

## Vigilance of kit foxes at water sources: A test of competing hypotheses for a solitary carnivore subject to predation

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### ABSTRACT

Animals that are potential prey do not respond equally to direct and indirect cues related to risk of predation. Based on differential responses to cues, three hypotheses have been proposed to explain spatial variation in vigilance behavior. The predator-vigilance hypothesis proposes that prey increase vigilance where there is evidence of predators. The visibility-vigilance hypothesis suggests that prey increase vigilance where visibility is obstructed. Alternatively, the refuge-vigilance hypothesis proposes that prey may perceive areas with low visibility (greater cover) as refuges and decrease vigilance. We evaluated support for these hypotheses using the kit fox (*Vulpes macrotis*), a solitary carnivore subject to intraguild predation, as a model. From 2010 to 2012, we used infrared-triggered cameras to record video of kit fox behavior at water sources in Utah, USA. The refuge-vigilance hypothesis explained more variation in vigilance behavior of kit foxes than the other two hypotheses (AICc model weight = 0.37). Kit foxes were less vigilant at water sources with low overhead cover (refuge) obstructing visibility. Based on our results, the predator-vigilance and visibility-vigilance hypotheses may not be applicable to all species of prey. Solitary prey, unlike gregarious prey, may use areas with concealing cover to maximize resource acquisition and minimize vigilance.

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### 1. Introduction

Risk of predation often varies spatially across landscapes (Laundré et al., 2010). Areas with high risk of predation can elicit an increase in the use of antipredator behavior (e.g., vigilance) of prey compared to areas with low risk. The way in which prey associate risk with different areas can depend on how they perceive direct and indirect cues related to risk of predation. Perception of these cues by prey species, however, is likely related to the type of predator (e.g., aerial vs. terrestrial, ambush vs. pursuit) that preys upon them. Given variation in predators and their hunting strategies, prey species likely do not respond equally to direct and indirect cues related to risk of predation (Verdolin, 2006).

Based on differential responses to direct and indirect cues, three hypotheses have been proposed to account for spatial variation in the use of vigilance, a common antipredator behavior.

The predator-vigilance hypothesis proposes that in areas where predators are present or where there is evidence of predators (direct cue of risk of predation), prey increase vigilance behavior (Adams et al., 2006; Hauser and Caffrey, 1994; Jones, 1998; Laundré et al., 2001; Parsons and Blumstein, 2010; Rainey et al., 2004; Wolff and Van Horn, 2003; Zuberbuhler et al., 1997). The visibility-vigilance hypothesis proposes that in areas with reduced or obstructed visibility (indirect cue of risk of predation) where it is difficult to visually detect predators, prey increase vigilance behavior (Arenz and Leger, 1997; Barri et al., 2012; Bednekoff and Blumstein, 2009; Goldsmith, 1990; Hernández et al., 2005; Martella et al., 1995; Metcalfe, 1984; Underwood, 1982; Whittingham et al., 2004). Alternatively, the refuge-vigilance hypothesis proposes that prey may perceive areas with low visibility (greater cover) as refuges (Kotler et al., 2002; Lima, 1990; Lima et al., 1987) and therefore may reduce vigilance. Vigilance behavior of prey may also be influenced by a combination of predator presence and visibility (Embar et al., 2011). These hypotheses concerning vigilance have been studied with many species of prey (e.g., birds, rodents, ungulates) in a variety of habitats. Nonetheless, we lack a general understanding of how presence of predators (direct cue) and visibility (indirect cue) influence vigilance of species occupying higher

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trophic levels that are also susceptible to predation (e.g., small carnivores).

Small carnivores are not generally considered prey, but they are often preyed on by larger carnivores. Moreover, within carnivore guilds there can be sufficient overlap in use of resources (e.g., habitat, food) to create intraguild conflict (Caro and Stoner, 2003). Intraguild conflict often results in larger dominant carnivores killing smaller subordinate carnivores (Palomares and Caro, 1999). To alleviate intraguild conflict and predation, subordinate carnivores have developed antipredator behaviors similar to those typical of prey species (e.g., herbivores; Frank and Woodroffe, 2001). For example, subordinate carnivores can make large-scale behavioral adjustments in how they partition resources to reduce potential encounters with larger, dominant carnivores over space and time (Brawata and Neeman, 2011; Creel and Creel, 1996; Kitchen et al., 1999). At a finer scale, subordinate carnivores likely use vigilance to minimize risk of intraguild predation (Jones, 1998; Switalski, 2003).

The use of vigilance, however, may result in a behavioral tradeoff between resource acquisition (e.g., foraging) and safety (Elgar, 1989; Quenette, 1990). To minimize costs associated with this tradeoff, some herbivorous and granivorous species “multitask” by handling food items while maintaining vigilance (Baker et al., 2011; Fortin et al., 2004). The ability to “multitask”, nevertheless, is influenced by qualities associated with different resources. With drinking water, for example, animals cannot “handle” water simultaneously while scanning their surroundings for predators as they can with some food items (e.g., chewing plants or manipulating seeds). Thus, drinking water likely creates a behavioral tradeoff. This tradeoff can be mitigated to some degree by gregarious species (Elgar, 1989). As group size increases, additional group members can help partition time for vigilance, thereby decreasing vigilance per individual (Quenette, 1990). Solitary species (e.g., small carnivores) may be at a disadvantage compared to gregarious species as they have no group dynamic to increase awareness of predators. This disadvantage may asymmetrically affect solitary species relative to gregarious species, particularly at areas of increased risk of predation such as water sources.

Water sources are unique landscape features that may be associated with increased risks of predation (Valeix et al., 2009). Unlike other resources (e.g., forage patch) where prey can spatially shift activities to avoid risk of predation, water sources are often discrete features on the landscape (Burger, 1992). Moreover, in arid and semiarid environments, drinking water is often a limiting factor for both prey and predator. Predators not only use water sources for drinking, but they also concentrate hunting and movement patterns near available water (Brawata and Neeman, 2011; Valeix et al., 2010). Thus, water sources can become flash points for predator-prey interactions. In addition, water sources often support dense vegetation and/or occur in areas where topographical features obstruct visibility of prey (Burger, 2001; de Boer et al., 2010). For some prey, reduced visibility can prevent them from detecting predators using cover around water sources for ambush or stalking. Despite the potential risk of predation associated with water sources, vigilance behavior of solitary carnivores at these unique landscape features is poorly understood.

