Patterns of Gray Wolf and White-tailed Deer Movement:

Local, County and Regional Camera-trap Data (2018-2025)

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Abstract

The gray wolf (*Canis lupus*) is the apex predator of white-tailed deer (*Odocoileus virginianus*), but on a single restored site it can be too rare to study. A year-round survey of about ten cameras at nine fixed stations on an approximately 100-ha prairie–savanna complex located within Washburn County, Wisconsin, yielded too few wolf detections over three years (11,473 animal detections, 2024–2026) to analyze wolf movement. The same camera-trap method was applied at a broader scale using data for Washburn County and too few detections were available for analysis (55 wolf detections, two sequential wolf–deer events). A wolf-enriched extract of the Snapshot Wisconsin citizen-science camera network for the five surrounding counties (Barron, Burnett, Bayfield, Douglas, and Sawyer; 525 cameras, 294,031 camera-days, 634,214 detections, 2018–2025; 1,856 wolf detections on 197 cameras) provided sufficient data for analysis. For each wolf detection the nearest deer within 30 min was scored as *co-occurrence*, *follow*, or *precede*. The results were tested against a day-reassignment permutation null (each wolf detection reassigned to a random day at the same camera and season). Wolves arrived after the deer in 75% of 116 sequential encounters (null 50%, P = 0.002; median lag 5.8 min, P = 0.002), most strongly in the spring denning and fall rut seasons (0.88 and 0.87, both P = 0.002; median lag 3.3 min in spring, 10.5 min in fall). Wolf detections were predominantly nocturnal (62.4% between dusk and dawn), with low diel activity overlap with humans (0.301) and high overlap with bucks (0.869). Antlered bucks were over-represented among deer nearest a wolf relative to availability - bucks were 14.3% of deer recorded but 26.3% of deer nearest a wolf (selection ratio 1.84, versus 0.89 for does and 0.52 for fawns; $\chi^2 = 12.53$), rising to 1.92 during the fall rut, remaining elevated within the night alone (1.67), indicating the association is not attributable solely to shared nocturnality. Deer returned to a site 2.24× more slowly after a wolf than on their baseline interval (110 cameras), a larger delay than after humans (1.83×, 432 cameras). Compared to this regional baseline, deer at the local stewarded home site returned close to their normal schedule (≈ 1.05). Two companion associations on the same trails — the wild turkey closely associated with does by day and the black bear following fawns in fall (0.82, P = 0.002) — provided some community context to interpret results. The results indicated that the regional wolf–deer relationship is structured by season, deer sex, and diel timing, in contrast to other species (bear, turkey), and that our local site-level deer tolerated us more than the deer tolerated people in the surrounding counties.

Keywords: camera trap; gray wolf; Canis lupus; Odocoileus virginianus; apex predator; predator–prey; sexual segregation; interspecific temporal association; site fidelity; Snapshot Wisconsin; prairie–savanna restoration.

Introduction

Researchers often use trail cameras to ask a question about a single species — where a deer goes, when a bear is active, what shapes a turkey's movement (e.g., Schuttler et al. 2017; Gaynor et al. 2018). However, the animals it records are not on the landscape by themselves. On both working and wild land, the movement of species concentrates on a finite set of trails, edges, and crossings. Many species pass the same camera because they are drawn to the same corridor. The temporal order in which they pass carries ecological information - one animal arriving shortly behind another can indicate commensal foraging (turkey and deer), a predator using its prey's routes (coyotes and rabbits), or two species independently drawn to the same landscape feature at overlapping hours (fox and skunk). If we use amethod that classifies the order of arrivals and controls for chance and for the numerical dominance of the commonest animal class, we can begin to distinguish these cases.

This paper is one of a linked series based on a single method applied at two different scales. In earlier work I found that white-tailed deer tolerance of people is strongly sex-structured. Bucks are roughly twice as wary as does when the measured currency is return-to-site rather than vigilance (e.g., Lashley et al. 2014), with the buck's wariness interpreted as a hunting-season response and the doe's tolerance as familiarity with a known human (Vraniak 2026). Here I ask the corresponding questions: when a deer walks a trail, does the wolf follow, how soon, toward which class of deer, and in which season, and how does the deer herd's displacement response to the predator compare with its response to humans?

