

Influence of Wind and Humidity on Foraging Behavior of Olfactory Mesopredators

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Many mammalian predators rely on scents to locate prey and weather conditions that affect an odor plume (i.e., scents suspended in air) or depositional odor (i.e., scents laid on the ground) should affect predator foraging behavior. We predicted that wind speed, wind direction, and humidity would influence the foraging behavior of olfactory mesopredators. We tested these predictions by conducting spotlight surveys for foraging Red Foxes (*Vulpes vulpes*), Striped Skunks (*Mephitis mephitis*), and Raccoons (*Procyon lotor*) along the dike surrounding Willard Bay Reservoir in Willard, Utah, from August 2008 to August 2009. We recorded predator species, locations, numbers, and weather conditions at the time each predator was observed. While humidity had no effect on foraging, wind speed and direction were significant predictors of a predator's nightly foraging activity, with most predators observed when wind speeds were 2 to 4 m/s and winds were blowing perpendicularly over the dike rather than parallel to the dike. Wind speed and direction also influenced where predators foraged on the dike, with predators being more likely to forage on the windward side of the dike when wind speeds were high enough to cause turbulence. We detected differences among predator species in their response to wind speed: Raccoons were more active than Striped Skunks and Red Foxes when the wind was calm and blowing parallel to the dike. Overall, our results indicate that these predator species alter their foraging behavior based on wind speed and wind direction. By foraging when winds were light and blowing perpendicularly over the dike, predators could likely enhance their ability to locate food using olfaction.

Key Words: Striped Skunk, *Mephitis mephitis*, Raccoon, *Procyon lotor*, Red Fox, *Vulpes vulpes*, mesopredator, olfaction, olfactory predator, Utah.

Foraging behavior of predators is a function of the predators themselves, their prey, and environmental conditions at the time of foraging (Schmidt 1999). Olfactory predators such as Raccoons (*Procyon lotor*), Red Foxes (*Vulpes vulpes*), and Striped Skunks (*Mephitis mephitis*) may employ all five senses to detect and locate prey, but they rely primarily on their acute sense of smell when conditions are favorable for its use (Conover 2007). For example, Raccoons are known to grope and probe with their forefeet to locate food underwater, but they generally detect prey using olfactory cues (Bowman and Harris 1980; McClearn 1992).

Although many studies have examined the effects of vegetation and prey distribution on predator behavior (Bowman and Harris 1980; Schmidt 1999), few studies have examined the effects of weather. We are aware of two studies that investigated the effects of weather on olfactory predator foraging. Jolly and Jolly (1992) found that wind direction affected the search time it took for captive Dingoes (*Canis lupus dingo*) to locate meat baits. Shivik (2002) found that search time of domestic dogs (*Canis lupus familiaris*) increased as circular standard deviation of wind direction increased.

Weather conditions that have an impact on odor plumes (i.e., scents suspended in the air) and depositional odors (i.e., scents laid on the ground or vegetation)

should affect predator foraging behavior. These weather conditions include temperature, cloud cover, humidity, wind speed, and wind turbulence. High temperatures and direct sunlight destroy odorants and decrease the scent available for a predator to detect, while low temperatures and humidity counteract these effects and keep odors viable (Gutzwiller 1990). Heavy rain or snow washes away or obscures depositional odor trails (Whelan et al. 1994). High wind velocities, turbulence, and shifting wind direction can dilute an odor plume beyond a predator's ability to detect it (Shivik 2002; Conover 2007; Borgo 2008). Moderate wind velocities, laminar flow, and constant wind direction result in a long, linear plume that can extend some distance downwind of the odor source. Predators are more likely to come into contact with an odor plume of this shape than a plume that is spherical and limited to the immediate vicinity of the odor source by lack of wind (Conover 2007; Borgo 2008). High wind speeds create turbulence and cause odor plumes to disintegrate. Hence, moderate wind speeds should create optimal conditions for predators to use olfaction to locate prey. Habitat features also influence odor plumes. Optimal habitat for the use of olfaction is where the upper surface of the ground or vegetation is smooth; surface features that protrude into the air, such as shelterbelts and

dikes, create areas of turbulence on their leeward side (Conover 2007).

