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Original Article

Wolves choose ambushing locations to counter and capitalize on the sensory abilities of their prey

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Comprehensive knowledge of ambush behavior requires an understanding of where a predator *expects* prey to be, which is generally unknowable because ambush predators often hunt mobile prey that exhibit complex, irregular, or inconspicuous movements. Wolves (*Canis lupus*) are primarily cursorial predators, but they use ambush strategies to hunt beavers (*Castor canadensis*). Terrestrial beaver activity is predictable because beavers use well-defined, conspicuous habitat features repeatedly. Thus, studying where wolves wait-in-ambush for beavers provides a unique opportunity to understand how predators choose ambush locations in relation to prey activity. We searched 11 817 clusters of GPS locations from wolves in the Greater Voyageurs Ecosystem, International Falls, MN, and documented 748 ambushing sites and 214 instances where wolves killed beavers. Wolves chose ambush locations: 1) with olfactory concealment to avoid detection from the highly developed olfactory senses of beavers and 2) close (generally <5 m) to beaver habitat features to take advantage of beavers' inability to visually detect motionless predators. Our work describes in detail the ambush strategies wolves use to hunt beavers and continues to overturn the traditional notion that wolves rely solely on cursorial hunting strategies. We also demonstrate that ambush predators can anticipate the movements and behavior of their prey due to a fundamental understanding of their prey's sensory abilities. Wolves, therefore, and likely ambush predators in general, appear capable of simultaneously accounting for abiotic and biotic factors when choosing ambush locations, ultimately allowing them to counter and capitalize on the sensory abilities of their prey.

Key words: **ambush hunting, hunting behavior, hunting mode, predation risk, sit-and-wait predator, wolf predation.**

INTRODUCTION

How predators hunt their prey provides insight into predator space use, energetics, and time budgets (Williams et al. 2014; Bryce et al. 2017). Predators are broadly categorized as either ambush predators (i.e., sit-and-wait or sit-and-pursue strategies) or cursorial predators (i.e., wide-ranging, active hunting strategy; Preisser et al. 2007; Schmitz 2008; Miller et al. 2014). Because predation is a strong evolutionary force, understanding predator hunting mode and the strategies predators use to hunt prey can reveal the behavioral adaptations prey use to minimize fatal encounters with predators (Romero and Koricheva 2011; Kohl et al. 2019). Predators that use ambush hunting strategies are more likely to lead to behavioral responses in prey compared to those that use cursorial strategies because ambush predators are more sedentary and their cues (e.g., scent) are concentrated in specific areas (e.g., ambushing locations) that likely signal high predation risk to prey (Miller et al. 2014). Cursorial predators, in contrast, cover large areas and, thus, their cues do not necessarily correspond to high predation risk for prey because the cues are dispersed throughout the landscape (Pressier et al 2007; Schmitz 2008). Despite this, ambush hunting—especially where and how predators decide to ambush prey—has received less attention and is more poorly understood than cursorial hunting behavior (Rossoni and Niven 2020), likely due to the challenges of studying cryptic ambush behavior (Li et al. 2003; González-Bernal et al. 2011).

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Where predators choose ambush locations is scale dependent because predators must choose where to wait at both macrohabitat (where predators focus ambushing on a home-range scale) and microhabitat (the specific locations predators choose to wait-in-ambush) scales (Rodríguez-Robles and Glaudas 2011; Clark et al. 2016). Macrohabitat selection by ambush predators is thought to be primarily a function of prey abundance, vulnerability, or accessibility (Hopcraft et al. 2005; Balme et al. 2007; Rodríguez-Robles and Glaudas 2011). When selecting ambush locations *within* macrohabitats (i.e., microhabitat selection), predators must balance the probabilities of: 1) being detected by prey (Li et al. 2003; Wilson 2007), 2) detecting their prey (Gall and Fernández-Juricic 2009), 3) encountering prey at a given location (i.e., encounter rates; Clark 2004; González-Bernal et al. 2011), and 4) killing prey at that location should an encounter occur (i.e., capture rates; Shine and Li-Xin 2002). Predators are likely under strong selective pressures to select optimal ambush locations given the amount of time necessary to wait for and capture prey via ambushing (Du et al. 2009). Thus, optimal ambush sites are generally considered those that maximize encounter and capture rates of prey while minimizing detection by prey (Wilson 2007; González-Bernal et al. 2011).

Systematically documenting ambush behavior is challenging as many ambush predators are difficult to observe because they often rely on secrecy and concealment to hunt prey (Rodríguez-Robles and Glaudas 2011). Furthermore, determining where predators anticipate or expect prey to appear is challenging and often unknowable because ambush predators often hunt mobile prey that exhibit complex, irregular, or inconspicuous movement patterns. Thus, relatively few studies have examined whether ambush strategies are specifically adapted to counter the antipredator behaviors and defenses of their prey. Although logistically challenging to document, such information is vital for a comprehensive understanding of the behavioral adaptations predators use to catch prey (Li et al. 2003) and where predators choose to wait-in-ambush.

Most research on ambush behavior at the microhabitat scale has focused on how herpetofaunal and arachnid predators, and, to a lesser degree, avian, fish, and other invertebrate predators, select ambush locations at this scale. However, there is little information on how terrestrial carnivores select ambush locations at the microhabitat scale. Part of this lack of information is because these smaller taxa are easier to observe and study in the field relative to larger predators (e.g., Schraft et al. 2019). Additionally, smaller taxa are often well suited for controlled experiments where ambush behavior can be examined under various conditions (Preisser et al. 2007; Schmitz 2008; Du et al. 2009; González-Bernal et al. 2011; Miller et al. 2014). Our understanding of carnivore ambush behavior is primarily based on anecdotal observations (Mech 2007; Eads et al. 2010; Gable, Stanger, et al. 2018) or by correlating predator movements or kill-site locations with coarse biotic and abiotic metrics (e.g., habitat type, vegetation density, and wind speed). For instance, researchers often assume that habitat selection by predators provides insight into where predators try to ambush prey (Hopcraft et al. 2005; Balme et al. 2007; Loarie et al. 2013) or that characteristics from kill sites are representative of where ambush predators choose to sit-and-wait (Lone et al. 2014; Donadio and Buskirk 2016; Lendrum et al. 2018). Such research might provide some general insights into predator ambush behavior but precludes a fine-scale or detailed understanding of carnivore ambush behavior. Consequently, the fundamental questions of where and how carnivores choose to wait-in-ambush for their prey remain unanswered (González-Bernal et al. 2011).