The wolf is a strong candidate for studying class-directed following. However, on our own cameras it appears only a few times a month. Even in Washburn County alone the Snapshot record provides only 55 wolf detections and two sequential wolf–deer events, too few to test. I therefore designed, with the help of the Wisconsin DNR Office of Applied Science, a wolf-enriched extract of the five counties surrounding our site, where wolves are recorded in sufficient numbers. This regional record provides enough wolf detections for analysis, and it also supplies the ordinary regional deer response against which the home herd's tolerance could be compared.

Materials and methods

Study system

The within-site record is our own year-round survey of roughly ten cameras at nine fixed stations on an approximately 100-ha restored tallgrass-prairie, pine- and oak-savanna, and adjacent-woodland home ground within Washburn County, Wisconsin (11,473 detections, 2024–2026), in which every frame is individually labelled and deer were sexed and aged in the field and from antler and body cues. The home site carried the full mesocarnivore guild, but few independent wolf detections in three years. The primary dataset is a wolf-enriched re-export of the Snapshot Wisconsin citizen-science camera network (WI DNR) for the five surrounding counties — Barron, Burnett, Bayfield, Douglas, and Sawyer — covering 525 cameras and 294,031 camera-days over 2018–2025 (634,214 detections; three files joined on camera with zero orphans). The data on deer arrived already resolved to antlered (buck), antlerless (doe), and fawn, with a per-trigger head-count, per-camera survey effort in camera-days, and a global human-modification (GHM) covariate at every camera. The extract carried 1,856 wolf detections on 197 of 525 cameras, present in every year 2018–2025.

Directional co-occurrence and permutation null

For each wolf detection the nearest deer was located at the same camera within a window W (30 and 60 min; 30 min reported for the wolf). Each was scored as co-occurrence if the nearest deer fell within 30 s — the threshold that separated simultaneous presence from sequential trail use — as *follow* if the deer preceded the wolf (deer → wolf), or as *precede* if the deer succeeded the wolf. Directional structure is the *follow* fraction, FOLLOW / (FOLLOW + PRECEDE), where 0.5 denotes equal likelihood of arriving before or after a deer. Because deer detections were dominated by does and seasonally clumped, significance was assessed against a day-reassignment permutation null: in each of 500 iterations every wolf detection was reassigned to a random active date at the same camera in the same season, its time of day preserved, and the classification recomputed. This held camera, season, diel phase, and true deer abundance fixed, isolating temporal association from availability. Nearest-deer class use was compared with class availability (all deer detections at the same cameras) as a selection ratio with a χ^2 test — each class scored against its own availability, not against another class. The average following time for an edge wass the median deer→follower interval on its *follow* events. Avoidance ratios were per-camera medians of the deer return interval after a disturber, divided by the deer's own baseline interval (30-min independence), computed only where a camera carries at least three independent baseline intervals and at least three post-disturber return events. Absolute return times are those same intervals in real units. Diel overlap is the histogram-intersection coefficient of two hourly activity distributions. The same analysis pipeline was used across scales, so values are comparable with the companion analyses; analyses were run in Python 3 (numpy, scipy, statsmodels).

Results

Directional following

Across 116 sequential wolf-and-deer encounters within 30 min, the wolf arrived after the deer 75% of the time, against a day-shuffled expectation of 50% (P = 0.002), at a median lag of 5.8 minutes — shorter than chance (P = 0.002). The directional signal was strongest in spring (0.88, P = 0.002) and fall (0.87, P = 0.002), the seasons of denning and the rut (Figure 1). Resolved by the class followed, the effect held for both sexes: wolf → doe 0.68 (n = 71, P = 0.004) and wolf → buck 0.79 (n = 28, P = 0.006). The wolf did not follow the coyote (0.43, n = 60, n.s.), so there was no apex-over-mesopredator following in this record. The median following interval — how far behind the deer the wolf arrived — was 5.8 minutes overall, shortest behind the doe (5.9 min) and longest behind the buck (10.5 min). The black bear trailed the fawn by a median 14 minutes, while the coyote's ~1-minute lag, with a non-significant fraction, indicates simultaneous presence rather than pursuit (Table 1).