We hypothesized a priori that more predators would be foraging when 1) it was humid, 2) wind speeds were between 1 and 3 m/s, and 3) the wind was blowing at right angles to the dike (across the dike) because such conditions are conducive to the use of olfaction to locate food (Conover 2007). The objective of this study was to test these predictions by observing olfactory mesopredators in their nightly foraging on Willard Bay Reservoir Dike in Willard, Utah. We also predicted that these predators would avoid foraging on the leeward side of the dike when wind velocities were high because this area would experience enough air turbulence to break up odor plumes.

Methods

Study area

This study took place at Willard Bay State Park and Reservoir (41°37N, 112°08W) in northern Utah, USA. The state park is located approximately 5 km south of the Bear River Migratory Bird Refuge at an elevation of 1287 m and is bordered on the east by Interstate 15 and on the west by the Great Salt Lake. The Arthur V. Watkins Dike runs approximately 11 km and separates the freshwater of Willard Bay from the Great Salt Lake (Figure 1). The reservoir side of the dike extends laterally 20 m and is lined with riprap consisting of boulders 0.5 to 3.0 m in diameter. The dry side of the dike, opposite Willard Bay Reservoir, also extends laterally approximately 20 m; it is earthen and covered with vegetation. The dike is approximately 15 m high, 11 m wide at the top, and 40 to 50 m wide at the base. The road on top of the dike is approximately 10 m wide and runs the length of the dike. The swath of land between the dike and the Great Salt Lake varies from 70 to 135 m in width, depending on the level of the Great Salt Lake. A row of tamarisk (*Tamarix* spp.) is present at approximately 70 m from the dry side of the dike and runs intermittently along most of the dike.

The vegetation on the top of the dike and on the slope of the dry side of the dike was dominated by Cheatgrass (*Bromus tectorum*), Crested Wheatgrass (*Agropyron cristatum*), and various bluegrass species (*Poa* spp.). The most common forbs on the dike were Dyer's Woad (*Isatis tinctoria*), Flixweed (*Descurainia sophia*), Red-stem Filaree (*Erodium cicutarium*), and Field Bindweed (*Convolvulus arvensis*). At the base of the slope, there is a 5-m-wide section of riprap constructed of boulders 0.5 to 1 m in diameter. Beyond the riprap, there was a 5-m-wide area of patchy grasses and forbs intermixed with stands of Common Reed (*Phragmites australis*) that extended the entire length of the dike. Off the dike on the dry side, there is a dirt road approximately 30 to 40 m in width that people use to access the dike for fishing. The most common forbs and grasses off dike were Cheatgrass, Inland Saltgrass (*Distichlis spicata*), Rabbitfoot Grass (*Polypogon mon-*

speliensis), Poison Hemlock (*Conium maculatum*), Dyer's Woad, Virginia Glasswort (*Salicornia virginica*), Matted Sandmat (*Chamaesyce serpens*), and knotweed (*Polygonum* spp.).

Field methods

We used a 1 000 000 candlepower spotlight from a truck driven at 15 km/h on top of the dike to observe predators located on top or on either side of the dike. The observer in the back of the truck scanned both sides of the dike, while the driver watched for predators on the road. Both observers scanned ahead in an effort to detect animals before they moved. Any animal that was obviously fleeing before it was sighted was excluded from the analysis. If a group of predators was observed, such as a family group of Raccoons, we counted this as one observation. Red Foxes, Striped Skunks, and Raccoons are secretive and nocturnal, and they make use of shelters or dens when not active. Therefore, we assumed predators were foraging when observed, unless it was obvious they were not (e.g., a litter of young Red Foxes in front of a den or a Raccoon in a tree cavity).

Our starting location on the dike, going either north or south, was randomly determined for each observation period (i.e., each night of spotlighting). Our observations began at 0.5 to 1 hour after sunset and continued until the entire dike had been surveyed (usually 2 to 3 hours). We made observations between 20 August 2008 and 18 August 2009. No observations were made between mid-February and the end of March 2009, when winter weather made the dike impassable. Observations were made weekly from 20 August 2008 to mid-February 2009, weekly between the end of March and the beginning of May 2009, and twice weekly from the beginning of May to 18 August 2009.