Wolves (*Canis lupus*) are primarily cursorial predators, but they have flexible hunting strategies and can switch to ambushing when targeting alternate prey, such as beavers (*Castor canadensis*) and freshwater fish (Gable, Windels, and Homkes 2018; Gable, Stanger, et al. 2018). Beavers are important summer prey for wolves in many ecosystems, constituting up to 42% of wolf diets during spring-fall (Gable et al. 2017; Gable, Windels, Romanski, et al. 2018). Wolves—the primary natural predator of beavers across the circumboreal ecosystem (Gable, Windels, Romanski, et al. 2018)—primarily hunt beavers as individuals, not as a pack (Gable et al. 2016; Gable and Windels 2018).

Beavers are unique prey for wolves given the short periods they spend on land close to water. When on land, beavers primarily cut woody vegetation for food and lodge/dam construction, to build or repair dams or lodges, or to create and maintain scent mounds that demarcate their territory (Baker and Hill 2003). Most notably, beavers use well-defined "feeding trails," which rarely exceed 40–60 m, to access and cut woody vegetation (Jenkins 1975; Novak 1987; Salandre et al. 2017). Where beavers, who are central place foragers, will be on land is predictable because they use the same habitat features repeatedly, and their terrestrial activity is conspicuous and confined to a small area (Baker and Hill 2003; Gable, Stanger, et al. 2018; Gable, Windels, Romanski, et al. 2018). To minimize fatal encounters with predators on land, beavers primarily rely on their highly developed olfactory senses to detect predators (Baker and Hill 2003; Rosell and Sanda 2006) and remain close to water to quickly escape should a predator be detected or encountered (Basey and Jenkins 1995; Campbell-Palmer and Rosell 2010; Gable, Stanger, et al. 2018).

Although the general strategy wolves use to hunt and kill beavers (i.e., waiting-in-ambush near active beaver features) is relatively well understood (Gable et al. 2016; Gable, Stanger, et al. 2018), specifics about how, when, and where wolves attempt to, and successfully do, ambush beavers are unknown. Fortunately, where wolves wait-in-ambush for beavers can be identified by searching clusters of locations from GPS-collared wolves (Gable et al. 2016). This approach allows us to determine not only where wolves choose to wait-in-ambush but also how they choose ambush locations relative to where they likely expect or anticipate beavers to be active on land (Gable et al. 2016; Gable, Windels, Romanski, et al. 2018).

Our primary objective was to describe the patterns of where and how wolves ambush beavers. Specifically, we sought to understand how wolves chose ambush locations in relation to terrestrial beaver activity, water, and wind direction and whether they killed beavers in the same habitats where they waited-in-ambush. We expected wolves to choose ambush locations that would allow them to counter the two main defense strategies of beavers: 1) using olfaction to detect predator odors (Campbell-Palmer and Rosell 2010) and 2) proximity to water to facilitate a quick escape (Basey and Jenkins 1995; Gable, Stanger, et al. 2018). Thus, we hypothesized that wolves would choose ambush locations with olfactory concealment (i.e., where the wind direction would not reveal the wolf's presence) that would also be farther from water, when possible. We also expected wolves would choose ambush locations close (<5 m) to beaver activity because beavers, which have poor eyesight, appear unable to visually detect motionless predators but can detect pursuing predators from >15 m away (Basey and Jenkins 1995; Gable, Stanger, et al. 2018). Finally, we expected to find differences between where wolves waited-in-ambush for and killed beavers as previous work has shown that a certain but unknown percentage of wolf-killed beavers are killed via opportunistic encounters and not via ambushing (Gable et al. 2016).

METHODS

Our study was conducted as part of the Voyageurs Wolf Project, located in the Greater Voyageurs Ecosystem (GVE), International Falls, MN, which is a southern boreal ecosystem that includes Voyageurs National Park and the area southerly adjacent to the park. The GVE is in the Laurentian Mixed Forest Province and is characterized by dense forests (deciduous, coniferous, and mixed) and abundant lakes, bogs, and wetlands interspersed with rocky ridges and outcrops from glacial activity (Gable, Johnson-Bice, et al. 2020). The GVE has sustained dense wolf (35–45 wolves/km^2; Gable et al. 2016) and beaver populations (>0.47–1.0 colonies/km^2; Gable and Windels 2018) for >30 years. Due to their abundance, beavers are valuable seasonal prey for wolves in the GVE with beaver constituting up to 42% of wolf pack diets from April to October (the ice-free season) when beavers are vulnerable to predation (Gable et al. 2017). For more information on the GVE, see Gable et al. (2016, 2017).

During 2015–2019, we used foothold traps and cable restraints to capture wolves and fit them with 20-min-fix-interval GPS collars (Institutional Animal Care and Use Committee protocol: MWR_VOYA_WINDELS_WOLF). In 2015, three wolves were fitted with collars that took fixes every 4–12 h (see Gable et al. 2016 for more details). We searched clusters of GPS locations from collared wolves during April-November to identify predation events. In 2015, we only searched clusters where a wolf had remained within a 200-m area for ≥4 h (Gable et al. 2016). Our objective in 2015 was to visit random GPS clusters in beaver habitats because we primarily wanted to locate where wolves killed beavers (Gable et al. 2016; Gable and Windels 2018). During 2016–2019, we adjusted our cluster criteria to be ≥2 consecutive locations (≥20 min) within a 200-m radius of one another (Gable, Windels, and Homkes 2018). In 2016–2017, we searched a random subset of clusters from GPS-collared wolves and, in 2018–2019, we visited every cluster from GPS-collared wolves. The change in cluster criteria and percentage of clusters searched represents our trial-and-error process for determining how to successfully study wolf predation on small prey from spring to fall in a southern boreal ecosystem, which had proven difficult prior to our research (Palacios and Mech 2010; Gable et al. 2016; Gable, Johnson-Bice, et al. 2020). The change in our cluster criteria over time should not bias our results in regards to wolf hunting or predation behavior on beavers as clusters in beaver habitats were visited randomly from 2015 to 2017 and every cluster during 2018–2019 was searched (Gable et al. 2016; Gable and Windels 2018; Gable, Johnson-Bice, et al. 2020).

