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The tangled web we weave: how humans influence predator-prey dynamics

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Abstract Large carnivores like gray wolves (*Canis lupus*) play key roles in regulating ecosystem structure and function. After being functionally extirpated from the United States by the early 1900s, wolves have recently recolonized portions of their historic ranges and are increasingly coming into contact with a rapidly-growing human population. When carnivores encounter humans, the way they behave, and therefore the way they shape ecosystems, is likely to change. Unfortunately, our ability to predict how wolves will affect ecosystems in human-dominated areas is limited by an incomplete understanding of how and why carnivores respond to human influence. We are therefore investigating wolf kill sites across Jackson Hole, Wyoming, where we can disentangle the effects of multiple simultaneous human influences. Specifically, we are evaluating whether and how spatiotemporal patterns of wolf predation may change in response to unnatural physical infrastructure, disturbance from general human activity, potential threat of mortality, and human-altered prey distributions. Our ongoing field study will help managers anticipate effects of wolf predation in and around human-influenced areas while contributing novel information to theories of predation risk and predator-prey interactions.

Introduction

Large carnivores regulate the abundance and distribution of herbivorous prey via direct predation (Berryman, 1992) and indirect behavioral effects (Laundré et al., 2001), thereby acting as key drivers of trophic dynamics and ecosystem productivity (Estes et al., 2011). Since the reintroduction of gray wolves (*Canis lupus*) to the Greater Yellowstone Ecosystem (GYE) in 1995, numerous studies have evaluated the effects of wolves on other species and ecosystems (Woodruff and Jimenez, 2019; Fortin et al., 2005; White et al., 2012; Kauffman et al., 2007; Ripple and Beschta, 2012). Far fewer studies, however, have assessed the degree to which human influences might alter these effects (Dellinger et al., 2018). As wolf populations expand beyond protected parks and remote wildernesses, human populations are also expanding into previously-undeveloped areas. Although it is generally assumed that predators like wolves avoid humans in shared landscapes, little research explicitly integrates humans into studies of trophic interactions. As a result, we lack a clear understanding of how humans affect carnivores, their prey, and ecosystems at large (Haswell et al., 2017).

The popular "human shield" hypothesis (Berger, 2007) posits that humans weaken predator-prey interactions by excluding carnivores and therefore increasing survival of prey. Though frequently cited, the human shield hypothesis has rarely been tested, and most tests have occurred in protected areas such as Grand Teton and Yellowstone National Parks where human influence is highly regulated. It is not known whether the "human shield" exists in the human-dominated landscapes adjacent to these parks into which wolf populations have more recently expanded, and there is some evidence that humans affect predator-prey dynamics differently outside protected areas (Dellinger et al., 2018). Further, despite the fact that prey survival comprises the core tenet of this hypothesis, very few studies test it using empirical information about predation. We are therefore gathering predation data across a gradient of human influences in Jackson Hole, Wyoming (Figure 1).

Specifically, we aim to determine whether wolves are more likely, less likely, or similarly likely to kill native ungulates when influenced by: 1) presence of anthropogenic structural developments, 2) physical presence of humans, 3) potential risk of human-caused mortality, and 4) supplemental ungulate feeding operations. Disentangling the effects of these human influences will go beyond merely supporting or refuting the human shield hypothesis, allowing us to identify which specific aspects of human influence most strongly alter predator behavior. This study will allow us to determine whether the predation risk for ungulates differs in and around the human-wildlife interface, and if so, what aspect(s) of human influence effect this change. Results will advance understanding of trophic dynamics in human-influenced systems, help guide management decisions by predicting effects of carnivore predation on native ungulates in anthropogenic areas, and lay the groundwork for developing and testing further hypotheses regarding human effects on predators, prey, and ecosystem function.

Methods

To determine how humans might influence wolf predation, we are investigating wolf kill sites across Jackson Hole, Wyoming, where human influences run the gamut from a developed town to relatively unused wilderness areas (Figure 1). Our fieldwork occurs during winter, because this is the season in which wolves affect ungulate survival most strongly and in which ungulates experience the strongest human influences. We began fieldwork in winter 2019 and plan to continue through winter 2021. Data collected in the field will allow us to quantify how spatiotemporal aspects of kill sites may change due to human influences (see Future Work).