To investigate the influence of wind speed and direction on where predators were foraging, we divided the dike into three sections, based on its orientation (Figure 1). Section 1 is oriented northeast/southwest, section 2 is oriented north/south, and 3 is oriented east/west. We classified the dike's cross-sectional terrain into one of four categories: reservoir side, top of the dike, slope of the dike on the dry side, or off of the dike on the dry side (Figure 1). When a predator was spotted, the truck was stopped at right angles to where the predator was first seen. We recorded the predator species, the section of the dike, the type of terrain in which the predator was located, and the distance in meters between the road and the predator's location using a Nikon Prostaff 550 range finder (Nikon Incorporated, Melville, New York). We then measured the direction of the wind using a compass and the wind speed (m/s) using a Kestrel 2000 weather meter (Nielsen-Kellerman, Boothwyn, Pennsylvania). We took four measurements of the wind speed at 15-second intervals at a height of 2 m above the ground at the top of the dike. We recorded the high, low, and mean wind speeds during this 1-minute period.

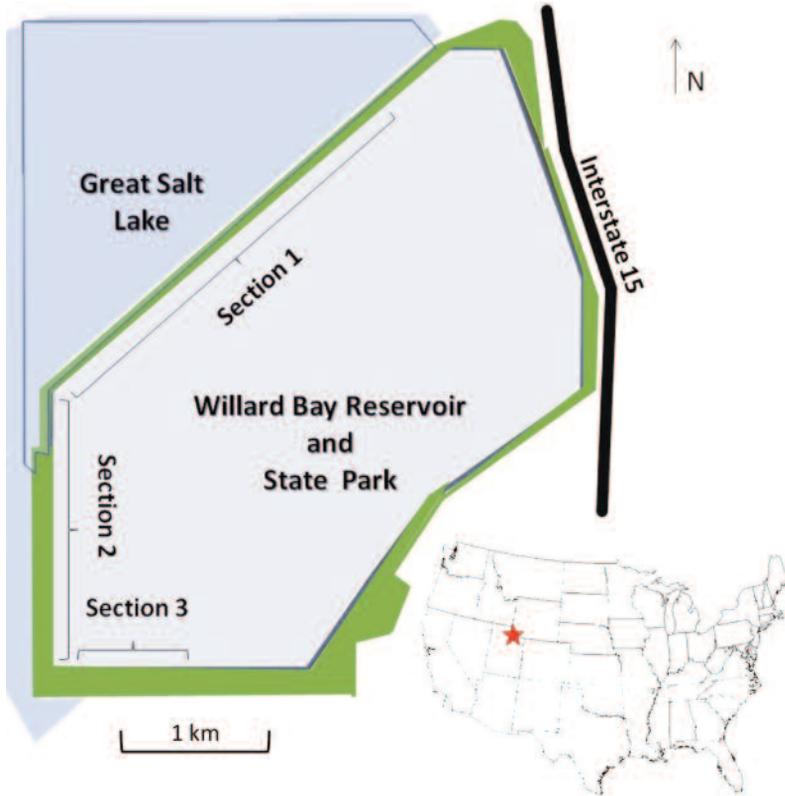


FIGURE 1. Overview of Willard Bay State Park and Reservoir, Utah, USA, showing sections of the Arthur V. Watkins Dike, where we conducted predator spotlighting surveys.

We selected 5 to 10 random locations along the dike using a random number chart to determine distances from the start. We measured wind speed and wind direction at these locations to capture their variation throughout the spotlighting run. We recorded relative humidity using a Kestrel 2000 weather meter. Precipitation was not a factor in our analysis because surveys were conducted only when it was not raining or snowing (due to poor visibility created by those conditions).

Data analysis

We used four different regression analyses to determine the effect of wind speed, the orientation of the wind relative to the dike, and humidity on the number, location, and species of predators we observed. We conducted a multiple linear regression in SAS (PROC REG, Version 9.2, SAS Institute, Cary, North Carolina) to model the number of predators observed as a function of wind speed, wind orientation, and humidity. We determined mean wind speed of each night spotlighting by averaging all wind measurements taken from the dike that night, including both predator observations and random points. Mean wind orientation for each night was calculated using the CIRCSTATS pack-

age in Program R (Version 2.9.2, R Foundation for Statistical Computing, Vienna, Austria). To include wind orientation as a continuous circular variable in the linear regression, we first converted it to radians and then calculated cosine and sine of the variable (Zar 1984). It was necessary to include both sine and cosine of wind orientation to describe accurately wind direction in the model. Therefore, we retained both variables if one was significant for all models that contained wind orientation.