Edge (follower → target)	n events	Follow fraction	Median follow lag	P
Wolf → deer (all)	116	0.75	5.8 min	0.002
Wolf → deer (spring)	33	0.88	3.3 min	0.002
Wolf → deer (fall)	30	0.87	10.5 min	0.002
Wolf → doe	71	0.68	5.9 min	0.004
Wolf → buck	28	0.79	10.5 min	0.006
Wolf → coyote	60	0.43	1.1 min	0.69 (n.s.)
Black bear → fawn (comparator)	45	0.82	13.8 min	0.002

Table 1. Directional following of the gray wolf on white-tailed deer, five-county Snapshot extract (W = 30 min). Follow fraction > 0.5 indicates arrival after the deer; median follow lag is the median deer→follower interval on the follow events (average following time); P is a one-sided day-reassignment permutation probability. The bear → fawn edge is shown for comparison.

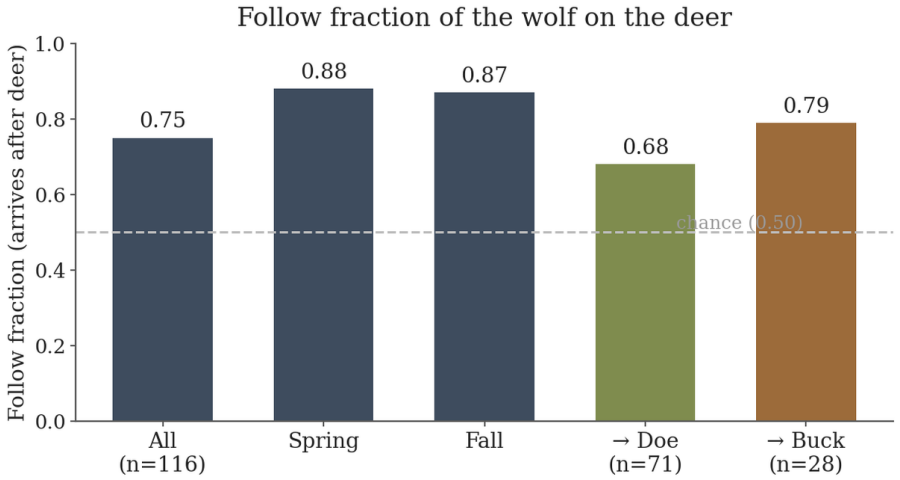

Figure 1. Follow fraction of the wolf on the deer, overall and by season and deer class, against the day-reassignment null (dashed line, 0.50). All edges shown are significant at P ≤ 0.006.

Diel activity and nearest-deer class selection

The wolf was predominantly nocturnal: 62.4% of its detections fell between dusk and dawn (the Washburn subset gave 63.6%, consistent with this value). Its diel activity overlap was lowest with people (0.301) and highest with the coyote (0.842) and the buck (0.869; Table 2, Figure 2). The fawn, the most diurnal deer class, showed the lowest overlap (0.701). The deer nearest each wolf detection was an antlered buck more often than availability predicted — selection ratio 1.84 for bucks against 0.89 for does and 0.52 for fawns ($\chi^2 = 12.53$), rising to 1.92 in the fall rut (Figure 3). Each ratio compares the share of the deer nearest a wolf that fall in a class against that class's share of all deer recorded at the same cameras: bucks 26.3% against 14.3% (1.84); does 69.7% against 77.9% (0.89); fawns 4.0% against 7.8% (0.52). A ratio of 1.0 indicates no preference. Because bucks are the most nocturnal deer class and therefore share the wolf's active hours most closely, this measures co-occurrence in space and time rather than active targeting.

To separate shared timing from over-representation, I recomputed the selection ratio within the night alone, when the wolf and the buck are both most active. At night the available deer are already more abundant with bucks — 18.7% of deer recorded at night are bucks, against 14.3% across the whole day — yet bucks remained over-represented among deer nearest a wolf: 31.2% of the deer beside a night-time wolf were bucks, a ratio of 1.67 ($\chi^2 = 6.57$, P = 0.037). By day the ratio was larger: 23.4% of the deer beside a daytime wolf were bucks against 10.7% of deer recorded by day, a ratio of 2.19 ($\chi^2 = 8.37$, P = 0.015). Shared

nocturnality increases how often a buck is available beside a wolf but does not account for the association: within each half of the day the deer nearest a wolf is still disproportionately an antlered buck.