To conduct field investigations, we first use GPS collar data from radio collared wolves to identify "clusters" of locations in which wolves are focusing their time. Then, we visit a randomly prioritized subsample of these cluster sites in the field to determine whether a predation event has occurred and to gather relevant environmental and prey-related data. Data gathered from prey includes identification of species and sex, teeth for aging, and bone marrow to estimate body condition at time of death. We also note the type of wolf activity at the cluster: bedding/resting, killing, scavenging a carcass they did not kill, revisiting an old cluster site, or insufficient evidence. Predation events are further delineated as likely (i.e., very strong evidence of wolf kill consisting of characteristic pre-mortem hemorrhaging and/or clear tracks and landscape cues leading to an obvious kill site) or possible (i.e., the site has characteristics typical of a wolf kill, but not enough remaining hide or snow to find definitive evidence).

Preliminary results

Cluster sites were identified from GPS collar locations of 18 unique individuals (10 wolves in 2019; 12 wolves in 2020) in 6 packs. During winter 2019 and 2020, we visited 634 cluster sites (287 in 2019; 347 in 2020) over 112 field days (58 in 2019; 54 in 2020). Clusters consisted of 60.4% beds or resting areas, 16.4% likely or potential kills, 4.2% scavenged carcasses, 1.6% revisits of previous clusters, and 17.4% other or unknown behaviors (Table 1).

Kills tended to occur at intermediate to low elevations relative to the overall study area (mean 2,219 m, range 1,915-2,677 m) and on moderate slope angles (mean 17 degrees, range 0-61 degrees). On average, kill sites were located 1.7 km from buildings (range 0.05–3.9 km), 2.1 km from plowed oversnow travel routes (range 0.05-7.8 km), and 7.0 km from paved roads (range 0.50-27 km). Elk comprised the vast majority of likely wolf kills (87%), followed by moose (10%), with 3% other species. Of these likely elk kills, approximately 19% were calves, 19% yearlings, 21% young adults (2-5 yrs), 21% adults (6-10 yrs), 11%