Each spotlighting event was considered an independent sample, although the observations were collected in a sequential manner. To account for autocorrelation of the response, we introduced a time variable, where one unit of time was one night of spotlighting. Quadratic terms of both wind speed and time were introduced to account for systematic variation in the residuals. Wind and time variables were also centered so that the scale among the variables would be similar for easier interpretation of diagnostics. For this and all other tests, we considered results to be significant when $P < 0.05$.

Two multinomial logistic regressions were used to model the dike section and terrain category where a

predator was observed as a function of wind speed, the orientation of the wind relative to the dike, humidity, species, and time (PROC LOGISTIC, SAS). The objective of this analysis was to determine whether predators changed their foraging location in response to weather conditions. Our operating hypothesis was that turbulence caused by air flowing at an angle to the dike would make foraging conditions poor in one area of the dike and predators would therefore choose to forage in another section or in another terrain category. In both regressions, we also included the interaction between wind speed and orientation. We did this to account for the fact that, at low wind speeds, the direction the wind is blowing relative to the dike is not likely to have an impact on predator foraging behavior because there will be very little turbulence. Thus, at low wind speeds, foraging conditions would be similar on all sections regardless of the direction the wind was blowing.

Predator species was included in these models to account for differences in habitat use among the species. For example, Raccoons often forage near water and would therefore be more likely to be observed on the reservoir side of the dike, regardless of the weather conditions. As species was a categorical variable, we used odds ratios calculated in SAS using PROC LOGISTIC to detail the relationship between predictor and response. We assumed that when the odds ratio confidence interval included 1.0, events were equally likely to occur. A multinomial logistic regression requires that one level of the response be designated the reference level to which the other levels of the response will be compared. Therefore, we arbitrarily chose section 1 and off the dike on the dry side to be the reference level.

For all regression analyses, we used a step-wise backward selection to identify the final model. We first ran the global model and then eliminated variables one at a time, based on their individual significance. In each case, terms with the highest P values were eliminated first, and the model was re-run following each elimination.

Results

We observed a total of 180 predators during 40 nights of spotlighting from 20 August 2008 to 18 August 2009: 87 Raccoons, 50 Red Foxes, and 43 Striped Skunks. During the sampling period, 61 nights of spotlighting were possible, however we only sampled on 40 occasions due to interference from weather. The number of predators to be observed decreased over the winter and then increased in late July and August of 2009 (Figure 2). After accounting for these seasonal changes in predator numbers, we found that most predators were observed at intermediate wind speeds (between 2 and 4 m/s) and when winds were blowing from the northwest. Overall, the model, including the time vari-

ables, was highly significant ($F_{6,32} = 20.89, P < 0.001$) with an adjusted $r^2 = 0.76$. Individually, the time variables were also highly significant (time: $t_1 = -5.41, P < 0.001$; time squared: $t_1 = 5.29, P < 0.001$). The wind factors (wind speed squared, wind speed, and sine of wind orientation) were all significant predictors of the number of predator observations per night (wind speed squared: $t_1 = -2.91, P = 0.006$; wind speed: $t_1 = 2.49, P = 0.018$; sine of wind orientation: $t_1 = 2.52, P = 0.017$). Cosine of wind orientation was non-significant (cosine of wind orientation: $t_1 = -0.27, P = 0.79$); however, we retained this variable in the model to preserve interpretation of wind orientation.

We observed an interactive effect of wind speed and orientation on predator location (Figure 3). This interactive effect was manifested in the significance of the three-way interaction among sine of wind orientation, cosine of wind orientation, and wind speed ($\chi^2_2 = 8.8, P = 0.01$) in the logistic regression describing dike section. The max-rescaled r^2 for this model was 0.22, and the percentage correctly classified was 72%. Humidity, time, and species were all non-significant predictors of the section of dike where a predator was observed (humidity: $\chi^2_2 = 2.06, P = 0.35$; time: $\chi^2_2 = 0.90, P = 0.64$; species: $\chi^2_4 = 3.50, P = 0.48$).

