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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.

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^2 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

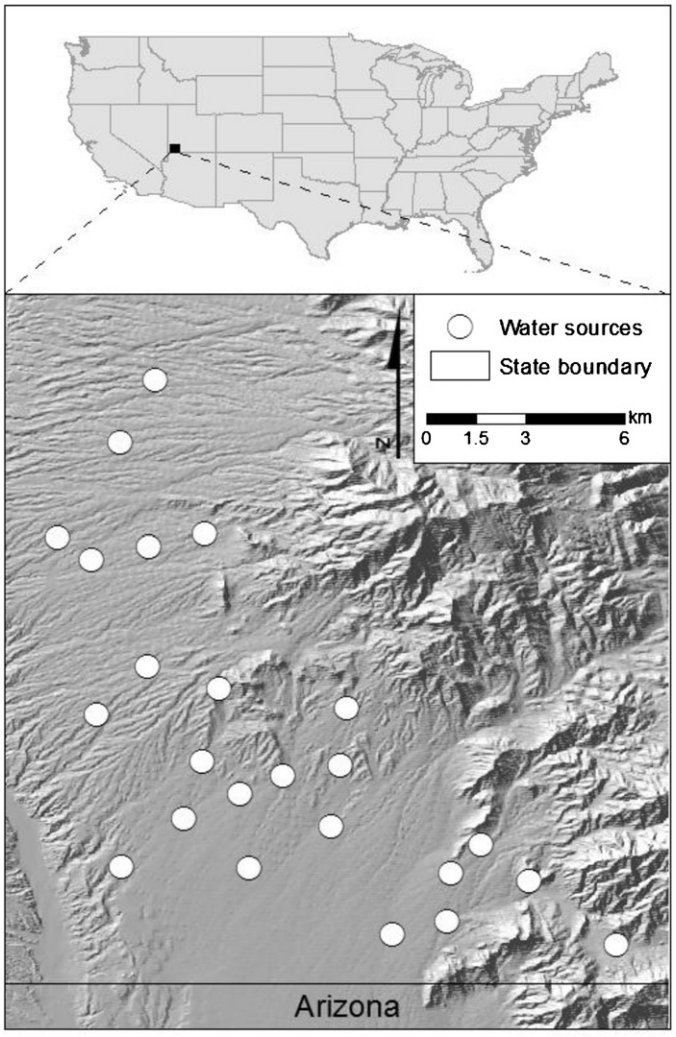

Fig. 1. Study area in Mojave Desert, Utah, USA where we evaluated kit fox (*Vulpes macrotis*) vigilance from May 2010 to January 2012. White circles represent locations of water sources used by kit foxes during our sampling period.