We systematically searched for evidence of predation events when at GPS clusters. We considered evidence of predation to be any cluster where there were fresh beaver remains, such as bones, fur, skull/lower mandible, stomach contents, and castor glands (Gable et al. 2016; Gable, Johnson-Bice, et al. 2020). Kill sites typically had depressed or disturbed vegetation that assisted in locating the kill and finding beaver remains. When we located wolf-killed beavers, we recorded the beaver habitat feature (e.g., feeding trails and dams) that the beaver was killed at or near (Gable et al. 2016). We considered there to be 12 habitat features a beaver could be killed at (see Supplementary Appendix 1). Although GPS collars provide us with ample, fine-scale information on wolf movements, using GPS data to locate and identify kill sites is nonetheless an indirect process. At kill sites, we were unable to determine whether bed sites found occurred before or after the kill (Gable et al. 2016; Gable, Windels, Romanski, et al. 2018). This prevented us from determining whether wolf-killed beavers were killed via ambush strategies or through fatal opportunistic encounters, ultimately precluding us from evaluating ambush hunting success rates. For more detailed information about our cluster and kill-site investigations, see Gable et al. (2016) or Gable, Windels, and Homkes (2018).

Beaver-hunting attempts

We identified "beaver-hunting attempts"—where wolves appeared to wait-in-ambush for beavers but where a kill was not found (i.e., ambush attempts that were unsuccessful)—when searching clusters of GPS locations (Figure 1; Gable et al. 2016). Generally speaking, a beaver-hunting attempt was a tight cluster of wolf locations near fresh beaver activity (Supplementary Appendices 2–4). Specifically, we defined a beaver-hunting attempt as ≥2 consecutive locations <25 m apart, of which >50% had to be ≤15 m from fresh beaver activity (e.g., fresh cuttings and mud on scent mound; Gable et al. 2016). When we identified beaver-hunting attempts, we searched intensively to find the specific spot (i.e., bed site) where the wolf had waited (Gable et al. 2016; Kusler et al. 2017). Wolf beds

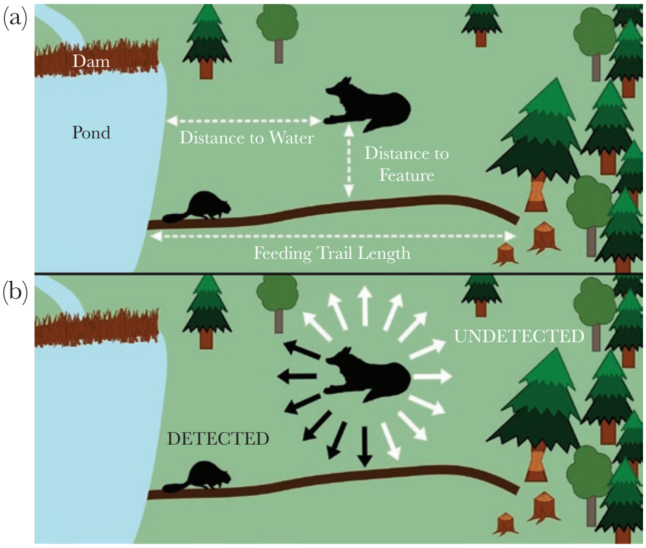

Figure 1
Diagram showing how we assessed whether wolves would have been likely detected or likely undetected by beavers at ambushing attempts. We first identified where the wolf was waiting-in-ambush based on bed-site location and then made a detailed map and video in the field of where the wolf waited in relation to terrestrial beaver habitat features (a feeding trail and dam in this example) as well as the aquatic features (a pond in this example; top panel, a). We then used the prevailing wind direction(s) during the hunting attempt based on the closest weather station to determine if the wolf's odor plume would have been blown over the terrestrial and aquatic beaver features (bottom panel, b). The white arrows indicate wind directions where we would have considered the wolf to likely have been undetected by beavers whereas black indicates wind directions where the wolf would likely have been detected. We assumed that once the beaver had traveled beyond the wolf, the wolf would be able to successfully ambush the beaver even if the beaver detected the wolf at that point.

were characterized by a circular area of depressed vegetation or earth with wolf hairs scattered on the ground (see Supplementary Appendix 2). We found bed sites at most hunting attempts; however, there were some attempts where we could not find a bed because of certain forest floor cover types (e.g., rock and compacted bare ground). If we could not find a bed site, we assumed that the bed site was at the centroid of the GPS locations associated with that hunting attempt (Vogt et al. 2018) as most located bed sites were <2 m from the centroid (T.D. Gable, pers. observation). We emphasize that hunting attempts were ambush sites where wolves were unsuccessful and did not kill a beaver. By contrast, kill sites were locations where wolves successfully killed a beaver.

When we documented beaver-hunting attempts, we recorded: 1) the beaver habitat feature(s) wolves waited by (Figure 1), 2) the distance (meters) between the wolf and the closest fresh beaver activity (i.e., how far the wolf was bedded down from where we surmised it expected beavers to be), 3) the distance (meters) between the wolf and deep water (>0.5 m deep), and 4) the time (beginning and end) the hunting attempt occurred based on GPS locations. When wolves waited by beaver feeding trails in 2018–2019, we measured the length of the trail to the nearest meter (these data were not recorded in 2015–2017). Additionally, we recorded videos of field investigations of most hunting attempt sites and created hand-drawn maps, based on field investigations, of each hunting attempt site to document pertinent information (e.g., where the wolf was waiting in relation to water and beaver activity; Figure 1). The combination of the hunting attempt measurements, maps, and videos (see Supplementary Appendices 2–4) allowed us to thoroughly document this behavior and determine where wolves waited to ambush beavers (Figure 1).

For analysis and comparison, we assigned kills and hunting attempts to six broader beaver habitat feature categories (see Supplementary Appendix 1): dams, foraging features, forest interior, lodges, shorelines, and waterways (e.g., streams and creeks). Wolves sometimes positioned themselves equidistant to two or three beaver habitat features during hunting attempts (e.g., a wolf bedded down next to a feeding trail below an active beaver dam). In such instances, we divided the attempt and assigned the resulting values to each feature the wolf waited next to (i.e., one attempt at two features = a value of 0.5 for each feature). We used Fisher's exact test to compare the habitat features where wolves waited to ambush beavers and where they killed beavers.

