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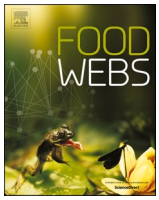

Video observations of wolves hunting ungulates on linear features

Thomas D. Gable [a,*], Sean M. Johnson-Bice [b], Austin T. Homkes [a], Joseph K. Bump [a]

[a] Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN, United States of America
[b] Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba, Canada

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ABSTRACT

Anthropogenic linear features allow wolves to travel faster and more efficiently, which is thought to increase wolf hunting efficiency of ungulates. Most previous studies have evaluated the role of linear features in wolf-ungulate dynamics by relying on indirect observations (e.g., GPS location data). Thus, there remains little direct observational data showing how wolves use linear features to hunt ungulates. Here, we present observational data (29 hunting sequences) of wolves using linear features to hunt ungulates. Linear features have largely been considered travel corridors that facilitate wolf movement and allow wolves to detect prey *near* (but not necessarily *on*) linear features. However, we clearly demonstrate wolves also use linear features as active hunting arenas where they detect, pursue, and kill prey that are also traveling *directly on* linear features. Our observations further suggest one of, if not the, primary way wolves detect ungulates on linear features is via olfactory cues.

Anthropogenic alterations to landscapes can dramatically change and shape predator-prey dynamics, which can alter food webs and ecosystem function through processes such as apparent competition (Labadie et al., 2021; Serrouya et al., 2021) and trophic cascades (Dorresteijn et al., 2015; Kuijper et al., 2016). Over the past decade, substantial effort has been made to understand how human modifications in boreal ecosystems affect wolf (*Canis lupus*)-ungulate dynamics (Mumma et al., 2018). One of the most persistent and pervasive human modifications to boreal landscapes are linear features (e.g., seismic lines, logging roads, power lines) created for access and resource extraction (DeMars and Boutin, 2017; Serrouya et al., 2020). The increase and accumulation of linear features has altered wolf movement patterns and in turn changed historical wolf-ungulate dynamics (Serrouya et al., 2020). Wolves can travel faster and more efficiently on anthropogenic linear features, and as a result, strongly select these features when moving (Latham et al., 2011; Dickie et al., 2017b). This increase in movement efficiency increases encounter rates of wolves with ungulate prey (Whittington et al., 2011; McKenzie et al., 2012), and likely increases wolf hunting efficiency (Dickie et al., 2017a). However, most of these previous studies have evaluated the role of linear features in wolf-ungulate dynamics by relying on indirect observations, such as movement patterns between GPS-collared wolves and ungulates (DeMars and Boutin, 2017; Mumma et al., 2018) or by relating linear features to locations of wolf-killed ungulates identified in the field (Whittington et al., 2011; McKay et al., 2021). Thus, there remains little direct observational data of wolves actively using linear features to hunt ungulates, which would ultimately provide empirical support for conclusions drawn from this previous body of work on wolf-ungulate-linear feature dynamics.

Herein, we present video evidence of wolves using anthropogenic linear features to hunt and kill ungulates. We opportunistically placed remote cameras (Browning Spec Ops models/Reconyx Hyperfire) on anthropogenic linear features (total of 616 camera deployments) in the Greater Voyageurs Ecosystem, MN, a southern boreal forest ecosystem, as part of the research and monitoring efforts of wolves by the Voyageurs Wolf Project (Gable et al., 2022). We defined anthropogenic linear features as any human-made landscape feature that is linear or curvilinear (e.g., roads, trails). We considered wolves to be actively chasing and pursuing deer on linear features when a wolf(ves) ran past a camera on a linear feature ≤5 min after a running deer did so (i.e., the wolf was chasing the deer and the two recordings were not independent events; (Iannarilli et al., 2019) (Fig. 1A-1C). We considered wolves to be tracking deer when wolves appeared to be following, but not in active pursuit, of deer (e.g., intensively smelling ground, examining deer trails) (Fig. 1D-1E). Although wolves almost certainly scent-track prey that have passed by a camera >30 min prior (Mech et al., 2015), we only considered tracking observations to be those where wolves passed by a camera ≤30 min after a deer. We developed these criteria for 'chasing' and 'tracking' using the most recent ethogram of wolf predation

* Corresponding author.
E-mail address: thomasd.gable@gmail.com (T.D. Gable).