Species of predators differed in their use of terrain types. Raccoons were 28 times more likely to be observed on the bay side than on the reference level (off-dike dry side) than Striped Skunks (95% CI = 3.5 – 231). Raccoons were 50 times more likely to be observed on the bay side than on the reference level (off-dike dry side) than Red Foxes (95% CI = 6 – 333). Raccoons were also 4.5 times more likely than Red Foxes to be observed on the dike than on the off-dike dry side (95% CI = 1.4 – 15).

Odds ratios for Red Foxes versus Striped Skunks indicated that they were equally likely to be seen on the bay side (0.58 [95% CI = 0.03 – 9.9]), on the dike (0.48 [95% CI = 0.1 – 1.8]), or on the slope of the dike on the dry side (0.58 [95% CI = 0.2 – 2.3]) when compared to the off-dike dry side. Raccoons were also equally likely as Striped Skunks to be seen on the dike (2.2 [95% CI = 0.7 – 7.0]) and the slope of the dike on the dry side (0.95 [95% CI = 0.2 – 3.8]), as well as Red Foxes on the slope of the dike on the dry side (1.6 [95% CI = 0.4 – 6.3]). Overall, in the terrain regression, species was the only significant predictor of terrain type where a predator was observed ($\chi^2_6 = 26.1, P < 0.001$). All other variables were non-significant: wind speed ($\chi^2_3 = 2.37, P = 0.49$), wind orientation (sine: $\chi^2_3 = 4.03, P = 0.26$; cosine: $\chi^2_3 = 7.76, P = 0.051$), temperature ($\chi^2_3 = 1.99, P = 0.57$), humidity ($\chi^2_3 = 0.95, P = 0.81$), and time ($\chi^2_3 = 5.2, P = 0.16$). The three-way interaction among wind speed, cosine wind orientation, and sine wind orientation was also non-significant in the terrain model ($\chi^2_2 = 1.76, P = 0.62$).

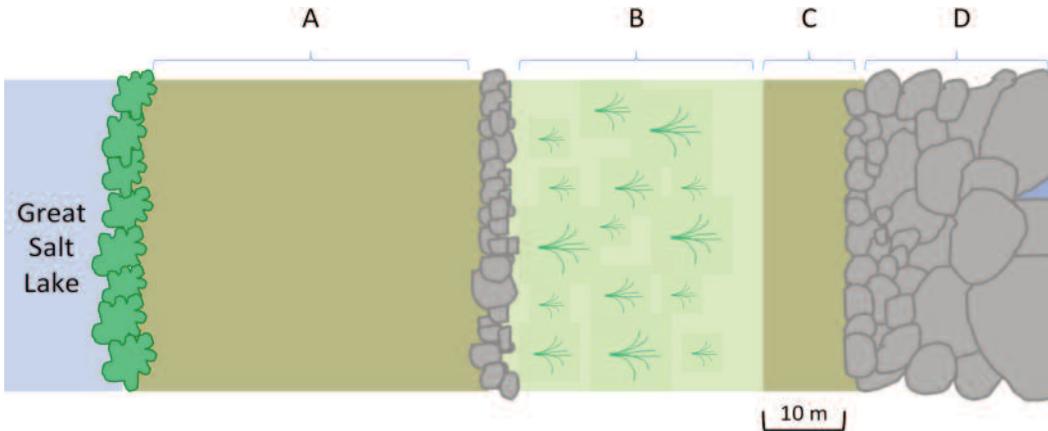


FIGURE 2. Cutout of Arthur V. Watkins Dike at Willard Bay State Park and Reservoir, Utah, USA, showing terrain types: A) off-dike on the dry side, B) slope of the dike on the dry side, C) top of the dike, and D) reservoir side.

Discussion

We did not conduct surveys when it was snowing, raining, or there was fog because poor visibility would have influenced our ability to locate predators. We do not believe that our ability to locate predators varied with wind speed, the orientation of the wind relative to the dike, or humidity. It is possible that at low wind speeds predators would have been able to hear our vehicle approaching from a greater distance and flee the area before we were able to observe them. However, this area is regularly driven by people fishing and other people using the dike. It is likely that predators are conditioned to the noise of vehicles and would have no reason to flee, because this area is not hunted.