To assess the relationship between feeding trail length and the distance wolves waited from water, we used a generalized least squares (GLS) model with a power variance structure and included a random effect for individual wolves (Zuur et al. 2009). We refer to this as the "observed data" model below. We used the "lme4" package to fit the GLS model (Bates et al. 2015). We had sufficient data from 11 wolves for this analysis because we only recorded feeding trail length at ambushing sites during 2018–2019. We then used a "null" model to determine what we would expect if ambush sites were chosen at random. To do this, we selected 20 randomly distributed values on feeding trails ranging from 1 to 80 m (e.g., 20 attempts on 1 m trails, 20 attempts on 2 m trails, and so on) and then created a "null" GLS model with a power variance structure. Given our definition of an ambushing attempt (i.e., the wolf had to be within 15 m of active beaver sign), we considered potential ambush locations to be 15 m beyond the end of any feeding trail. For example, on a 50-m trail, potential ambush locations were 0–65 m from water. We then assessed whether the slope of the "null" model fell within the confidence intervals (CIs) for the slope of the "observed data" model to determine if there was a difference between the two models.

We used a feeding trail index (index = bed site distance from water/feeding trail length) to assess the distance wolves waited from water relative to the length of the feeding trail they were waiting next to. A feeding trail index >1 indicated that a wolf waited farther from water than the end of the feeding trail, whereas an index <1 indicated a wolf waited somewhere between water and the end of the trail. A feeding trail index of 1 indicated the wolf waited at the end of the trail. We fit these data with a locally weighted smoothing regression line to visualize the trend. All analyses were conducted in the program R version 3.5.2.

Wind direction and olfactory concealment

We used wind direction data collected hourly from a weather station in Voyageurs National Park (station name: VOYA-SB, station site code: 27-137-0034) to estimate wind direction during hunting attempts. We used both the mean hourly wind direction (in degrees) and the overall range of wind direction during the attempt. If the attempt took <1 h, we used the wind direction data from the nearest hour for our analysis. In three instances, wind direction data were not available for specific periods, so we used wind direction data recorded hourly at the Falls International Station at Falls International Airport (KINL), which is ~18 km west of Voyageurs National Park.

We then qualitatively evaluated whether wolves would have been detected via olfaction by beavers at each hunting attempt. Assessing whether a wolf would have been detected required understanding not only how wolves positioned themselves relative to terrestrial beaver features that they waited by but also how they positioned themselves relative to nearby aquatic features (e.g., ponds, streams, and canals) that beavers used for traveling to terrestrial features (Figure 1). For instance, a wolf might correctly position itself relative to a beaver feature (e.g., feeding trail) given the wind direction, but if the wind blows the wolf's odor over the water that the beaver must travel through to reach that feature, then the beaver would detect the wolf before it ever comes ashore. We relied on the detailed information we recorded in the field (i.e., maps and videos of hunting attempts detailing pertinent beaver activity and where a wolf bedded in relation to that) to assess whether the wolf would have likely been detected at each attempt (Figure 1). In particular, we plotted the prevailing wind direction(s) during the attempt and assessed whether the wolf's odor plumes would have been dispersed over pertinent aquatic and terrestrial beaver features (see Figure 1). We assumed that beavers could detect wolves at any distance so long as they were downwind of the wolf's odor plume (i.e., we did not assume a threshold distance after which wolf scent would be deemed undetectable by beavers). Our aim in using these qualitative assessments was to understand whether wolves chose ambush locations based on olfactory concealment. While our approach does not capture all of the nuances of wind turbulence and direction during hunting attempts, it allowed us to assess how prevailing wind direction influences ambush behavior at a finer scale than any previous study we are aware of (Conover 2007; Cherry and Barton 2017).

When assessing how wolves waited in relation to wind direction, we categorized hunting attempts as: wolf likely undetected by beaver, wolf likely detected by beaver, or unknown (Figure 1). Attempts assigned as "unknown" were those where we were unable to make a clear decision due to a variety of different factors, such as variable wind direction during the attempt, no wind during the attempt (wind direction was generally not recorded at weather station when wind speeds were <0.5 m/s), and uncertainty about how the beaver would have approached the location where the wolf was waiting-in-ambush. We calculated the percentage of total attempts in each of these groups (likely detected, likely undetected, and unknown) and used those percentages to assess how wolves chose to wait-in-ambush in relation to wind direction. We used nonparametric bootstrapping to get CIs for our detection estimates (Fieberg et al. 2020). We omitted a small number of attempts from our analysis because detailed information on the attempt was not recorded.

RESULTS

We searched 11 817 clusters of GPS locations in the field from 32 wolves during 2015–2019. In doing so, we documented 214 wolf-killed beavers and 748 beaver-hunting attempts (i.e., instances where wolves attempted to ambush beavers) from 28 different wolves (i.e., we did not identify ambush attempts from 4 of the 32 wolves studied). Wolves generally waited-in-ambush a mean distance of 2.5 m (standard deviation [SD] = 3.3 m; median = 3.5 m) from beaver activity (Figure 2) and 7.0 m (SD = 10.1; median = 10.1 m) from water (Figure 3). Wolves waited a mean distance of 3.0 m (SD = 3.5; median = 4.0 m) from water when not waiting at feeding trails (Figure 3a). Ambushing attempts lasted anywhere from 0.3 to 30.0 h with an average duration of 4.0 h (SD = 3.7 h; median = 2.7 h).

We measured 316 feeding trails that wolves bedded down along to ambush beavers. There was a positive relationship between the length of a feeding trail and the ambush site's distance from water (Figure 4a and Figure 5d; Distance to Water ~ 4.31 + 0.44 × Feeding Trail Length; 95% CI for β_0 and β_1 was 2.76–5.86 and 0.38–0.51, respectively; $P < 0.001$). However, the slope of our null model (0.49) fell within the 95% CI of the slope from our "observed data" model (0.38–0.51), indicating that ambushing locations were chosen at random. Interestingly, however, at short trails (<9 m long, n = 47), wolves generally waited beyond the end of the trail, whereas, at trails >9 m long (n = 269), wolves generally waited an average of 50–70% of the way down the trail (Figure 4c). Along the longest feeding trails (>35 m, n = 69), wolves never waited beyond the end of the trail.