Class	Diel overlap with wolf	Nearest-deer selection ratio
Antlered buck	0.869	1.84 (1.92 in fall rut)
Antlerless doe	—	0.89
Fawn	0.701	0.52
Coyote	0.842	—
People	0.301	—

Table 2. Activity overlap with the wolf (the share of the daily active hours the two hold in common) and nearest-deer class selection ($\chi^2 = 12.53$). Each selection ratio is the share of the deer nearest a wolf that fall in a class, divided by that class's share of all deer recorded at the same cameras: bucks 26.3% against 14.3% (1.84), does 69.7% against 77.9% (0.89), fawns 4.0% against 7.8% (0.52). A ratio of 1.0 is no preference; above 1 is over-representation near the wolf. Wolf nocturnality: 62.4% of detections between dusk and dawn.

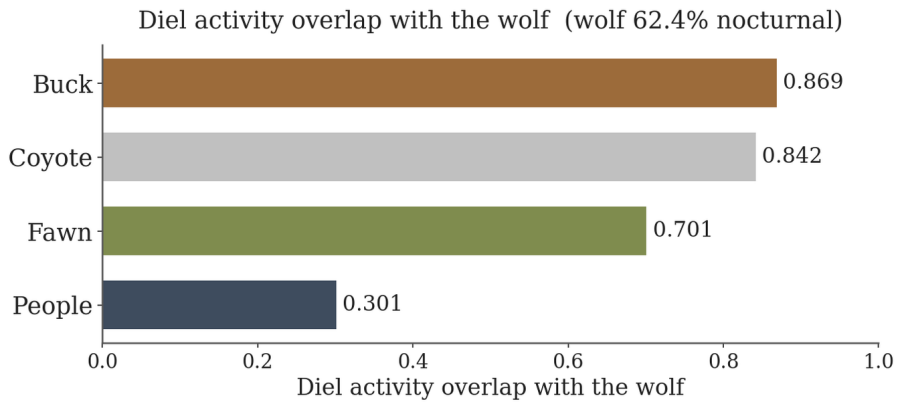

Figure 2. Diel activity overlap between the wolf and each class. The wolf shares most of its hours with the nocturnal buck and coyote, and least with people.

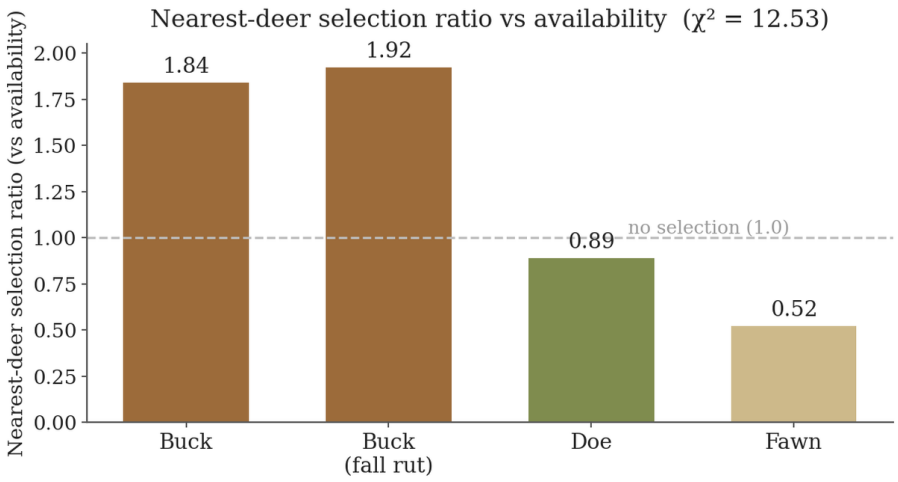

Figure 3. Nearest-deer class use versus availability (selection ratio; dashed line, 1.0 = no selection). The antlered buck is over-represented near the wolf, most strongly at the fall rut.

Deer return times (displacement)

Measured as displacement — the time deer take to return to a camera after a disturbance, the record shows its clearest contrast. Region-wide, deer returned 1.83× more slowly after a person (432 cameras) and 2.24× more slowly after a wolf (110 cameras): the wolf was given a wider berth than the human (Figure 4). Resolved by class, doe avoidance (1.81) is the reliable comparator, because does are present year-round and their baseline is stable. The buck (5.08) and fawn (8.66) ratios are higher but are inflated by a sparse, seasonal baseline and are reported as directionally consistent rather than as clean magnitudes. The five surrounding counties broaden the distribution against which the home site is compared: regional deer avoidance is 1.83 (interquartile 1.147–3.199), against 1.42 for Washburn alone.