We were unable to estimate how our ability to detect predators varied across species. We believe that our detection probability was the highest for Red Foxes. Red Foxes are larger than Striped Skunks and Raccoons and are easily visible in all terrains. Their behavior also increased their visibility, as they would often freeze and look at the spotlight before running. Raccoons tended to freeze and look at the spotlight as well, and their medium size made them easy to detect. On the reservoir side of the dike, the large rocks and crevices make it possible for Raccoons to hide, and it is likely that there were more Raccoons present there than we observed. Given this, Raccoon use of the reservoir side of the dike may have been even greater than what we recorded. Striped Skunks did not tend to look at the spotlight, and they were probably underrepresented in the survey. However, these discrepancies in predator counts had minimal effect on our results. We were not interested in estimating the predator population, only in comparing changes in predator behavior with varying wind conditions.

One limitation of our study is that it was an observational study, and many factors besides weather may have influenced the predators we observed. We also

assumed that most predators were foraging when we observed them at night but some undoubtedly were searching for mates or patrolling their territories. In spite of all this extraneous “noise” surrounding our findings, the results still demonstrate that wind speed and the orientation of the wind relative to the dike affected how many, where, and which predators were observed. Together with time variables, these weather factors explained >75% of the variation in the number of predators observed per night.

Effect of wind speed and the orientation of the wind relative to the dike on predator numbers

We observed the most predators when wind speeds were moderate (2 to 4 m/s); we saw few predators at low or high wind speeds. These results support our a priori prediction that optimal foraging conditions for olfactory predators should occur at wind speeds between 1 and 3 m/s. When there is little or no wind, odor plumes are small and localized, and this decreases the probability that predators will be able to detect a prey's odor unless they are very close to it. Predators also have difficulty using olfaction to locate prey when the wind speed becomes fast enough to create turbulence, because turbulence causes odor plumes to disintegrate (Conover 2007). An alternate hypothesis is that olfactory predators avoid foraging when the conditions are windy because the wind increases ambient noise levels, making it more difficult to hear their prey or an approaching predator. However, this hypothesis also predicts that the number of foraging predators should peak when there is no wind, but we found that predator numbers peaked at moderate wind speeds.

For wind orientation, most predators were observed when winds came from the northwest and flowed at right angles to section 1 of the dike, so that the dry side of the dike was on the windward side. This would give predators a large area to forage in (i.e., the dry side of sections 1 and 2), where their efforts would not be