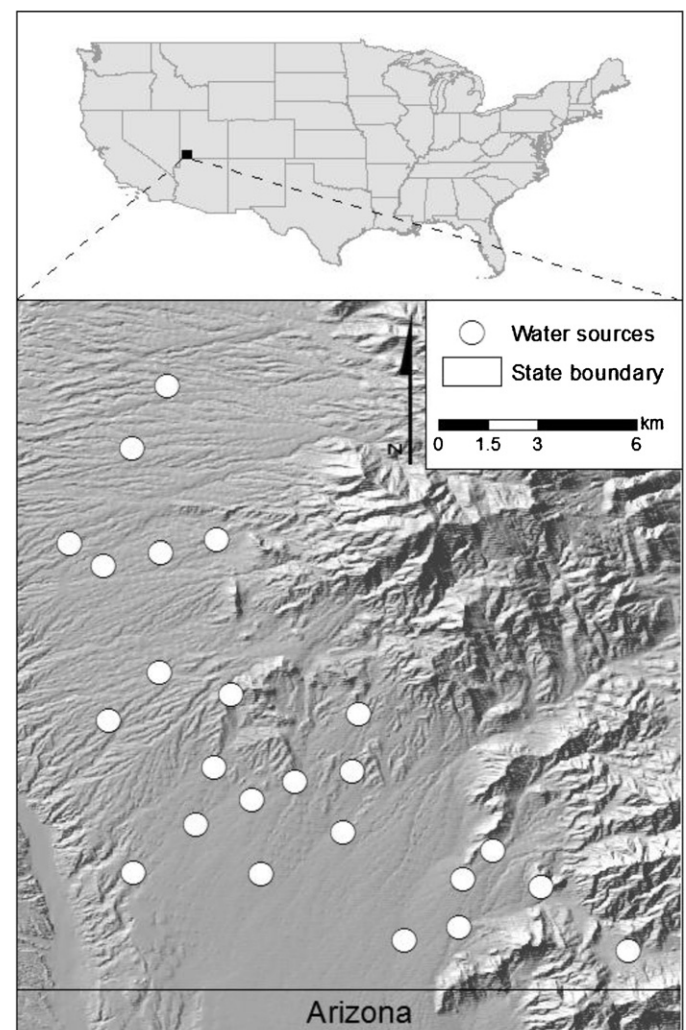
Our objective was to evaluate relative support for the predator-vigilance, visibility-vigilance, and refuge-vigilance hypotheses using a subordinate, solitary carnivore subject to intraguild predation as a model. Specifically, we wanted to determine which of the hypotheses best explained vigilance behavior at water sources. To evaluate support for these hypotheses, we monitored vigilance behavior of the kit fox (*Vulpes macrotis*), a small, solitary carnivore that is preyed upon by several intraguild carnivores (Cypher et al., 2000). If vigilance behavior of kit foxes is related to direct cues of predation risk (i.e. frequency of visitation by predators), we

expect vigilance to increase at water sources where predator visitation is greater (predator-vigilance hypothesis; Periquet et al., 2010). However, if vigilance behavior of kit foxes is driven by detectability of predators, we expect vigilance to increase at water sources with less visibility (visibility-vigilance hypothesis; Burger, 2001). Alternatively, if concealing cover provides refuge (refuge-vigilance hypothesis; Lima et al., 1987), we expect vigilance to decrease at water sources where visibility is obstructed.

## 2. Methods

### 2.1. Study site

We conducted this study in the Mojave Desert, Utah, USA (37°05'N, 113°56'W; Fig. 1). Our study area consisted of 398 km<sup>2</sup> of public land managed by the United States Department of Interior, Bureau of Land Management. This portion of the Mojave Desert was grazed seasonally by livestock from October to May during our study period. Our study area was characterized by rolling hills/ridges and dry desert washes radiating from the Beaver Dam Mountains to the northeast and draining into the Beaver Dam Wash to the southwest near the Utah, Nevada, and Arizona state borders (Fig. 1). Elevations across the study area ranged from approximately



**Fig. 1.** Study area in Mojave Desert, Utah, USA where we evaluated kit fox (*Vulpes macrotis*) vigilance from May 2010 to January 2012. White circles represent locations of water sources used by kit foxes during our sampling period.

900 to 1300 m. Annual climate consisted of mean air temperatures of 20.1 °C and mean precipitation of 12.7 cm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). Native vegetation in our study area was predominantly creosote (*Larrea divaricata*), Joshua-tree (*Yucca brevifolia*), and black-brush (*Coleogyne ramosissima*). A large portion of this study area has experienced several wildfires over the last decade. In burned areas, exotic grasses (e.g., *Bromus rubens*) were prevalent and interspersed among surviving communities of native vegetation.

## 2.2. Vigilance behavior monitoring

Based on preliminary monitoring, we identified 25 water sources used by kit foxes within our study area (Fig. 1). These water sources included 15 water developments for wildlife, seven drinking troughs for livestock, and three water storage tanks for livestock (Fig. 2). Due to logistical constraints, we did not sample all 25 water sources continuously. Instead, we randomly sampled water sources with replacement (each water source was eligible to be re-sampled). During May to Jan 2010–2012, we accrued 25 sample periods (approximately 21 days per sample) and each water source was sampled  $\geq$  two times. We randomized sampling effort by first creating a random point within our study area using ArcGIS® (ArcMap, version 10.0, Environmental Systems Research Institute, Redlands, CA). We then identified the nearest water source to the random point and sampled that site and surrounding water sources.