The proportion of hunting attempts (i.e., where wolves waited-in-ambush but did not successfully kill a beaver) at habitat features was

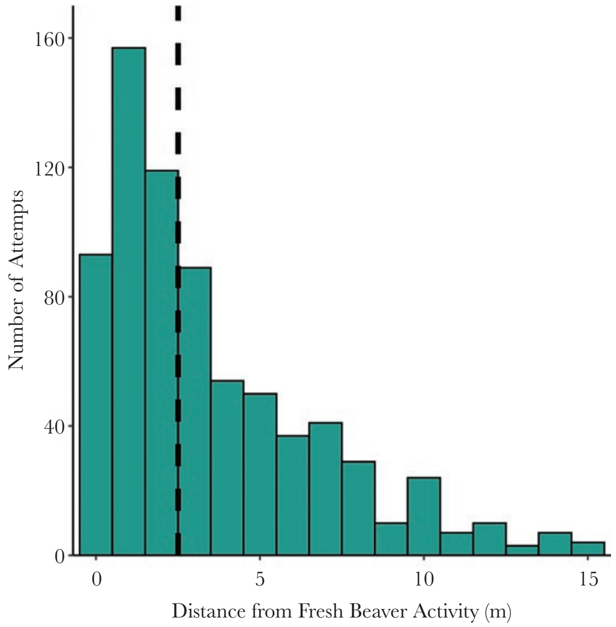

Figure 2
The distance that wolves waited-in-ambush (n = 748) from fresh beaver activity when hunting beavers in the Greater Voyageurs Ecosystem, International Falls, MN, between 2015 and 2019. Dashed line represents the median.

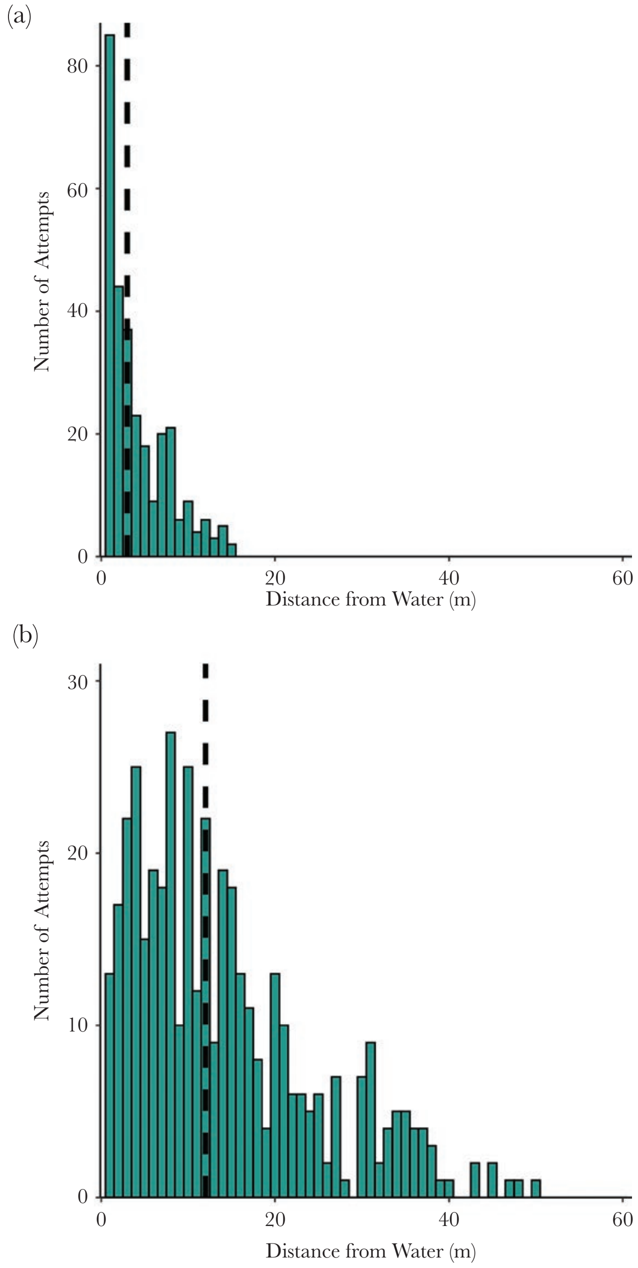

Figure 3
The distance wolves waited-in-ambush from water when hunting beavers in the Greater Voyageurs Ecosystem, International Falls, MN. Panel a shows the distribution of all (n = 317) ambushing attempts that were not along beaver feeding trails, whereas Panel b shows the distribution of ambush attempts along feeding trails (n = 422). Dashed lines represent the median.

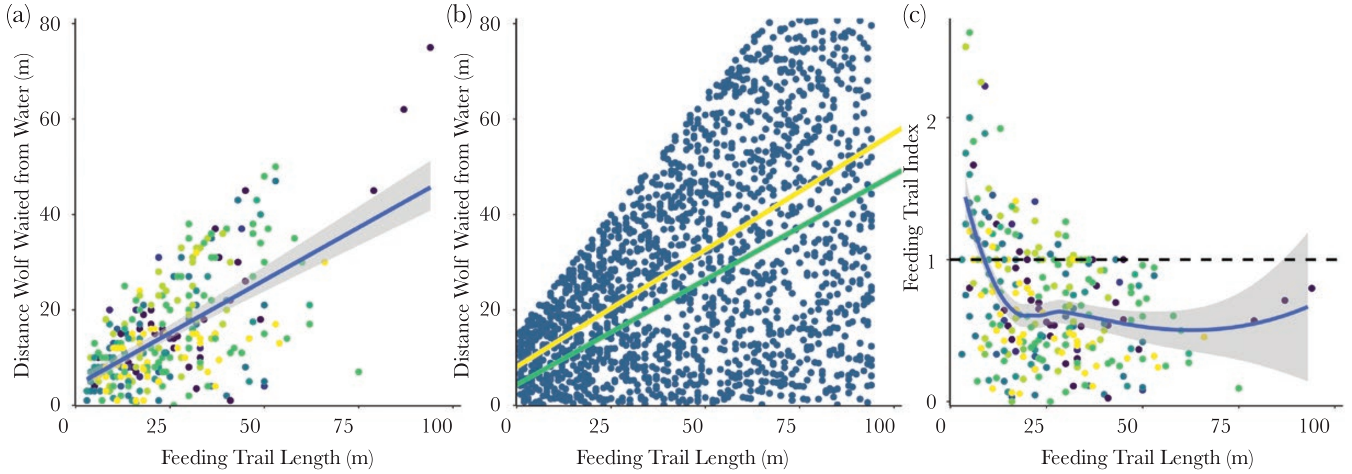

Figure 4

Where wolves choose to wait-in-ambush at beaver feeding trails in the Greater Voyageurs Ecosystem, International Falls, MN, based on 316 ambushing attempts from 2018 to 2019. The different colored points in Panels a and c correspond to individual wolves (*n* = 11 wolves). Though wolves generally waited further from water on longer feeding trails (a), this is largely a result of the fact that wolves have a greater variety of distances they can wait from water as a trail gets longer (b). Panel B represents what we would expect if ambush sites were chosen at random with respect to water (the points represent randomly distributed values on feeding trails). The yellow line represents the null model and the green line represents the GLS model from Panel a. The feeding trail index in Panel c represents how far down a feeding trail relative to the length of the trail a wolf chose to wait-in-ambush (i.e., index = distance wolf waited from water/length of feeding trail). Index values >1 indicate that a wolf waited further from water than the end of the feeding trail, whereas index <1 indicate a wolf waited somewhere between water and the end of the trail. A feeding trail index of 1 (dashed line in Panel b) indicate that the wolf waited at the end of the trail. Shading represents 95% CIs.