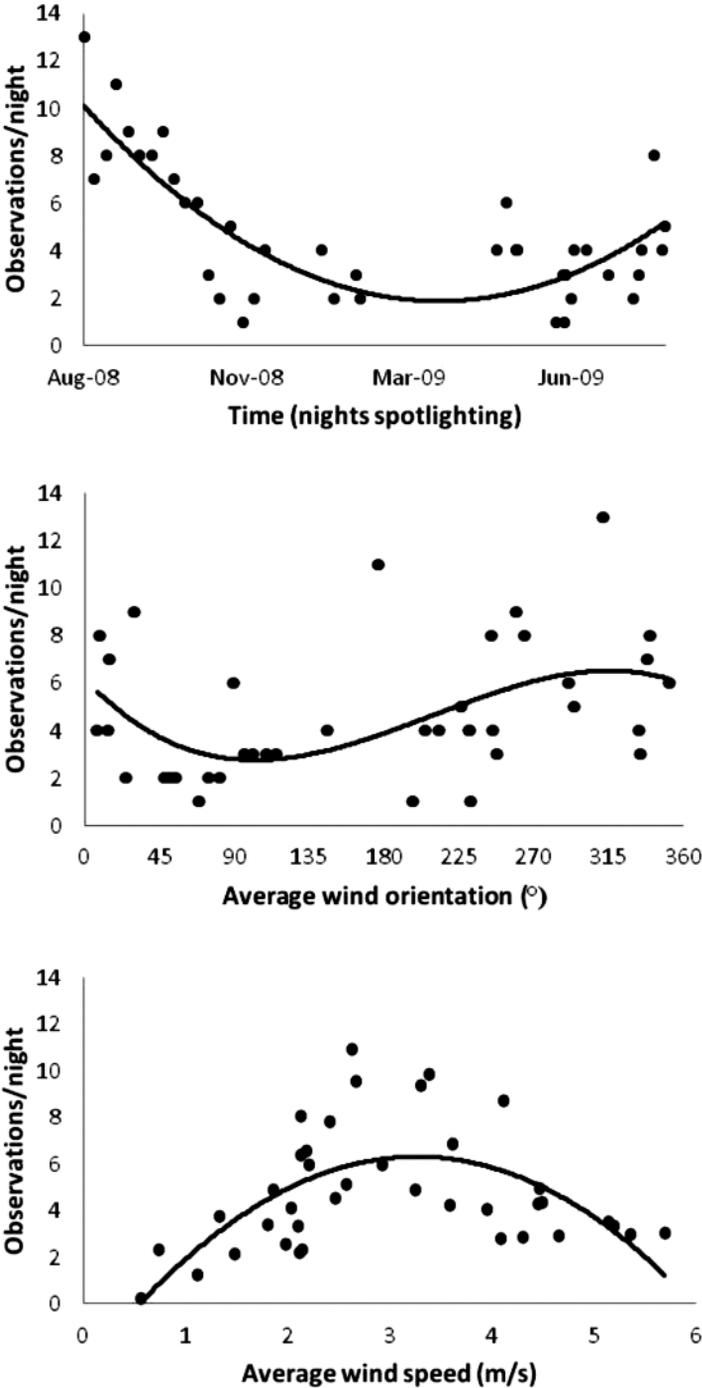


FIGURE 3. Number of olfactory predators observed (•) during nocturnal spotlighting over time (where one unit of time represents one night of spotlighting), average orientation of the wind relative to the dike per night, with 0° and 360° being North, and average wind speed per night (m/s). Predicted values (—) were obtained from a multiple linear regression of the number of predators observed per night on time, orientation of the wind relative to the dike, and wind speed. Data were collected during spotlighting surveys from August 2008 through August 2009 at Willard Bay State Park and Reservoir, Utah.