At each sampled water source, we set up an infrared-triggered camera (Cuddeback®). We used cameras to avoid the potential effects of direct observation by humans on the behavior of animals (Bridges and Noss, 2011) and assumed any bias associated with cameras was consistent across water sources. When cameras were triggered, they recorded one photo and then 20–30 s of video. Cameras had a minimum delay of one minute between sequences of photos and videos. We placed cameras approximately 2 m away from each water source so that the camera's field of view captured all activity along the edge of the water where animals drank. At larger water sources (i.e., water storage tanks for livestock), we

placed cameras near drinking ramps where kit foxes could access water.

Using The Observer® X10 behavioral analysis software, we analyzed videos of kit fox behavior. We generally defined vigilance behavior as the head above the shoulders (Quenette, 1990), but also considered distinct scanning motions or periods of direct staring while motionless as vigilance even if the head was below the shoulders. During video analysis it was difficult to discern if a kit fox was vigilant while walking or running, therefore we excluded these behaviors from statistical analysis. Since we could not differentiate between individuals across seasons, we summed the amount of time spent vigilant for each water source and calculated a single measure of the proportion of time spent vigilant and proportion of time spent drinking by kit foxes for each water source. Water sources were  $\geq$  1.2 km apart which coincided with the size of core home ranges for kit foxes (Zoellick et al., 2002). Thus, we considered each water source an independent sampling unit in reference to vigilance behavior of kit foxes.

It became apparent that kit foxes visited some water sources more than others, which in turn resulted in unequal numbers of videos and length of monitoring time across water sources. To determine the minimum number of videos that adequately represented vigilance behavior for each water source, we randomly selected 2, 5, 10, 20, and 30 videos from 10 water sources that had  $\geq$  30 videos and repeated this process 30 times. Using the proportion of time spent vigilant for each sample of videos, we calculated sample variances for each quantity of videos. We then conducted pairwise *F*-tests (with a Bonferroni correction) for equal variances across quantities of videos. We found no significant differences in variances between quantities of videos except the quantity with two videos. Therefore we used data from water sources with at least five videos.

## 2.3. Predator data

As an index of predator presence at water sources, we used photos from the cameras that also recorded video data. We

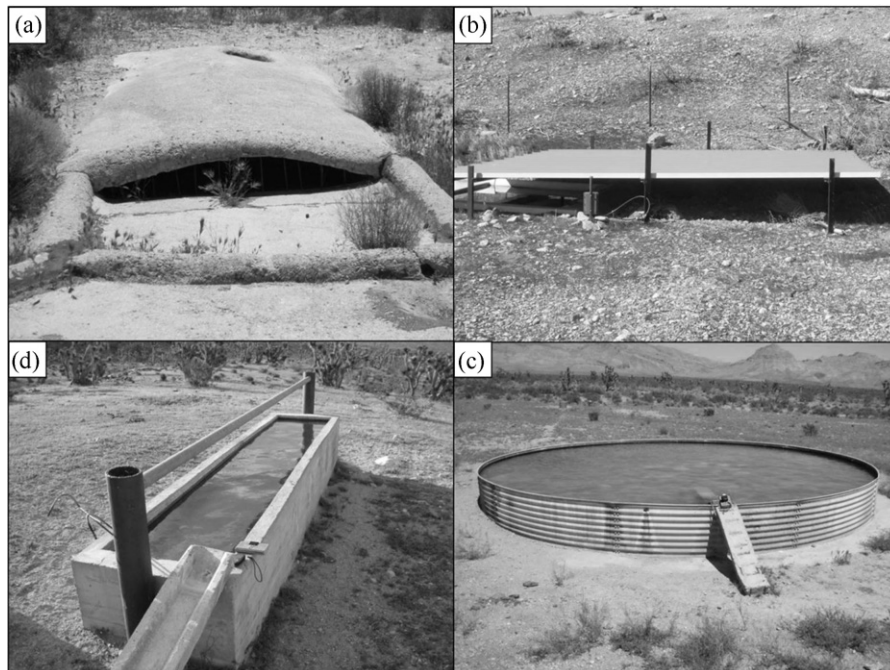


Fig. 2. Different types of water sources used by kit foxes (*Vulpes macrotis*) in Utah, USA between May 2010 and January 2012. (a) Concrete earthen tank, (b) fiberglass catchment with metal roof, (c) metal water tank for livestock, and (d) concrete drinking trough for livestock.

identified potential predators of kit foxes to species. We then calculated frequency of visitation for each species of predator at each water source by dividing the number of visits by the number of days that cameras were operable. We defined a visit as all photo occurrences of a single species within 0.5 h and considered these to be independent events (Michalski and Peres, 2007). Both mammalian and avian predators have been implicated in predation events on kit foxes (Cypher et al., 2000). Therefore, we calculated overall frequency of visitation for all mammalian and avian predators as well as all predators combined. Our estimate of frequency of visitation by avian predators was likely conservative since cameras may have underestimated the presence of avian predators that flew overhead, but did not actually visit the water source. We assumed this potential bias was similar across water sources.

#### 2.4. Visibility data

To determine relative visibility for each water source, we conducted geospatial analysis, measured height of vegetation, and assessed any other potential obstructions to visibility. Previous work indicates that the distance of “awareness” for kit foxes is approximately 150 m (Kozlowski et al., 2008). Thus, we focused our efforts within 150 m around each water source. We used ArcGIS to calculate topographical obscurity (view-shed) around water sources at 25 m intervals using a 10 m resolution digital elevation model. To measure height of vegetation, an observer positioned himself near the ground (to approximate the height of a kit fox) and recorded vegetation measurements from a Robel pole (Robel et al., 1970) that another observer placed at 25 m intervals radiating away from the water source in all four cardinal directions. Some water sources had structural roof cover that obstructed visibility and we captured this variation by categorizing each water source as covered or uncovered (see Table 1 for details about explanatory variables).