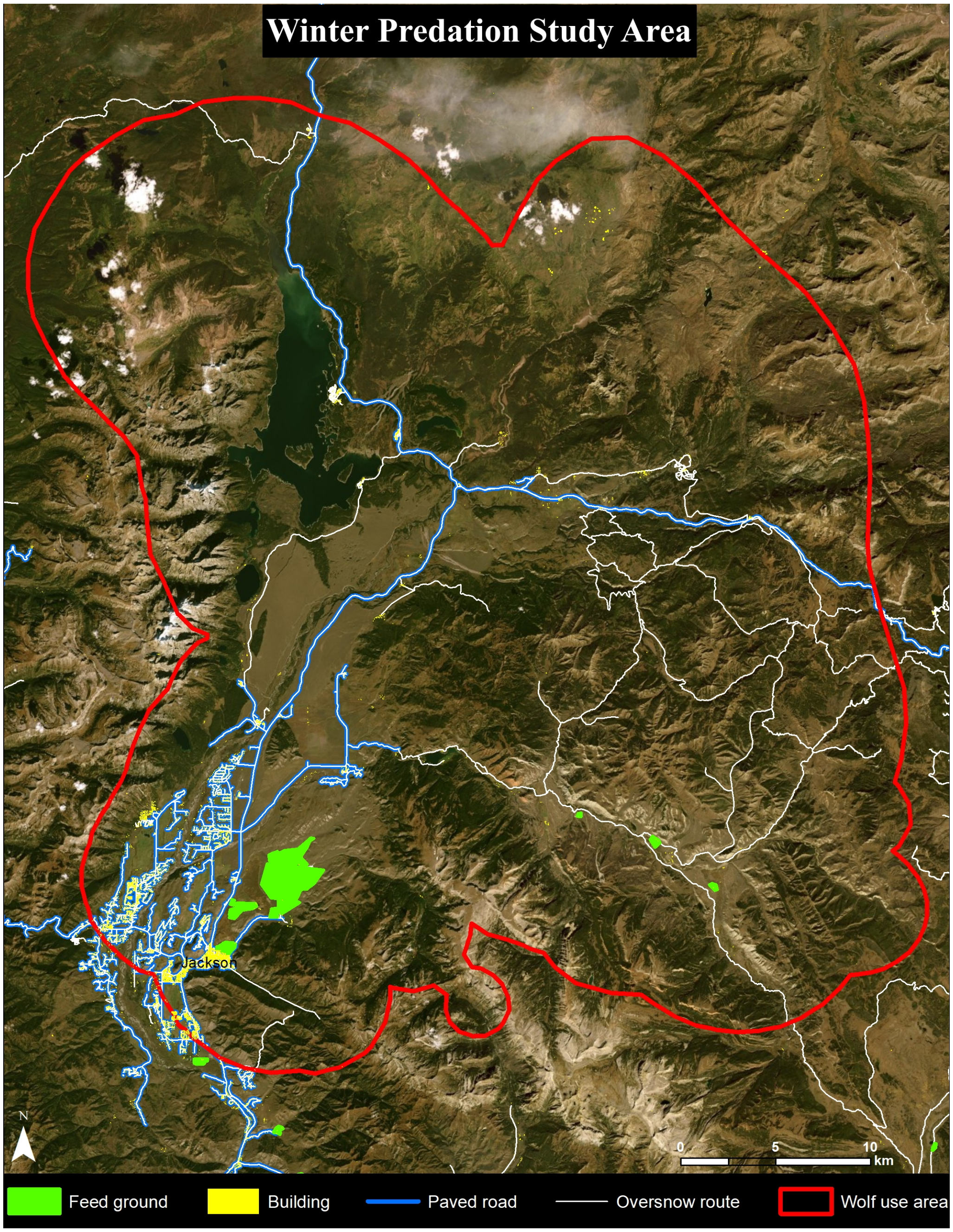

Figure 1. Across Jackson Hole, Wyoming, patterns of wolf predation on native ungulates may change in response to human influences including paved roads, plowed oversnow routes, buildings and other infrastructure, and elk feeding areas.

old adults, and 9% unknown. Ages were estimated in the field based on tooth wear; these preliminary results are subject to change following laboratory aging of tooth samples.

Conclusions

Because current sample sizes preclude our ability to run statistically rigorous models, we are unable to draw definitive conclusions at this time. After the winter 2021 field season, we anticipate a sufficient sam-

Cluster Type	2019	2020	Total
Bed	177	206	383
Kill (likely or potential)	48	56	104
Scavenge	13	14	27
Revisit	4	6	10
Other/unknown	45	65	110
Total	287	347	634

Table 1. Cluster sites investigated during winter 2019 and winter 2020.

ple size of predation events to build robust models capable of evaluating the influences of both environmental and human-related factors.

Future work

After completing fieldwork, we will use logistic regression models to estimate the probability of predation occurring in a given area by comparing characteristics of kill sites (i.e., "used" locations) to characteristics of sites where no kills were observed (i.e., "available" locations; Manly et al., 2002). Available locations will be randomly drawn from wolves' winter ranges (i.e., 95% utilization distributions; Fieberg and Kochanny, 2005). Characteristics considered will include both environmental and human-related factors in order to evaluate how human influences might alter natural patterns of predation.

We will use a two-tiered approach to assess whether and how human influence alters wolf predation. First, we will identify the combination of environmental covariates that best explains the probability of predation (Hosmer Jr et al., 2013). Then, we will compete this environmental model against other models that include additive and interactive effects of different types of human influences to determine whether the addition of human influence appreciably improves our ability to explain wolf predation (Hooten and Hobbs, 2015). Specifically, we will use spatial data to determine whether the probability of wolf predation increases, decreases, or remains the same as the proximity to buildings, roads, oversnow travel routes, and ungulate feeding areas increases. We also anticipate evaluating potential effects of time of day (i.e., whether kills are less likely to occur during the day when humans are most active) and risk of human-related mortality (i.e., hunting or control removals).

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