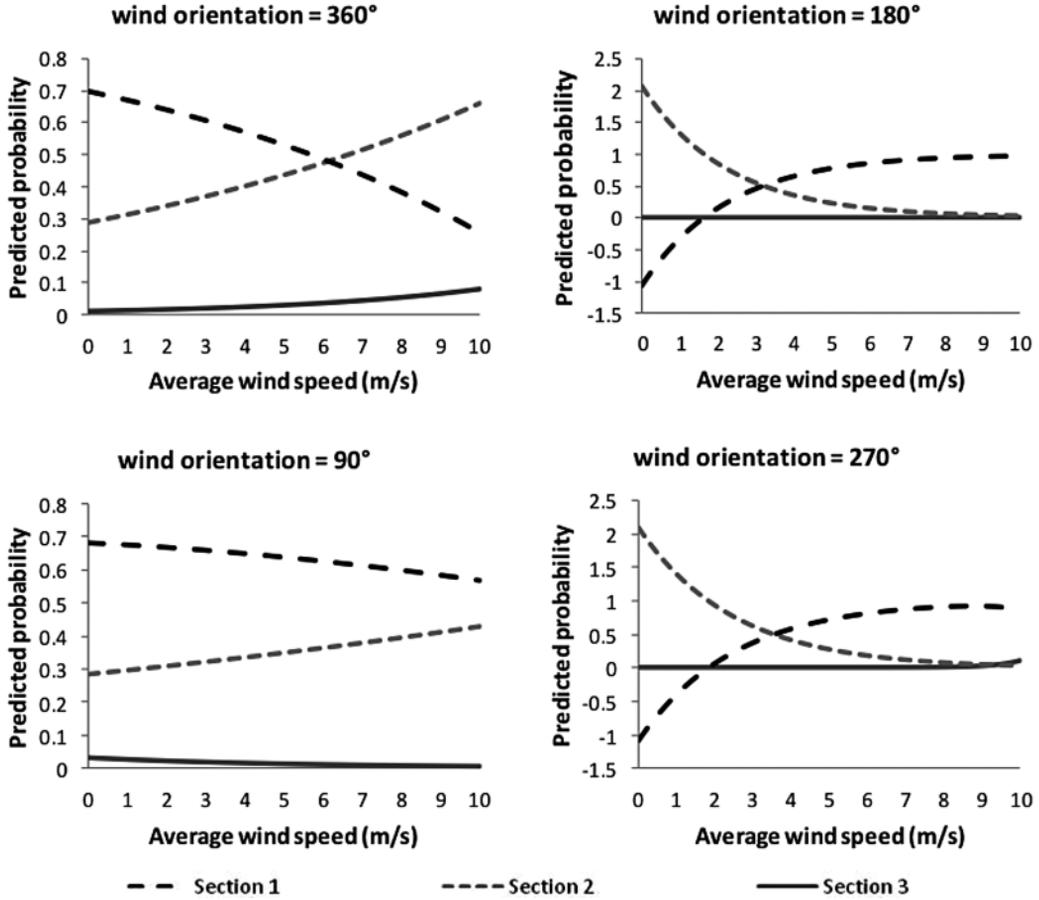


FIGURE 4. Predicted probabilities of observing a predator calculated from a multinomial logistic regression where the section of dike (1, 2, or 3) a predator was observed on was modeled as a function of the orientation of the wind relative to the dike and the wind speed. Predicted probabilities are shown across all wind speeds for four values of wind direction: North (0°), East (90°), South (180°), and West (270°). Data were collected during spotlighting surveys from August 2008 through August 2009 at Willard Bay State Park and Reservoir, Utah.

impeded by turbulence caused by the dike because these areas were on the windward side of the dike.

Seasonal variation in predator numbers

From August 2008 to June 2009, the number of predators we saw decreased, with a small increase in July and August 2009. Several factors could be responsible for this pattern, including seasonal variation in predator activity. Striped Skunks and Raccoons often become inactive for days or weeks during the winter (Dustin et al. 1997; Huxoll et al. 1998). Seasonal changes in predator populations may also have contributed to this pattern. Utah's cold temperatures and deep snow during winter kill many predators. There also was an outbreak of sarcoptic mange in the Salt Lake Valley during the course of the study (Ron Merrill, United States Department of Agriculture/Animal

and Plant Health Inspection Service (APHIS)/Wildlife Services, personal communication), and this could have contributed to increased predator mortality (Lindström et al. 1994). The increase in the number of predators in July and August likely reflects juvenile predators beginning to forage.

Effect of wind speed and the orientation of the wind relative to the dike on predator locations

Wind speed and the orientation of the wind relative to the dike had an interactive effect on the locations where we observed predators. We hypothesized that the mechanism driving predator location in response to wind speed and orientation would be the orientation of the wind relative to the dike and wind turbulence patterns that result from the dike-to-wind angle. This turbulence does not occur below a certain wind speed

(Conover 2007). Therefore, it is likely that, at low wind speeds, orientation of either the dike or wind matters less than at high wind speeds. Section 1 was the most probable location to observe a predator at low wind speeds when the wind was blowing from the north or east. However, our model broke down at low wind speeds for south and west winds, predicting probabilities less than one and greater than zero for sections 2 and 3. We did not find this surprising, given the small sample size for these wind directions. We conclude from our data that there is an interaction between wind speed and wind orientation (given the significance of the term) that affects the section of dike where predators forage, but it is impossible to determine the intricacies of the effect with our data set.

Raccoons were the most commonly observed predator on the dike. Several attributes of Raccoon behavior and of Willard Bay likely combined to draw Raccoons to the area. Raccoons often forage along the edge of water bodies because they are adept at using their front paws to grasp items in shallow water such as mollusks, crayfish, and other invertebrates and will even catch fish (McClearn 1992). Raccoons generally choose these aquatic animals if they are available, and Raccoons spend a disproportionate amount of time in wetland habitat compared to upland habitat (Fritzell 1978). Likewise, we found that Raccoons were 28 times more likely than Striped Skunks and 50 times more likely than Red Foxes to be observed on the reservoir side of the dike.

We detected no differences between Red Foxes and Striped Skunks in their use of the terrain. Both species were more likely to be seen on the dry side of the dike than were Raccoons. Striped Skunks and Red Foxes commonly employ a wide-area search strategy for food (Crabtree et al. 1989; Jędrzejewski and Jędrzejewski 1992), and the dry side of the dike was more suited to their hunting methods. Neither species is known to prefer aquatic prey. Red Foxes and Striped Skunks typically avoid entering water (Sargeant et al. 1984; Lokemoen and Woodward 1993), and Red Foxes prefer open habitats for foraging (Jędrzejewski and Jędrzejewski 1992).

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