#### 2.5. Statistical analysis

To evaluate support for each of the hypotheses, we used general linear models (response variable was proportion of time spent vigilant) and model selection (Burnham and Anderson, 2002; Symonds and Moussalli, 2011). We used a general linear model because residuals associated with our response variable were normally distributed. Model selection provided a statistical environment in which we could quantify the relative ability of each hypothesis to account for variation in vigilance response of kit foxes. We used a two-stage approach (Carpenter et al., 2010) to assess support for each risk-related factor: predators and visibility. In the first stage, we constructed univariate models using the variables associated with predators (i.e., frequency of visitation by various species of predators) and those associated with visibility (i.e., vegetation, topography, structural roof cover) to explain the proportion of vigilance behavior associated with each water source (Table 1). We then used Akaike's Information Criterion adjusted for small sample size (AICc) to compare univariate models within each category (Burnham and Anderson, 2002). We considered models to be competing if they were within two  $\Delta$ AICc values of the model with the lowest AICc value (Burnham and Anderson, 2002). After the first stage, we advanced the competing univariate models from each category to the next stage of analysis.

For the second stage of model selection, we first evaluated the potential for multicollinearity (correlation between explanatory variables) by evaluating correlation coefficients. When explanatory variables were highly correlated ( $|r| > 0.7$ ), we retained the explanatory variable with the lowest AICc value from the first stage of univariate model comparison (Carpenter et al., 2010). After discarding correlated explanatory variables, we used the remaining

**Table 1**

Explanatory variables (visibility and predator) measured at water sources where we evaluated proportion of time spent vigilant by kit foxes (*Vulpes macrotis*). Mean values represent mean proportion ( $\pm$ SE) for visibility variables and mean frequency ( $\pm$ SE) of visitation to water sources by species for predator variables. Data were collected in Utah, USA from May 2010 to January 2012.

Explanatory variables	Mean	SE
<b>Visibility</b>		
Structural roof cover <sup>a</sup>	0.41	0.11
Viewshed 25 m radius <sup>b</sup>	0.00	0.00
Viewshed 50 m radius	0.07	0.02
Viewshed 75 m radius	0.18	0.02
Viewshed 100 m radius	0.25	0.03
Viewshed 125 m radius	0.35	0.03
Viewshed 150 m radius	0.42	0.03
Vegetation height 25 m radius <sup>c</sup>	0.34	0.04
Vegetation height 50 m radius	0.62	0.05
Vegetation height 75 m radius	0.75	0.04
Vegetation height 100 m radius	0.79	0.04
Vegetation height 125 m radius	0.83	0.04
Vegetation height 150 m radius	0.86	0.04
<b>Predators<sup>d</sup></b>		
Badger	0.10	0.03
Bobcat	0.02	0.01
Coyote	0.04	0.02
Domestic dog	0.01	0.01
Golden eagle	<0.01	<0.01
Gray fox	<0.01	<0.01
Great horned owl	0.10	0.06
Red-tailed hawk	0.08	0.07
Raptors	0.19	0.13
Mammals	0.19	0.04
Predators	0.37	0.15

<sup>a</sup> Presence (1) or absence (0) of roof cover.

<sup>b</sup> Proportion of pixels visible around each water source.

<sup>c</sup> Height of vegetation measured in all four cardinal directions around each water source.

<sup>d</sup> Frequency of visitation based on photo-captures from infrared-triggered cameras.

explanatory variables from the top competing univariate models to build all pairwise combinations of multivariate models (Carpenter et al., 2010). We limited ourselves to models with two variables given our modest sample size ( $N = 22$ ) and general rules of thumb regarding model selection and linear models. Using AICc values and model weights ( $\omega_i$ ), we ranked competing models from this list of univariate and multivariate models (Burnham and Anderson, 2002). We then evaluated both the log likelihood and AICc values associated with top models to identify any models with uninformative parameters. We judged parameters as uninformative when competing models differed from the top model by a single parameter and little to no improvement in log likelihood was evident (Anderson, 2008; Arnold, 2010; Burnham and Anderson, 2002). This two-step process allowed us to determine relative support for variables associated with predators (direct cues) and visibility (indirect cues) characteristics associated with each water source and make inference about which best explained vigilance behavior in kit foxes. We performed statistical analyses using Program R (R Development Core Team, 2008).

### 3. Results

In 4222 camera nights we obtained 851 videos (total of 6.59 h) of kit foxes at 25 water sources. However, three water sources had fewer than five videos so we excluded these from analysis, leaving 22 water sources that we used for subsequent analyses. Kit foxes comprised 57% of the 2116 total visits to water sources by members of the carnivore guild. We identified eight potential predators of kit foxes in photos at water sources: badgers (*Taxidea taxus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), domestic dogs

**Table 2**

AICc,  $\Delta$ AICc, log likelihood (LL), number of parameters ( $K$ ), and model weights ( $\omega_i$ ) for models of kit fox (*Vulpes macrotis*) vigilance as a function of predator and visibility explanatory variables. We advanced competing models (within two  $\Delta$ AICc values of the top model) to stage two of analysis. Vigilance behavior data were collected on kit foxes in Utah, USA from May 2010 to January 2012.

Model	AICc	$\Delta$ AICc	LL	$K$	$\omega_i$
<b>Visibility models</b>					
Structural roof cover	−30.64	0.00	18.63	2	0.76
Vegetation height 125 m	−24.85	5.79	15.74	2	0.04
Vegetation height 100 m	−24.10	6.54	15.36	2	0.03
Vegetation height 50 m	−23.70	6.94	15.16	2	0.02
Viewshed 50 m	−23.49	7.15	15.06	2	0.02
Viewshed 150 m	−23.45	7.19	15.04	2	0.02
Viewshed 100 m	−23.22	7.42	14.92	2	0.02
Vegetation height 150 m	−23.09	7.55	14.86	2	0.02
Vegetation height 25 m	−23.04	7.60	14.83	2	0.02
Viewshed 125 m	−23.00	7.64	14.82	2	0.02
Vegetation height 75 m	−22.85	7.79	14.74	2	0.02
Viewshed 75 m	−22.69	7.95	14.66	2	0.01
<b>Predator models</b>					
Red-tailed hawk	−24.37	0.00	15.50	2	0.13
Bobcat	−24.36	0.01	15.50	2	0.13
Predators	−24.16	0.21	15.39	2	0.12
Raptors	−24.02	0.35	15.32	2	0.11
Domestic dog	−23.72	0.65	15.18	2	0.09
Great horned owl	−23.60	0.77	15.11	2	0.09
Mammals	−23.48	0.89	15.05	2	0.08
Badger	−23.14	1.23	14.89	2	0.07
Coyote	−23.01	1.36	14.82	2	0.07
Gray fox	−22.79	1.58	14.71	2	0.06
Golden eagle	−22.68	1.69	14.65	2	0.06