On a common scale, these return-time ratios increase with distance from the local home-stewarded site: the home herd returned close to its ordinary schedule (≈ 1.05× its own baseline interval). The ordinary Snapshot deer of Washburn at our home site's own county at 1.42×, and the five surrounding counties at 1.83×. These three levels represent the herd's ordinary avoidance of everyday, largely human disturbance, increasing with distance from the stewarded ground. The delay after a wolf was greater still at 2.24×. Deer were most tolerant, quickest to return, on our family's own landscape, somewhat slower across our county, and slower again in the surrounding counties.

In absolute time (Table 4), on the 110 cameras that qualify for the avoidance test, a deer returned within six hours after a wolf about one time in five (18.1%) and within a day about 45% of the time (45.2%). The median wait was close to 29.9 h, although the quietest tenth of sites remained empty for two weeks or more. That absolute clock must be read against each camera's own baseline (median 18.1 h), because the raw interval is confounded by where wolves and people occur — wolf cameras sit in denser-deer country, so the raw time can appear shorter after a wolf than after a person until it is normalized. The ratio in Table 3 is that normalization, and it is where the wolf's wider berth appears. In practical terms for a trail-camera or hunting stand, a passing wolf does not empty a site for weeks — a deer often returns the same day — but it roughly doubles the ordinary wait.

Unlike the typical Northwoods deer, which take about 80% longer to return after a person, the our local home-site deer sit further into the tolerant range than the regional deer, they returned to a known family and its machines close to schedule at roughly 1.05. In absolute time our home site doe returned to a camera a median 11.3 h after a large canid and 11.7 h after a person, close to her 10.8 h baseline (return indices 1.05 and 1.08). The home buck return was longer (28.4 h after a large canid, index 1.92 against the buck's own, wider baseline — a per-camera median rather than the two medians divided). Deer responded to home machines sorted by sound continuity rather than by fuel type. Our deer avoided only the intermittent machine, the ATV. The continuous electric utility vehicle and the steady gas mower drew the home site doe back on or ahead of her ordinary schedule (return index 0.85), while the intermittent gas ATV raised it to 1.66 — the continuous-versus-ATV difference significant even pooled across three years ($P = 0.0005$ for does, 0.0022 for all deer). Sound continuity, not fuel type, predicted the response - the gas mower patterned with the electric cart rather than the gas ATV. None of the machines, including the ATV, approached the berth the herd gave the wolf. On our ground, a disturbance did not seem to be a threat; only the intermittent engine sound was associated with delayed return. The full home-ground machine analysis, resolved by sex and machine, is reported in the companion home study (Vraniak 2026). Figure 5 shows the

same result across all four machine classes for pooled deer — on foot 1.02, electric cart 0.83, gas mower 0.73, and gas ATV 1.64.

Disturber / herd	Return-time ratio	Cameras / note
After a person (regional)	1.83×	432 cameras
After a wolf (regional)	2.24×	110 cameras
Doe (reliable comparator)	1.81×	year-round baseline
Buck	5.08×	inflated by sparse baseline
Fawn	8.66×	inflated by sparse baseline
Home-ground herd (known family)	≈ 1.05×	returns on schedule
Washburn County (home county)	1.42×	Snapshot; intermediate rung

Table 3. Deer return-time ratios (median return interval after a disturber ÷ the deer's own baseline interval). A ratio near 1 is no delay; higher is a wider berth. Regional five-county deer avoidance 1.83 (IQR 1.147–3.199); Washburn alone 1.42. Home-ground rungs are drawn from the companion home study (Vraniak 2026).

Percentile	Time to first deer return after a wolf
10th	3.4 h
25th	9.8 h
50th (median)	29.9 h (≈ 1.25 days)
75th	102 h (≈ 4.3 days)
90th	384 h (≈ 16 days)

Table 4. Distribution of the absolute time to the first deer detection after a wolf, pooled over the 110 cameras that qualify for the avoidance test (n = 1,676 wolf→deer return events). A deer is back within 6 h 18.1% of the time, within 24 h 45.2%, within 48 h 60.7%, within 72 h 70.0%. Read against each camera's own baseline (median 18.1 h); note the 2.24× ratio of Table 3 is the median of the per-camera ratios (each camera's return interval ÷ its own baseline), not these pooled medians divided (29.9 ÷ 18.1 = 1.65×).