different from the proportion of kills at those same features (Figure 6; $P < 0.001$). In particular, 65% of beaver-hunting attempts occurred around features beavers used for foraging (e.g., feeding trails, feeding canals, and feeding areas), whereas only 32% of kills occurred at these features. In contrast, 15% and 20% of kills occurred in the forest interior and at small waterways, respectively, but only 0% and 3% of all hunting attempts occurred at these features (Figure 5). Wolves focused much of their ambushing behavior at feeding trails as 49% ($n = 368$) of all hunting attempts occurred near feeding trails.

Wolves primarily chose ambush locations where beavers would likely have been unable to smell them (89% of hunting attempts; 95% CI: 86.0–91.0%). At 5% (95% CI: 3.7–7.0%) of hunting attempts, wolves waited where they likely would have been detected by beavers. We classified the remaining 6% of hunting attempts as unknown (95% CI: 4.4–7.9%). Given that wolves primarily waited in a downwind or undetected position, we suspect that, at most of these "unknown" hunting attempts, wolves waited in undetected or downwind positions. If we omit these unknowns (or assume that the other hunting attempts are representative of the unknowns), then wolves waited downwind or in undetected positions at 94% of hunting attempts and upwind or in detected positions at 6% of attempts. In 22 cases, we failed to record adequate data for such an assessment, so we omitted these from the olfactory analysis. Patterns of where individual wolves (only includes wolves that made >10 ambushing attempts; $n = 15$) waited-in-ambush for beavers were markedly similar in regards to olfactory concealment, distance from fresh beaver activity, and distance from water (Figure 5).

DISCUSSION

We have demonstrated that wolves primarily ambush beavers by waiting near beaver features for substantial periods (mean duration of 4.0 h, though some attempts last up to 30 h) in locations that account for wind direction, distance from beaver activity, and the beaver habitat feature they are waiting next to. The similarity in ambushing patterns of individual wolves from different packs provides evidence that this ambush behavior is widespread throughout, and likely beyond, our study area (Figure 5). Our work continues to overturn the traditional notion that wolves rely solely on cursorial hunting strategies (Mech et al. 2015; Gable et al. 2016; Gable, Stanger, et al. 2018). Instead, wolf hunting strategies appear highly flexible with wolves able to switch between hunting modes depending on the prey. Moreover, when using ambush strategies, wolves are capable of choosing locations to counter and capitalize on their prey's sensory abilities.

Wolves appear to choose ambush locations to counter beavers' primary sensory defense, olfaction (Novak 1987; Campbell-Palmer and Rosell 2010). To prevent detection, wolves predominantly chose ambush locations that had olfactory concealment (89–94% of attempts) where beavers likely could not detect them. Although this was expected, empirically demonstrating how wind direction influences the ambush behavior of carnivores has been difficult, at best, with most studies only able to correlate habitat selection or hunting success with wind speed or direction (Stander and Albon 1993; Conover 2007; Cherry and Barton 2017). To our knowledge, this is the only study that demonstrates that carnivores can choose ambush locations with olfactory concealment from their prey (see Conover 2007 and Cherry and Barton 2017 for a review of olfaction in predator–prey interactions).

To exploit a key sensory deficiency of their prey, wolves appear to choose ambush locations to capitalize on the poor eyesight and visual acuity of beavers. That is, wolves likely have learned that beavers cannot see a motionless predator (Gable, Stanger, et al. 2018) as wolves generally waited close (1–5 m) to beaver features (Figure 2), commonly with little-to-no visual cover Supplementary Appendix 2; Video S2, Gable, unpublished data). Waiting close to a feature minimizes the period between when wolves leave their ambush location and when they encounter beavers, likely