(*C. lupus familiaris*), golden eagles (*Aquila chrysaetos*), gray foxes (*Urocyon cinereoargenteus*), great-horned owls (*Bubo virginianus*), and red-tailed hawks (*Buteo jamaicensis*). We did not observe any attempted predation on kit foxes, but there were three instances where a kit fox quickly departed from a water source as a badger approached.

In stage one (univariate analyses within categories) of our analysis for the predator category we considered all models as competitors since they were within two  $\Delta$ AICc values of one another (Table 2). For the visibility category, we identified structural roof cover at water sources as the sole competing model, accounting for 76% of AICc weight (Table 2). The next potential competing model for visibility was 5.79  $\Delta$ AICc values greater than that of the structural roof cover model with a model weight of only 4% (Table 2). For stage two of model selection (competing models across categories), predator models received very little individual support. Structural roof cover at water sources was the best approximating model that contributed most to the explanation of proportion of time spent vigilant by kit foxes (Table 3). This model resulted in the lowest AICc value and majority of model weight (Table 3). Although there were other models that received some AICc weight, (e.g., structural roof cover + red tailed hawk,  $\Delta$ AICc = 1.92), the top six models (93% of AICc weight) all contained structural roof cover (Table 3). For models 2–6, predator variables were added to the structural roof cover model. In each of these cases, the predator variable was an uninformative parameter because addition of these variables resulted in little improvement to log likelihood and each differed from the top model by a single parameter (Anderson, 2008; Arnold, 2010; Burnham and Anderson, 2002). Without inclusion of structural roof cover, models with predator variables accounted for very little AICc weight (Table 3). Kit foxes spent less time vigilant and more time drinking at water sources with structural roof cover (reduced visibility) compared to uncovered water sources (Fig. 3).

**Table 3**

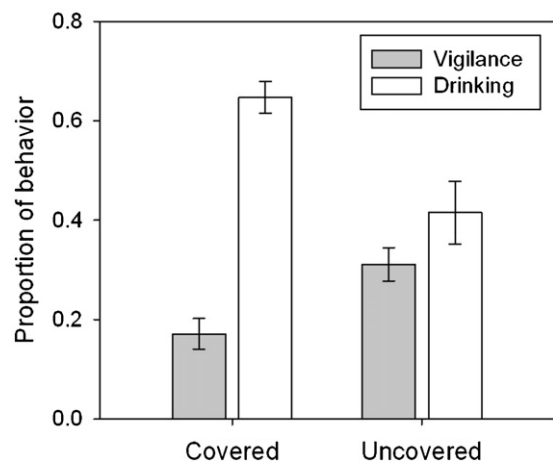
AICc,  $\Delta$ AICc, log likelihood (LL), number of parameters ( $K$ ), and model weights ( $\omega_i$ ) for combined (stage two) models of kit fox (*Vulpes macrotis*) vigilance as a function of predator and visibility explanatory variables. Vigilance behavior data were collected on kit foxes in Utah, USA from May 2010 to January 2012.

Model	AICc	$\Delta$ AICc	LL	$K$	$\omega_i$
Structural roof cover	−30.64	0.00	18.63	2	0.37
Structural roof cover + Red tailed hawk	−28.72	1.92	19.02	3	0.14
Structural roof cover + Mammals	−28.32	2.32	18.82	3	0.11
Structural roof cover + Golden eagle	−28.26	2.38	18.80	3	0.11
Structural roof cover + Gray fox	−28.09	2.55	18.71	3	0.10
Structural roof cover + Coyote	−27.94	2.70	18.64	3	0.10
Red-tailed hawk	−24.37	6.27	15.50	2	0.02
Mammals	−23.48	7.16	15.05	2	0.01
Coyote	−23.01	7.63	14.82	2	0.01
Gray fox	−22.79	7.85	14.71	2	0.01
Red tailed hawk + Coyote	−22.02	8.62	15.68	3	0.01
Golden eagle	−22.68	7.96	14.65	2	0.01
Red tailed hawk + Gray fox	−21.88	8.76	15.61	3	0.00
Red tailed hawk + Golden eagle	−21.68	8.96	15.51	3	0.00
Coyote + Gray fox	−20.46	10.18	14.89	3	0.00
Coyote + Golden eagle	−20.32	10.32	14.82	3	0.00
Gray fox + Golden eagle	−20.09	10.55	14.71	3	0.00

#### 4. Discussion

Our findings provide novel information about vigilance behavior of kit foxes, but more importantly they demonstrate how indirect cues (i.e., visual obstructions) can influence perceived risk of predation at water sources for a solitary carnivore subject to intraguild predation. We found strong support for the refuge-vigilance hypothesis (Kotler et al., 2002; Lima, 1990; Lima et al., 1987) for kit foxes at water sources as vigilance decreased at covered water sources (obstructed visibility). Burger (2001) found that coatis (*Nasua narica*) and white-faced capuchins (*Cebus capucinus*) both increased vigilance and decreased drinking behaviors at water where visibility was obstructed. We observed the opposite relationship. At water sources with obstructed visibility, kit foxes exhibited proportionally less vigilance and more drinking than at water sources with more visibility.