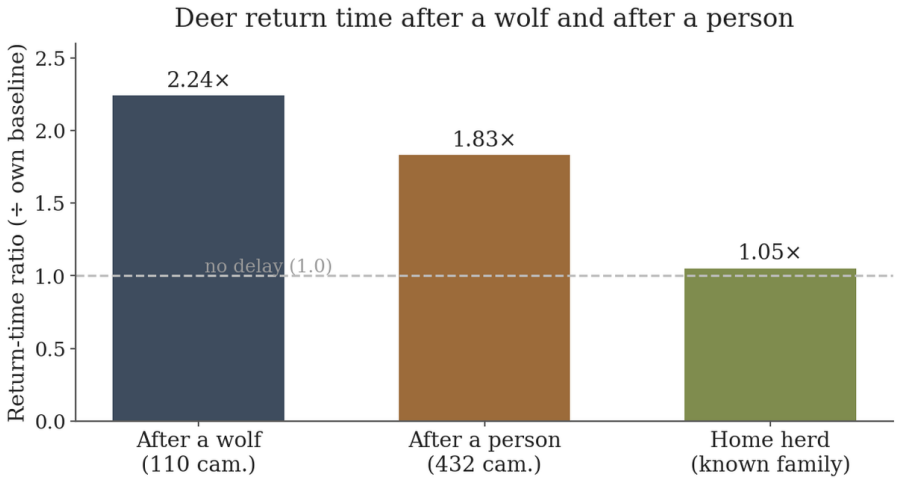

Figure 4. Deer return-time after a wolf and after a person across the five counties (dashed line, 1.0 = no delay), with the home-ground herd marked. The regional deer give the wolf a wider berth than people; the home herd returns on schedule.

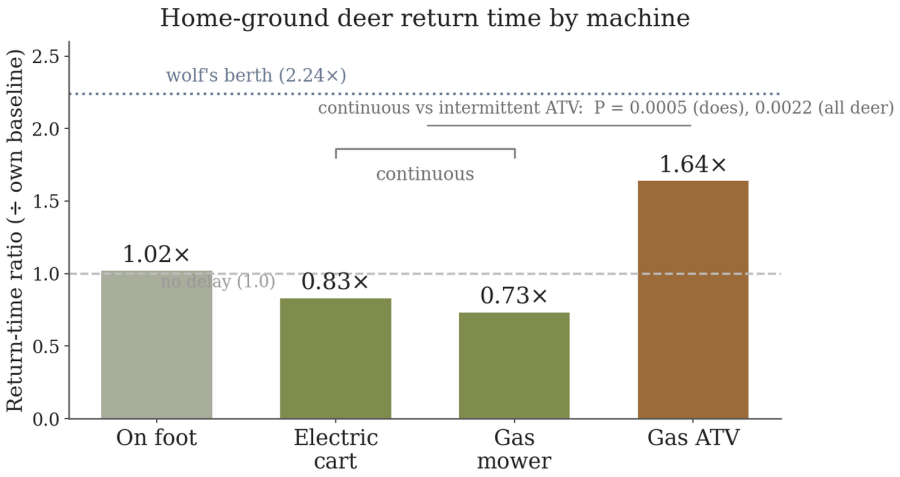

Figure 5. Home-ground deer return-time after each kind of disturbance, resolved by machine (return-time ratio ÷ the deer's own baseline; dashed line, 1.0 = no delay). The deer come back on or ahead of schedule after the continuous electric cart and the even-sounding gas mower, but give the intermittent gas ATV a wider berth: sound continuity rather than fuel type predicts the response (continuous vs ATV p = 0.0005 for does, 0.0022 for all deer). No machine, even the ATV, approaches the berth the regional herd gives the wolf (dotted line, 2.24×). Home-ground data from the companion study (Vraniak 2026).

Community context: three interspecific associations

The community pattern resolves into three interspecific associations around one deer herd, differing in kind, when we add in the apex predator, the wolf. The wild turkey companionably shares the doe's day without tracking her: it overlaps her daylight almost completely (97% diurnal), whereas the wolf, with 62.4% of its detections between dusk and dawn, barely overlaps it; however, the turkey follows the doe no more than chance (directional fraction 0.53, n = 1,163), consistent with a foraging commensal rather than a pursuer (Domínguez et al. 2023; Mikula et al. 2018). The black bear does follow, in the fall, toward the fawn (0.82, P = 0.002, a median 14 minutes behind). The gray wolf follows the deer, arriving a median six minutes behind and longest behind the buck (10.5 minutes). The three associations are therefore company by shared schedule (turkey–doe), the bear following the fawn, and the wolf following the buck. On our own ground, we are the resident family as an additional follower on the deer's trail — the one the herd does not avoid. Notably, on our home ground the turkey is the community's most people-averse member, yet still does not leave the doe's shared daylight (Vraniak 2026).