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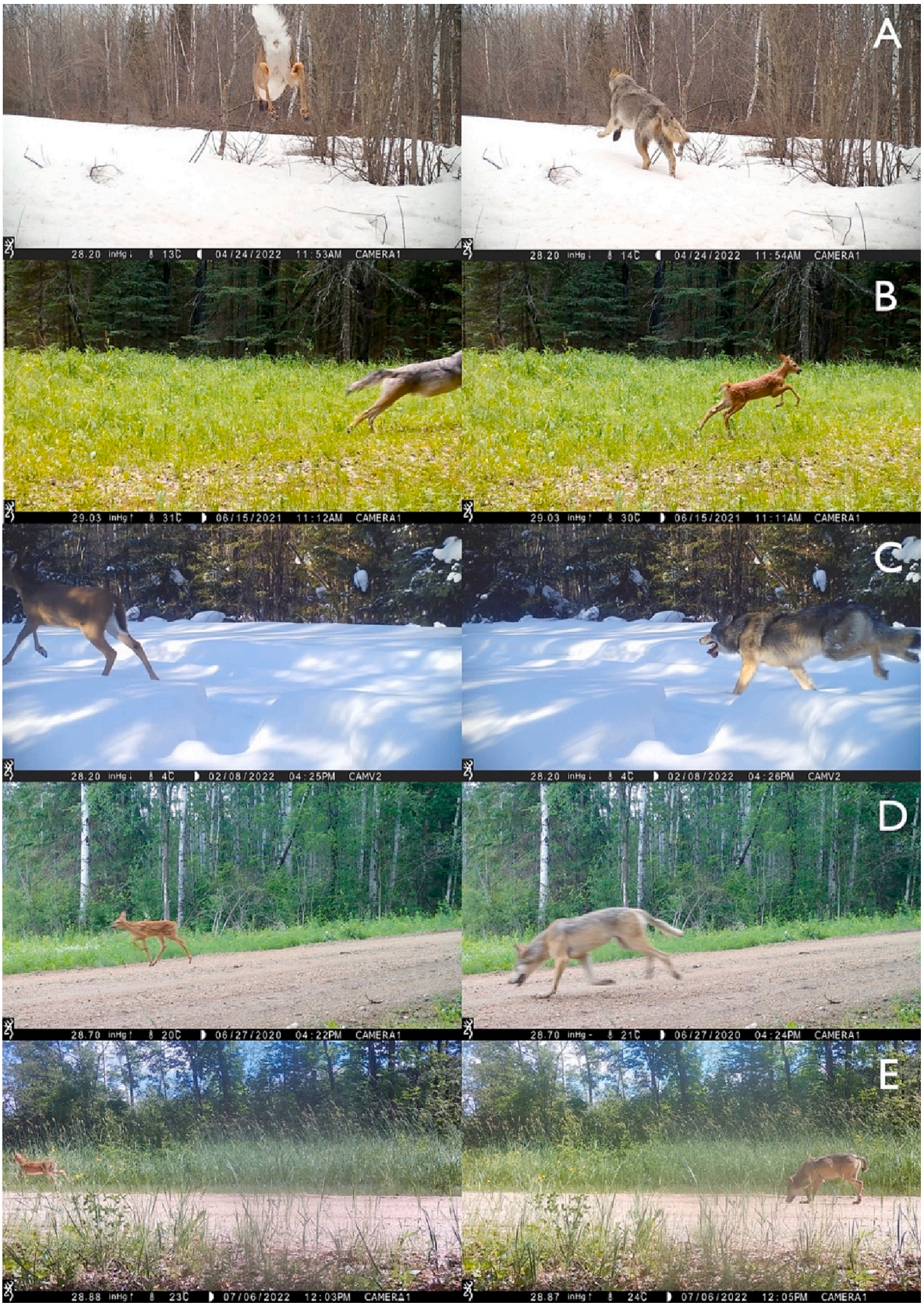

Fig. 1. Still frames from 5 video sequences showing wolves hunting white-tailed deer along anthropogenic linear features in the Greater Voyageurs Ecosystem, Minnesota, USA during 2020–2022. In Panels A-C, wolves are actively chasing and pursuing deer along linear features. We confirmed in the field that wolves in panels B & C successfully killed the deer they were chasing. In panels D & E, the wolves' posture indicated they are tracking white-tailed deer fawns using olfactory cues. These stills are from 5 of the 29 sequences that we documented. Video footage of all 29 sequences can be seen in Appendix A.

behavior by MacNulty et al. (2007) and based on numerous aerial observations of wolves hunting deer as reported in Mech et al. (2015).