Decreased visibility associated with obstructive cover does not necessarily result in increased levels of vigilance for all species. Uinta ground squirrels (*Spermophilus armatus*), for example, were thought to need open habitat with low cover to detect predators (Hannon et al., 2006). Yet, Hannon et al. (2006) found no relationship between visibility and vigilance across sites with varying levels of visual obstruction. Examples of species that have



**Fig. 3.** Proportions ( $\pm$ SE) of vigilance behavior and drinking by kit foxes (*Vulpes macrotis*) at water sources with ( $N=9$ ) and without ( $N=13$ ) structural roof cover from data collected in Utah, USA from May 2010 to January 2012.

demonstrated decreased vigilance under cover (reduced visibility) include baboons (*Papio cynocephalus ursinus*) (Cowlshaw, 1998), brush tail possums (*Trichosurus vulpecula*) (Nersesian et al., 2012), house sparrows (*Passer domesticus*) (Lima, 1987), and Siberian jays (*Perisoreus infaustus*) (Griesser and Nystrand, 2009).

Previous work with kit foxes has identified how at least two antipredator behaviors are interrelated with habitat. First, kit foxes select open areas with low cover thought to maximize visibility of approaching predators (Egoscue, 1956). Kit foxes may be using vigilance behavior in the open (more visibility) where it can be most effective. Embar et al. (2011) observed a similar relationship with gerbils (*Gerbillus andersoni allenbyi*); when sightlines of gerbils were obscured, vigilance decreased. These authors concluded that when gerbils were under obstructive cover and visually undetectable to predators, vigilance was less effective and gerbils spent more time foraging. Second, kit foxes use dens and burrows to not only minimize water loss to evaporative cooling but also to escape predation (Egoscue, 1962). Similar to the concealing nature of a den or a burrow, water sources with structural roof cover may also serve as concealment (refuge).

Cover that obstructs visibility can serve dual roles for prey. Obstructive cover can conceal the whereabouts of prey from a predator or prevent prey from visually detecting predators (Hannon et al., 2006). Prey that have evolved with predators that use dense cover for ambush or stalking may increase vigilance in areas with cover (Lima, 1987). The negative correlation we observed between vigilance and cover that obstructs visibility suggests that kit foxes are not generally victims of ambush attacks. Of the potential predators of kit foxes, bobcats are the primary predator that uses cover for ambush. However, bobcat predation constitutes only a small portion of recorded mortality of kit foxes (Cypher et al., 2000). Thus, areas with obstructive cover may not be perceived as risky by kit foxes.

Prey that coevolved with avian predators often use overhead cover to minimize risk of avian predation (Boinski et al., 2003). For instance, gerbils were less vigilant and foraged more under the cover of low overhead vegetation when owls (*B. bubo*, *Tyto alba*, and *Athene noctua*) were present (Embar et al., 2011; Kotler et al., 1991). In addition, squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*) and fat sand rats (*Psammomys obesus*), which are preyed on by raptors, were less vigilant under overhead cover (Boinski et al., 2003; Tchabovsky et al., 2001). Raptors are known to prey on kit foxes (Cypher et al., 2000) and have negatively impacted other species of related fox (Coonan et al., 2005; Moehrensclager et al., 2007). The decrease in vigilance by kit foxes under structural roof cover is similar to what others have found for prey that experience avian predation.

Coyotes are the most commonly reported predator of kit foxes (Cypher et al., 2000), however, we found no model support indicating that coyotes influenced vigilance behavior of kit foxes. The difference between coyote predation and our results may reflect the evolutionary history of canid communities prior to European settlement (Clark, 2007). During this time, wolves (*C. lupus*) occupied the majority of the contiguous USA (Mech, 1974). Wolves probably did not directly interact with kit foxes, but may have indirectly benefited them by providing scavenging opportunities and suppressing coyotes via interference competition (Berger and Gese, 2007; Clark, 2007). In areas with wolves, coyotes may have been less of a threat to smaller mesocarnivores, including the kit fox (Clark, 2007). Thus, kit foxes may not yet have fully developed vigilance behavior to minimize the risk of predation by coyotes.

The lack of support for the predator-vigilance hypothesis in our study conflicts with what has been found with large carnivores and their prey in Africa (Periquet et al., 2010). This discrepancy could be due to a relatively sparse distribution of water sources compared to our study area (Periquet et al., 2010). As water is more distantly

spaced and therefore spatially limited in arid landscapes, there are fewer locations where prey consistently visit. Frequent visitation by prey to fewer water sources results in predators focusing on these areas for hunting (de Boer et al., 2010; Valeix et al., 2010). Density of water sources in our study area was nearly 50 times greater (0.183 water sources/km<sup>2</sup>) than that of northwestern Zimbabwe (0.004 water sources/km<sup>2</sup>) where Periquet et al. (2010) conducted their work on the influence of predators on vigilance behavior of prey. Increased density of water sources lowers the probability of a predator encountering prey since there are more potential locations for prey to access water. Thus, arid landscapes with many water sources provide predators with fewer focal points for hunting and may influence vigilance behavior differently compared to arid landscapes with fewer water sources. The apparent low impact of presence of predators on vigilance behavior of kit foxes may reflect a diluted risk of predation at water sources.

An alternative explanation for lack of model support for the predator-vigilance hypothesis could relate to the diversity of cues left by multiple species of predator. For example, mice (*Peromyscus leucopus* and *P. polionotus*) and voles (*Microtus* spp.), which are preyed on by several predators, did not alter foraging behavior in response to scents of multiple predators (Fanson, 2010; Orrock et al., 2004; Pusenius and Ostfeld, 2002). Orrock et al. (2004) concluded that relying on direct cues may be less effective for prey with multiple predators. Focusing on indirect cues, such as habitat type or structure, is likely a more reliable method for some species of prey to assess the relative risk of predation (Verdolin, 2006).

Based on our results, the refuge-vigilance hypothesis best explained vigilance behavior in kit foxes. The other hypotheses may not be applicable to all species of prey, particularly solitary carnivores. Without the advantages of group living, solitary prey may use areas with concealing cover as refuge to minimize the behavioral tradeoff between resource acquisition and vigilance. Our study suggests that environmental factors (e.g., density of water sources in arid landscapes) and natural history of solitary prey (e.g., coevolution with predators, use of refuges) can influence vigilance behavior.

