in 2019–20, 2.54× in 2022–23, 2.30× in 2024–25; P = 0.45), unlike the suggestion of strengthening in the five-county record (Table 2).

Across the five species, the delay after a person forms a ranking (Table 3, Figure 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 species delayed after a person beyond its own baseline (all Wilcoxon $P < 10^{-50}$). The ranking

closely follows how heavily each species is hunted. The turkey and the bear — hunted intensively and directly, by calling and stalking, and by baiting and hounds — showed the longest delays. The wolf, whose legal hunting has been episodic, sits in the middle. The bobcat, lightly harvested, sits at the deer's level. Coyotes and bobcats also delayed after a wolf passed, but less than deer did: 1.57× (326 cameras, $P < 10^{-9}$) and 1.43× (232 cameras, $P < 10^{-6}$).

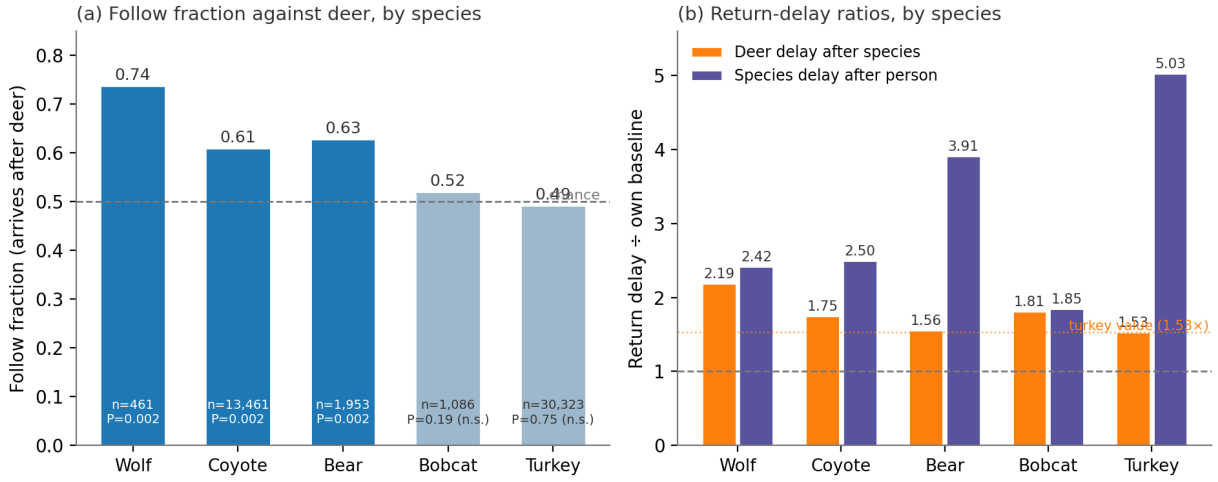


*Figure 5. (a) Follow fraction against deer, by species, with permutation P; the turkey control sits at chance. (b) Deer return delay after each species (orange) and each species' return delay after a person (purple). The dashed line is baseline; the dotted line is the turkey value (1.53×). Data: statewide Snapshot Wisconsin extract, 2018–2025.*

## Tables

**Table 1. Directional following by group (wolf): sequential encounters (n), follow fraction, and one-sided permutation P for groups or Fisher's exact P for contrasts. Data: statewide Snapshot Wisconsin extract, 2018–2025.**

| Group | n | Follow fraction | P |
|---|---|---|---|
| Statewide overall | 461 | 0.74 | 0.002 |
| 2019–20 (before harvest) | 101 | 0.63 | — |
| 2022–23 (after harvest) | 115 | 0.83 | 0.0019 (vs before) |
| 2021 (hunt year, excluded) | 61 | 0.87 | — |
| 2024–25 (held-out years) | 167 | 0.68 | 0.43 (vs before) |
| 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. Return-delay ratios for the three main relationships (median return after the disturber ÷ own baseline; qualifying cameras in parentheses). Data: 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) |
| 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) |
| 2019–20 window | — | — | 2.06× (68) |
| 2022–23 window | — | — | 2.54× (98) |
| 2024–25 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 return delay after each species, and each species' return delay after a person. Data: statewide Snapshot Wisconsin extract, 2018–2025.**