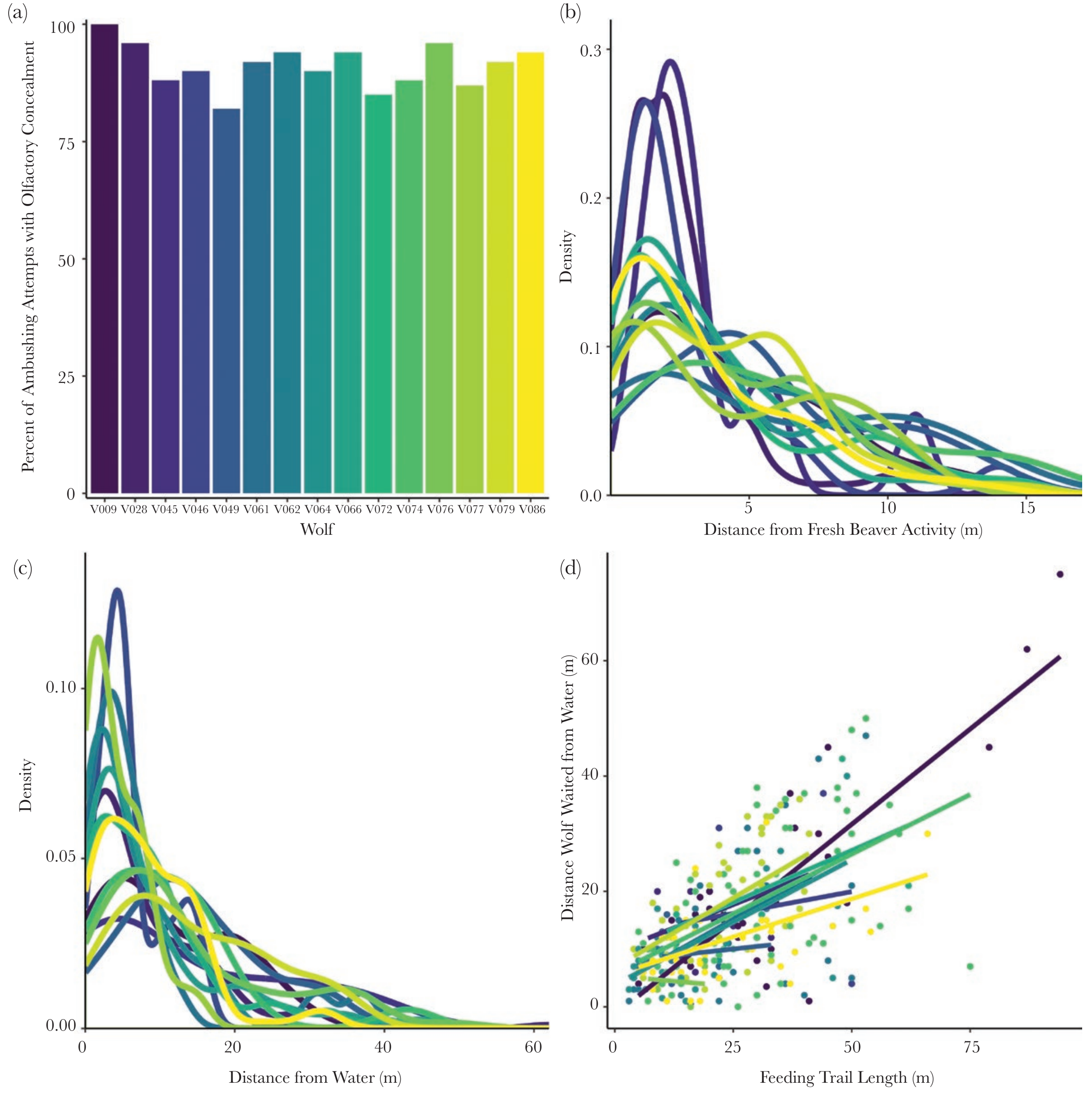

Figure 5

The similarity in where individual wolves (each colored bar/line represents a unique wolf; *n* = 15) waited-in-ambush for beavers relative to: (a) wind direction, (b) distance from fresh beaver activity, (c) distance from water, and (d) length of beaver feeding trails. We assessed where wolves waited in relation to wind direction (a) by determining whether wolves would have had olfactory concealment (i.e., have been undetected via scent) from beavers at ambushing attempts. We only included data from wolves that had >10 ambushing attempts (*n* = 15 wolves). For Panel d, we only had sufficient data for 11 wolves.

reducing the probability of being detected prior to an attack and, in turn, the beaver escaping to water (see Video S1 in Gable, Stanger, et al. 2018). Indeed, a wolf in Quebec was observed using this strategy by waiting motionless for a beaver to get within 2 m before attacking (Gable, Stanger, et al. 2018).

Although wolves appear to account for the sensory abilities of beavers, contrary to our hypothesis, they do not appear to choose ambushing locations to minimize the physical challenges of killing a beaver before it reaches water. A key assumption in our initial hypothesis was that beavers are more vulnerable to predation with increasing distance from water and, therefore, we expected wolves to wait farther from water on longer feeding trails to reduce the probability of a beaver escaping during an encounter. Typically, prey that rely largely on refuge for protection, instead of well-developed physical defenses, have increased predation risk as distance from the refuge increases (McLean and Goden 1989; Pokallus and Pauli 2016). Although there is consensus in the scientific literature that beavers are indeed more vulnerable to predation

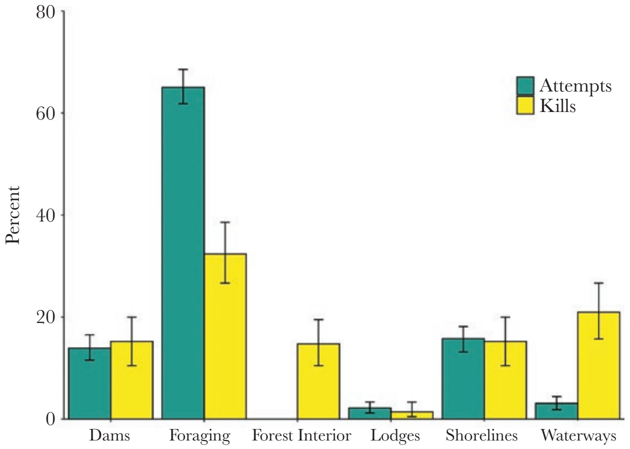

Figure 6
The habitat features where wolves attempted to ambush and successfully killed beavers in the Greater Voyageurs Ecosystem, International Falls, MN, during 2015–2019. Attempted ambushes were ambush sites where wolves were unsuccessful and did not kill a beaver. By contrast, kill were locations where wolves successfully killed a beaver. However, we were unable to determine whether wolf-killed beavers were killed via ambush strategies or through fatal opportunistic encounters (i.e., opportunism). That is, though we could locate kills, we were unable to ultimately identify ambushing attempts that were successful because of the limitations and indirect nature of studying wolf predation via GPS collars (Gable et al. 2016; Gable, Windels, Romanski, et al. 2018). The "foraging" habitat feature includes all attempts and kills around feeding trails, feeding areas, and feeding canals. The error bars represent 95% CIs.

farther from water (Basey and Jenkins 1995, Gable et al. 2018), there is no empirical data that supports this assertion—it has simply been assumed. Where wolves choose to wait-in-ambush along feeding trails appears random with respect to distance from water suggesting that either 1) wolves do not understand beavers are more vulnerable with increasing distance from water or 2) beavers are not more vulnerable at increasing distances from water and, thus, wolf ambush strategies reflect this fact. It remains unclear which explanation is more probable, highlighting the value of empirical data to support or reject long-held assumptions about the behavior of predators and prey alike.

Encounter rates, capture rates, and opportunism

Habitat-mediated differences in encounter and capture rates, in addition to opportunistic predation, likely explain the difference between where wolves attempted to kill beavers and where they were successful (Figure 6). Otherwise, the proportion of kills at each habitat should be similar to that of hunting attempts. When choosing ambush locations, wolves must balance the probability of encountering a beaver (i.e., encounter rates) with the probability of killing a beaver if an encounter occurs (i.e., capture rates). Capture rates could increase with increasing distance from water (but see above), whereas encounter rates likely vary by habitat feature. Unfortunately, gathering data on wolf encounter and capture rates of beavers is extremely challenging (see below).