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## References

- Adams, J.L., Camello, K.W., Orique, M.J., Blumstein, D.T., 2006. Does information of predators influence general wariness? *Behav. Ecol. Sociobiol.* 60, 742–747.
- Anderson, D.R., 2008. *Model-based Inference in the Life Sciences: A Primer on Evidence*. Springer, New York.
- Arenz, C.L., Leger, D.W., 1997. Artificial visual obstruction, antipredator vigilance, and predator detection in the thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*). *Behaviour* 134, 1101–1114.
- Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manage.* 74, 1175–1178.
- Baker, D.J., Stillman, R.A., Smart, S.L., Bullock, J.M., Norris, K.J., 2011. Are the costs of routine vigilance avoided by granivorous foragers? *Funct. Ecol.* 25, 617–627.
- Barri, F.R., Roldan, N., Navarro, J.L., Martella, M.B., 2012. Effects of group size, habitat and hunting risk on vigilance and foraging behaviour in the lesser rhea (*Rhea pennata pennata*). *Emu* 112, 67–70.
- Bednekoff, P.A., Blumstein, D.T., 2009. Peripheral obstructions influence marmot vigilance: integrating observational and experimental results. *Behav. Ecol.* 20, 1111–1117.

- Berger, K.M., Gese, E.M., 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? *J. Anim. Ecol.* 76, 1075–1085.
- Boinski, S., Kauffman, L., Westoll, A., Stickler, C.M., Cropp, S., Ehmke, E., 2003. Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedi*, *S. boliviensis*, and *S. sciureus*). *Behaviour* 140, 1421–1467.
- Brawata, R.L., Neeman, T., 2011. Is water the key? Dingo management, intraguild interactions and predator distribution around water points in arid Australia. *Wildl. Res.* 38, 426–436.
- Bridges, A.S., Noss, A.J., 2011. Behavior and activity patterns. In: O'Connell, A.F., Nichols, J.D., Karanth, K.U. (Eds.), *Camera Traps in Animal Ecology, Methods and Analyses*. Springer, New York.
- Burger, J., 1992. Drinking vigilance and group size in white-tipped doves and common ground-doves in Costa Rica. *Wilson Bull.* 104, 357–359.
- Burger, J., 2001. Visibility, group size, vigilance, and drinking behavior in coati (*Nasua narica*) and white-faced capuchins (*Cebus capucinus*): experimental evidence. *Acta Ethol.* 3, 111–119.
- Burnham, K.P., Anderson, D.A., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer, New York.
- Caro, T.M., Stoner, C.J., 2003. The potential for interspecific competition among African carnivores. *Biol. Conserv.* 110, 67–75.
- Carpenter, J., Aldridge, C., Boyce, M.S., 2010. Sage-grouse habitat selection during winter in Alberta. *J. Wildl. Manage.* 74, 1806–1814.
- Clark Jr., H.O., 2007. Hypothetical relationships between the San Joaquin kit fox, California grizzly bear, and gray wolf on the Pre-European California landscape. *Endangered Spec. Update* 24, 14–19.
- Coonan, T.J., Schwemm, C.A., Roemer, G.W., Garcelon, D.K., Munson, L., 2005. Decline of an island fox subspecies to near extinction. *Southwest. Nat.* 50, 32–41.
- Cowlishaw, G., 1998. The role of vigilance in the survival and reproductive strategies of desert baboons. *Behaviour* 135, 431–452.
- Creel, S., Creel, N.M., 1996. Limitation of African wild dogs by competition with larger carnivores. *Conserv. Biol.* 10, 526–538.
- Cypher, B.L., Warrick, G.D., Otten, M.R.M., O'Farrell, T.P., Berry, W.H., Harris, C.E., Kato, T.T., McCue, P.M., Scrivner, J.H., Zoellick, B.W., 2000. Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. *Wildl. Monogr.* 145, 1–43.
- de Boer, W.F., Vis, M.J.P., de Knegt, H.J., Rowles, C., Kohi, E.M., van Langevelde, F., Peel, M., Pretorius, Y., Skidmore, A.K., Slotow, R., 2010. Spatial distribution of lion kills determined by the water dependency of prey species. *J. Mammal.* 91, 1280–1286.
- Egoscue, H.J., 1956. Preliminary studies of the kit fox in Utah. *J. Mammal.* 37, 351–357.
- Egoscue, H.J., 1962. Ecology and life history of the kit fox in Tooele County, Utah. *Ecology* 43, 481–497.
- Elgar, M.A., 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.* 64, 13–33.
- Embar, K., Kotler, B.P., Mukherjee, S., 2011. Risk management in optimal foragers: the effect of sightlines and predator type on patch use, time allocation, and vigilance in gerbils. *Oikos* 120, 1657–1666.
- Fanson, B.G., 2010. Effect of direct and indirect cues of predation risk on the foraging behavior of the white-footed mouse (*Peromyscus leucopus*). *Northeast. Nat.* 17, 19–28.
- Fortin, D., Boyce, M.S., Merrill, E.H., Fryxell, J.M., 2004. Foraging costs of vigilance in large mammalian herbivores. *Oikos* 107, 172–180.
- Frank, L.G., Woodroffe, R., 2001. Behaviour of carnivores in exploited and controlled populations. In: Gittleman, J.L., Funk, S.M., Macdonald, D.W., Wayne, R.K. (Eds.), *Carnivore Conservation*. Cambridge University Press, London.
- Goldsmith, A.E., 1990. Vigilance behavior of pronghorns in different habitats. *J. Mammal.* 71, 460–462.
- Griesser, M., Nystrand, M., 2009. Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. *Behav. Ecol.* 20, 709–715.
- Hannon, M.J., Jenkins, S.H., Crabtree, R.L., Swanson, A.K., 2006. Visibility and vigilance: behavior and population ecology of Uinta ground squirrels (*Spermophilus armatus*) in different habitats. *J. Mammal.* 87, 287–295.
- Hauser, M.D., Caffrey, C., 1994. Anti-predator response to raptor calls in wild crows, *Corvus brachyrhynchos hesperis*. *Anim. Behav.* 48, 1469–1471.