Through this effort, we documented 29 observations of wolves hunting white-tailed deer (*Odocoileus virginianus*) on linear features during 2020–2023 (Video S1). In 15 instances, wolves actively chased and pursued deer on linear features and in the other 14 instances wolves tracked or followed deer (Video S1). During chases, wolves were on average 1.5 min (range: 0–5) behind fleeing deer. Of the 29 hunting observations, 28% (8) occurred on well-maintained logging roads, 24% (7) on ATV trails (6 of which were former logging roads), 24% (7) on snowmobile trails, 21% (6) on hiking trails, and 3% (1) on a regenerating logging road. Using GPS data from collared wolves and remote cameras, we confirmed in the field that wolves successfully killed deer (1 adult deer and 1 deer fawn) on or adjacent to anthropogenic linear features in 13% (2/15) of documented chases. We do not know the outcome of the other 27 hunting sequences.

Wolves hunted deer of all age-classes (22 adult/adult-sized deer, 7 fawns, and one mother-fawn pair) and sex (2 males, 14 females, and 13 of unknown sex). We documented hunting observations during every month of the year except May and November, and during both day and night. There was snow cover in 45% of hunting observations and no snow in the other 55% of observations. Wolves hunted deer by themselves in all observations ($n = 16$) during summer (i.e., snow-free periods) but hunted with other pack members in 38% ($n = 5$) of observations during winter. We observed up to 4 wolves hunting deer together.

We provide direct behavioral observations that confirm and support the conclusions of earlier indirect quantitative work, which indicated linear features directly influence wolf hunting behavior of ungulates (Whittington et al., 2011; DeMars and Boutin, 2017; McKay et al., 2021). Notably, many previous studies concluded linear features facilitate detection and encounter rates of wolves with ungulates, but there was little direct evidence demonstrating the specific behavioral mechanism underlying these conclusions. In other words, how wolves detect or encounter ungulates when on linear features was not well understood. For example, do wolves detect ungulates on or near linear features via olfactory or visual cues? Are wolves using linear features as travel corridors to hunt ungulates in close proximity (but not on) linear features, or do wolves use linear features as active hunting grounds where they can directly encounter ungulates also traveling on these features?

We clearly demonstrate that wolves use linear features as active hunting arenas where they detect, pursue, and kill prey that are also traveling *directly on* linear features themselves (Fig. 1; Video S1). The 13 chasing sequences we observed clearly show ungulates running down the linear feature followed shortly by a pursuing wolf (or wolves) – not to mention the two predation events we verified in the field – which indicates that wolves do detect and encounter ungulates directly on linear features. This observation is not surprising because white-tailed deer often select for linear features despite wolf predation risk (Darlington et al., 2022). Thus, in wolf-deer systems, linear features likely represent the best of both worlds for wolves: easy and efficient travel through high-quality habitats where prey are congregated. We suspect this explains, in part, why wolves in the Greater Voyageurs Ecosystem hunt and kill deer fawns closer to linear features than would be expected based on availability (Homkes, 2021).

In addition to directly encountering ungulates on linear features, our observations suggest that one of, if not the primary way wolves detect ungulates along linear features is via olfaction. We documented several sequences of deer traveling down linear features followed shortly thereafter by wolves traveling and intensively smelling the area where the deer had just travelled, indicating wolves were tracking olfactory cues left by deer moving along these features (Fig. 1D and E). Although all of our observations were of wolves detecting olfactory cues left on linear features, we think it highly likely that wolves also use linear features as travel corridors where they can detect odor plumes from prey near but not on linear features. As a result, wind direction when wolves are traveling is likely an important aspect of how wolves detect prey when using linear features.

As linear features continue to be created and accumulate on the landscape, they will continue to alter wolf-ungulate dynamics unless remediated or allowed to regenerate (Finnegan et al., 2018; Serrouya et al., 2020). Our observations suggest that wolves hunt deer on most linear features in our system ranging from small-scale, low-impact features such as hiking trails to large, well-maintained gravel roads. However, one of the most common linear features we observed wolves hunting deer on were former logging roads maintained by recreational off-road vehicle (ORV; includes all-terrain and utility terrain vehicles) users to access remote areas, typically for hunting ruffed-grouse (*Bonasa umbellus*) and white-tailed deer. Although much work has examined how anthropogenic linear features created for resource extraction and exploration influence wolf-ungulate dynamics, and in turn food webs, very little work has examined how recreational use of linear features facilitates the persistence and accumulation of linear features on landscapes (Pigeon et al., 2016). We suggest, given the substantial increase in ORV users in Minnesota and elsewhere (Kennedy, 2021) that future work is needed to understand how this booming recreational industry will shape and alter wolf-ungulate-linear feature dynamics.

Declaration of Competing Interest

We have no conflicts of interest to report for this manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2023.e00297.

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