Wolves focused most ambush efforts around beaver foraging features (65% of attempts; Figure 6) but only 32% of kills occurred around these features. We suspect only part of this difference is attributable to capture and encounter rates and that opportunistic predation of beavers explains some, if not most, of the disparity between where hunting attempts and kills occurred. Most kills in the forest interior and along small waterways are the result of wolves opportunistically encountering dispersing beavers traveling through small, shallow waterways or forested areas where they are readily killed by wolves because they cannot escape to deep water (Figure 6; Gable et al. 2016). However, beyond this, quantifying what percentage of kills are opportunistic is difficult from GPS-collar data alone (Gable et al. 2016), and we do not know whether most predation events were the result of successful ambushes or opportunistic encounters. Ultimately, the inability to parse opportunistic and ambush kills limits our ability to disentangle the extent to which encounter/capture rates and opportunism are driving the disparity between where attempts and kills are occurring. Developing methods using accelerometer data from GPS collars could be beneficial toward this end (Gable, Windels, Romanski, et al. 2018).

Despite our work on wolf ambush behavior, how wolves assess and decide where the best locations to wait-in-ambush are remains unknown. Understanding this is complicated by the fact that wolves must make both pond-level (where to wait around an active beaver pond) and territory-level (what pond to wait at) decisions when choosing ambush locations (i.e., two-level spatial selection; Rodríguez-Robles and Glaudas 2011). Thus, how wolves decide to wait at a particular location at a given pond, instead of a potentially better location at a different pond, remains unknown and is an outstanding challenge to understand.

Prey responses to ambush predators?

Determining how predators hunt their prey is crucial for understanding prey antipredator behaviors (Preisser et al. 2007; Miller et al. 2014). Several studies have examined how beavers alter their foraging and scent-marking behavior when wolf odors (e.g., urine and feces) are placed directly on beaver features (Engelhart and Müller-Schwarze 1995; Severud et al. 2011; Salandre et al. 2017). Such work has demonstrated that beavers can detect wolf odors, but inference beyond this is limited because the study design(s) did not simulate how wolves actually appear to hunt beavers. That is, the chemical cues often used do not match the intensity or type of sensory cue (Weissburg et al. 2014; Moll et al. 2017; Parsons et al. 2018; Peers et al. 2018) that beavers would likely encounter in natural settings because wolves generally choose ambushing locations in areas with olfactory concealment from beavers. Without accurate information on predator ambush strategies, studies examining antipredator behavior run the risk of being biologically flawed because they fail to mimic how ambush predators hunt their prey and, consequently, the strategies prey have evolved to avoid ambush predators (Weissburg et al. 2014; Moll et al. 2017; Prugh et al. 2019).

Identifying how ambush carnivores influence the behavior of their prey, and how their prey perceive predation risk of ambush predators, is challenging. Two common approaches for quantifying predation risk are: 1) creating models that predict where kills are most likely to occur based on habitat characteristics at kill sites and then assuming that habitats with a higher probability of kill occurrence have higher predation risk (Lone et al. 2014; Donadio and Buskirk 2016; Lendrum et al. 2018; Prugh et al. 2019) and 2) using GPS locations from predators to predict predator space use and assuming riskier habitats are those where predators spend more time (Moll et al. 2017; Kohl et al. 2019). Our work suggests that where ambush predators successfully kill their prey can be different from where they hunt prey (Figure 6), which is likely a result of opportunistic predation as well as habitat-mediated variations in encounter and capture rates. If only one of these components was examined, we would not have fully captured wolf predation pressure on beavers. Thus, studies examining nonconsumptive effects and predation risk of ambush predators on their prey should strive to decouple where and when ambush predators spend time waiting-in-ambush from where they spend time overall. However, identifying ambush attempts is extremely challenging for many predator–prey systems, so studies that account for both ambush predator space-use and kill-site characteristics (e.g., Smith et al. 2020) will be most useful for understanding how ambush predators influence prey behavior.

CONCLUSION

We have demonstrated how an ambush predator can choose ambush locations and adapt hunting behaviors in response to the antipredator defenses and sensory deficiencies of their prey. Understanding, with certainty, where predators expect their prey to be is impossible. However, evaluating how wolves hunt beavers presents a unique opportunity to study ambush predator–prey interactions because beavers use the same, conspicuous habitat features repeatedly and their activity is predictable. Therefore, we could reasonably infer where wolves *expected* beavers to be when waiting-in-ambush (Supplementary Appendices 2–4), allowing us to simultaneously infer the behavior of both predator and prey, as well as the influence of abiotic factors—providing rare insight into how a terrestrial carnivore chooses ambush locations at the microhabitat scale.

Ambush strategies and site selection are likely under intensive selective pressure in order to maximize hunting success (Shine and Xi-Lin 2002), so it is not surprising that ambush strategies have been evolutionarily honed to counter and capitalize on the sensory abilities of their prey (González-Bernal et al. 2011; Clark et al. 2016). However, in many regards, ambush behavior remains understudied—especially for large carnivores—largely due to the challenges of studying the complexities of ambush behavior. As a result, there is little empirical evidence to demonstrate how the hunting strategies of ambush predators are specifically tailored to capture particular prey. In this regard, we echo Rossoni and Niven (2020) when they state “sit-and-wait predators have been largely overlooked, their strategies often characterized as stereotyped.”

Therefore, we urge researchers to consider how predators select ambush locations not only based on habitat type, habitat features (e.g., physical cover), and environmental conditions (e.g., light, temperature, and wind) but also based on their prey’s sensory abilities. Such an approach will allow ambush site selection to be understood in its proper context (e.g., an ambush predator hunting a specific prey) and will ultimately provide a more robust understanding of how ambush predators maximize the probability of detecting prey while minimizing the probability of being detected by prey.

Ambush predators across various taxa have likely evolved analogous ambush strategies to counter the defenses and exploit the deficiencies of their prey (Du et al. 2009; González-Bernal et al. 2011). For example, *Phaeacius* spp., sit-and-wait jumping spiders, recognize different prey species and change their ambushing strategy based on the visual abilities of each prey (Li et al. 2003). Whether ambush behavior and strategy are innate, learned from conspecifics, or learned through prior interactions with prey—or a combination of these—is unknown, but understanding this is valuable for determining how hunting strategies persist in predator populations. To this end, we think our general approach can be useful for elucidating where and how other large carnivores ambush prey, which is valuable for understanding their functional role(s) in ecosystems (Schmitz 2008; Romero and Koricheva 2011; Miller et al. 2014).

SUPPLEMENTARY MATERIAL

Appendix 1. Description of beaver habitat feature classes used for analysis.

Appendix 2–4. Examples of videos taken in the field showing how beaver-hunting attempts were identified and documented in the field.

Supplementary data are available at *Behavioral Ecology* online.

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Data availability: Analyses reported in this article can be reproduced using the data provided by Gable, Homkes, et al. (2020). We intend to archive all data and code used for analysis via Dryad Repository upon acceptance.

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