Discussion

Analyzed at a wider scale a single home ground cannot reach, the gray wolf behaves as an apex predator is expected to. The wolf follows the deer above chance, is predominantly nocturnal, occurs nearest the antlered buck more than availability predicts, and is given a wider berth by the herd than people are. The buck association links this paper to its companion study on human tolerance. There I found the buck to be the wary sex when the currency is return-to-site. Here at home the buck is the class nearest the wolf and the most nocturnal. Both results indicate that the buck is the wide-ranging, night-moving, displacement-prone sex, consistent with sexual-segregation and reproductive-strategy models (Bowyer 2004; Ruckstuhl & Neuhaus 2002; Main 2008), in which the sexes manage risk differently because they solve different problems. I cannot overgeneralize the relationships I am seeing: bound as it is to shared nocturnality, the nearest-deer co-occurrence is spatial–temporal association rather than demonstrated targeting, and a wolf-specific

predation test would require individual resolution or GPS-collar movement covariates that the camera record cannot supply.

Direction is only part of what this return lag records. The wolf not only arrived after the deer; on the follow events it arrived sooner than a day-shuffled distribution would place it — a median 5.8 minutes behind, shorter than chance at the same P = 0.002 that certifies the direction. A purely spatial following, the same trails walked in the same order, would suggest the deer's own timing and sit at the null; this distribution is tighter than that. The compression is not uniform - the doe was followed closely and quickly (5.9 min), while the buck was followed at a longer interval (10.5 min), consistent with a longer assessment of the more dangerous, wider-ranging animal. Direction indicates who follows whom, and the compressed lag indicates that the follow interval is shorter than the surrounding traffic of the site would predict.

The displacement result carries the study's central contrast. Regional deer avoided both the human and the wolf — the human at 1.83×, the wolf more strongly at 2.24× — while the deer of one restored and stewarded home ground returned close to schedule (≈ 1.05). That gap is visible because the surrounding cameras record the ordinary Northwoods case so clearly. It is the empirical shape of a learned relationship - a herd that has known a particular family over years responds to it as neither predator nor stranger. Across the gradient the disturbance is nearly constant while the response varies. On our family's own landscape he same kind of passage that empties a stranger's camera for a day in the surrounding counties is associated with little delay. Displacement therefore measures the herd's response to a disturbance as much as the disturbance itself. The apex predator, too few on the home record and more present in the regional one, is the component that lets the coexistence result span the whole guild — turkey with the doe, bear with the fawn, wolf with the buck, and the resident family as the one follower the deer allow behind them. On the wider gradient of human disturbance — from the general shift of wildlife into the night under human pressure (Gaynor et al. 2018) to the community-scale displacements recorded under the war in Ukraine and around Chornobyl (Kudrenko et al. 2026) — a herd that returns on schedule to a known family marks the tolerant extreme. On this evidence, the difference between the response at our home and the regional response lies less in the deer than in the identity of the disturber and its behavioral characteristics.

Data and code availability

The five-county extract is drawn from the Snapshot Wisconsin citizen-science camera network (Wisconsin Department of Natural Resources, Office of Applied Science). The underlying home-ground camera records and analysis pipeline — including the machine (continuous-vs-intermittent) and sex-structured tolerance results reused here — are reported in the companion home study (Vraniak 2026) and are otherwise held by the authors and available on reasonable request. Exact localities of sensitive species are withheld for conservation reasons.

Acknowledgments

This work draws on a long-term, family-stewarded prairie–savanna restoration and on the regional camera record of Snapshot Wisconsin. We thank Eli Wildey and the Wisconsin DNR Office of Applied Science for the wolf-enriched five-county extract designed with us, J. Stenglein for the Snapshot program, and the household that maintains the home station network and contributed to frame identification.

Author contributions

D.A.V. conceived the study, conducted and stewarded the long-term camera survey, collected and identified the field data, obtained and specified the Snapshot Wisconsin extract, directed all analyses, and is responsible for the content of this manuscript. All methods, statistics, results, and interpretations were specified, verified, and approved by the author, and this final text was written and edited by the author.

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