- Hernández, L., Laundré, J.W., Gurung, M., 2005. Use of camera traps to measure predation risk in a puma-mule deer system. *Wildl. Soc. Bull.* 33, 353–358.
- Jones, M.E., 1998. The function of vigilance in sympatric marsupial carnivores: the eastern quoll and the Tasmanian devil. *Anim. Behav.* 56, 1279–1284.
- Kitchen, A.M., Gese, E.M., Schauster, E.R., 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. *Can. J. Zool.* 77, 1645–1656.
- Kotler, B.P., Brown, J.S., Dall, S.R.X., Gresser, S., Ganey, D., Bouskila, A., 2002. Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evol. Ecol. Res.* 4, 495–518.
- Kotler, B.P., Brown, J.S., Hasson, O., 1991. Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72, 2249–2260.
- Kozłowski, A.J., Gese, E.M., Arjo, W.M., 2008. Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. *Am. Midl. Nat.* 160, 191–208.
- Laundré, J.W., Hernández, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the landscape of fear in Yellowstone National Park, U.S.A. *Can. J. Zool.* 79, 1401–1409.
- Laundré, J.W., Hernández, L., Ripple, W.J., 2010. The landscape of fear: ecological implications of being afraid. *Open Ecol.* 3, 1–7.
- Lima, S.L., 1987. Distance to cover, visual obstructions, and vigilance in house sparrows. *Behaviour* 102, 231–238.
- Lima, S.L., 1990. Protective cover and the use of space: different strategies in finches. *Oikos* 58, 151–158.
- Lima, S.L., Wiebe, K.L., Dill, L.M., 1987. Protective cover and the use of space by finches: is closer better? *Oikos* 50, 225–230.
- Martella, M.B., Renison, D., Navarro, J.L., 1995. Vigilance in the greater rhea: effects of vegetation height and group size. *J. Field Ornithol.* 66, 215–220.
- Mech, L.D., 1974. *Canis lupus*. *Mamm. Species* 37, 1–6.
- Metcalfe, N.B., 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? *Anim. Behav.* 32, 981–985.
- Michalski, F., Peres, C.A., 2007. Disturbance-mediated mammal persistence and abundance-area relationships in Amazonian forest fragments. *Conserv. Biol.* 21, 1626–1640.
- Moehrenschrager, A., List, R., Macdonald, D.W., 2007. Escaping intraguild predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift foxes. *J. Mammal.* 88, 1029–1039.
- Nersesian, C.L., Banks, P.B., McArthur, C., 2012. Behavioural responses to indirect and direct predator cues by a mammalian herbivore, the common brushtail possum. *Behav. Ecol. Sociobiol.* 66, 47–55.
- Orrock, J.L., Danielson, B.J., Brinkerhoff, R.J., 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Behav. Ecol.* 15, 433–437.
- Palomares, F., Caro, T.M., 1999. Interspecific killing among mammalian carnivores. *Am. Nat.* 153, 492–508.
- Parsons, M.H., Blumstein, D.T., 2010. Feeling vulnerable? Indirect risk cues differentially influence how two marsupials respond to novel dingo urine. *Ethology* 116, 972–980.
- Periquet, S., Valeix, M., Loveridge, A.J., Madzikanda, H., Macdonald, D.W., Fritz, H., 2010. Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Anim. Behav.* 79, 665–671.
- Pusenius, J., Ostfeld, R.S., 2002. Mammalian predator scent, vegetation cover and tree seedling predation by meadow voles. *Ecography* 25, 481–487.
- Quenette, P.Y., 1990. Functions of vigilance behavior in mammals – a review. *Acta Oecol.* 11, 801–818.
- R Development Core Team, 2008. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, ISBN 3-900051-07-0 <http://www.R-project.org>
- Rainey, H.J., Zuberbühler, K., Slater, P.J.B., 2004. Hornbills can distinguish between primate alarm calls. *Proc. R. Soc. Biol. Sci. Ser. B* 271, 755–759.
- Robel, R.J., Briggs, J.N., Dayton, A.D., Hulbert, L.C., 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *J. Range Manage.* 23, 295–297.
- Switalski, T.A., 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. *Can. J. Zool.* 81, 985–993.
- Symonds, M., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21.
- Tchabovsky, A.V., Krasnov, B., Khokhlova, I.S., Shenbrot, G.I., 2001. The effect of vegetation cover on vigilance and foraging tactics in the fat sand rat *Psammomys obesus*. *J. Ethol.* 19, 105–113.
- Underwood, R., 1982. Vigilance behaviour in grazing African antelopes. *Behaviour* 79, 81–107.
- Valeix, M., Fritz, H., Loveridge, A.J., Davidson, Z., Hunt, J., Murindagomo, F., Macdonald, D.W., 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? *Behav. Ecol. Sociobiol.* 63, 1483–1494.
- Valeix, M., Loveridge, A., Davidson, Z., Madzikanda, H., Fritz, H., Macdonald, D., 2010. How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landsc. Ecol.* 25, 337–351.
- Verdolin, J.L., 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behav. Ecol. Sociobiol.* 60, 457–464.
- Whittingham, M.J., Butler, S.J., Quinn, J.L., Cresswell, W., 2004. The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. *Oikos* 106, 377–385.
- Wolff, J.O., Van Horn, T., 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Can. J. Zool.* 81, 266–271.
- Zoellick, B.W., Harris, C.E., Kelly, B.T., O'Farrell, T.P., Kato, T.T., Koopman, M.E., 2002. Movements and home ranges of San Joaquin kit foxes (*Vulpes macrotis mutica*) relative to oil-field development. *West. N. Am. Nat.* 62, 151–159.
- Zuberbühler, K., Noe, R., Seyfarth, R.M., 1997. Diana monkey long-distance calls: messages for conspecifics and predators. *Anim. Behav.* 53, 589–604.