| Species | Encounters | Follow ff (perm. P) | 2019–20 / 2022–23 ff | Deer delay after | Delay after person |
|---|---|---|---|---|---|
| Wolf | 461 | 0.74 (0.002) | 0.63 / 0.83 * | 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 (n.s.) | 0.60 / 0.51 | 1.81× (1,125) | 1.85× (901) |
| Turkey (control) | 30,323 | 0.49 (n.s.) | 0.49 / 0.50 | 1.53× (3,499) | 5.03× (2,847) |

** Fisher's exact P = 0.0019; the window contrasts of all other species are not significant, except the bobcat's (P = 0.037, in the opposite direction; see text).*

## 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 thirty 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 exactly at chance across thirty thousand 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 twelve-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 completed the comparison, and the species ranking changed its frame. Within the deer–wolf–human triangle, the wolf remains the most person-avoidant of the three relationships, and its avoidance varies with settlement: strongest where the landscape is most developed, mildest in the emptiest public forest. Predators avoiding people is the mechanism assumed by the human-shield hypothesis, here measured directly in the predator (Berger 2007; Suraci et al. 2019; Kuijper et al. 2016). This result also renames the five-county north–south pattern: at state scale, the gradient follows settlement rather than latitude, although the recolonization-history reading (Wydeven

et al. 2009) cannot be fully separated from settlement, because wolves are newest in the most settled areas. Across all five species, however, the wolf is not the most person-avoidant animal in the record. The ranking — turkey, bear, coyote, wolf, deer, bobcat — closely follows the intensity and directness of each species' hunting. The deer's response to people is the most uniform in the record: identical across zones, and stable on a long-stewarded home ground in the companion study (Vraniak 2026a). In this record, avoidance of people corresponds to each species' history of being hunted rather than to its size or diet — an extension of the finding that large carnivores treat humans as a dominant threat (Suraci et al. 2019) to a full set of co-occurring species. It could support a separate report. The Central Forest result — wolves delaying only slightly after people in the state's large public-forest blocks — survived the corrected covariate. It is not explained by the development of the cameras themselves, which matches the Northern Forest, and the within-zone development splits are flat. What distinguishes the Central Forest is the character of the surrounding region: contiguous public land, where the people a wolf meets are passing visitors rather than residents. This reads as further evidence that the wolf's avoidance of people is learned at the scale of the landscape it lives in, not at the sites it passes through.

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 a mile. 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 person-avoidance ranking, the hard-antler buck selection, the development gradient in deer displacement), and the one nominal surprise (the bobcat's window drift) is reported and not pursued. Class-resolved analysis beyond the results reported here (hard-antler buck selection; bear–fawn following; the class-paired turkey references; the doe-direction reading of the development gradient) is deferred to the companion re-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 parent pipeline, on consistency of direction across independent partitions — zones, density thirds, clean and simple windows — on the specificity check across species, on the turkey reference value, and on agreement with prior work that predicted responses of this kind would be visible at fine time scales.

## Data and code availability

The statewide extract is drawn from the Snapshot Wisconsin citizen-science camera network (Wisconsin DNR, Office of Applied Science). The analysis pipeline extends the parent studies' (Vraniak 2026b, 2026c), was validated by exact reproduction of their published values, and is held by the author and available on reasonable request. Exact localities of sensitive species are withheld for conservation reasons.

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## Author contributions and disclosure

D.A.V. conceived the study, obtained and specified the Snapshot Wisconsin extract, directed all analyses, and is responsible for the content of this manuscript. Analysis code (Python) was computer-assisted; all methods, statistics, results, and interpretations were specified, verified, and approved by the author, and the final text was reviewed and edited by the author.

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