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The Influence of Anthropogenic Development of Water on Coyotes and Kit Foxes in the Great Basin and Mojave Deserts

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A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

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ABSTRACT

The Influence of Anthropogenic Development of Water on Coyotes and Kit Foxes in the Great Basin and Mojave Deserts

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Master of Science

Anthropogenic provisioning of water (water developments) to enhance abundance and distribution of wildlife is a common management practice in arid regions where water is limiting. Despite the long-term and widespread use of water developments, little is known about how they influence distribution, competition dynamics, and behavior of native species. To elucidate the potential influences of water developments on native species, we tested hypotheses concerning the occurrence and behavior of native kit foxes (*Vulpes macrotis*). First, we tested the indirect effect of water hypothesis (IEWH) which proposes that water developments negatively affect the arid-adapted kit fox by enabling a water-dependent competitor (i.e., coyote; *Canis latrans*) to expand distribution in arid landscapes. We tested the two predictions of the IEWH (i.e., coyotes will visit areas with water more frequently and kit foxes will avoid coyotes) and evaluated relative use of water by canids in the Great Basin and Mojave Deserts from 2010 to 2012. We established scent stations in areas with (wet) and without (dry) water and monitored visitation by canids to scent stations and water sources using infrared-triggered cameras. There was no difference in the proportions of visits to scent stations in wet or dry areas by coyotes or kit foxes at either study area. There was no correlation between visits to scent stations by coyotes and kit foxes. Visitation to water sources was not different for coyotes between study areas, but kit foxes visited water sources more in Mojave than Great Basin. The intense visitation to water by kit foxes in Mojave challenges our understanding that this species does not readily drink water. Our results did not support the IEWH in the Great Basin or Mojave Deserts for these two canids.

Second, we tested three hypotheses that have been proposed to explain spatial variation in vigilance behavior. The predator-vigilance hypothesis (PVH) proposes that prey increase vigilance where there is evidence of predators. The visibility-vigilance hypothesis (VVH) suggests that prey increase vigilance where detection of predators is impeded or visibility is obstructed. The refuge-vigilance hypothesis (RVH) 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, 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 developments in the Mojave Desert. The RVH 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 developments with low overhead cover (refuge) obstructing visibility. Based on our results, the PVH and VVH 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.

Keywords: carnivore, coyote, indirect effect, intraguild predation, kit fox, predation, refuge, remote camera, scent station, vigilance, visibility, water development, water source

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CHAPTER 1

WATER DEVELOPMENTS AND CANIDS IN TWO NORTH AMERICAN DESERTS: A TEST OF THE INDIRECT EFFECT OF WATER HYPOTHESIS

ABSTRACT

Anthropogenic modifications to landscapes to benefit wildlife may negatively influence communities. Anthropogenic provisioning of free water (water developments) to enhance abundance and distribution of wildlife is a common management practice in arid regions where water is limiting. Despite the long-term and widespread use of water developments, little is known about how they influence native species. Water developments may negatively influence arid-adapted species (e.g., kit fox, *Vulpes macrotis*) by enabling water-dependent competitors (e.g., coyote, *Canis latrans*) to expand distribution in arid landscapes (i.e., indirect effect of water hypothesis; IEWH). We tested the two predictions of the IEWH (i.e., coyotes will visit areas with free water more frequently and kit foxes will avoid areas with coyotes) and evaluated relative use of free water by canids in the Great Basin and Mojave Deserts from 2010 to 2012. We established scent stations in areas with (wet) and without (dry) free water and monitored visitation by canids to these sites and visitation to water sources using infrared-triggered cameras. There was no difference in the proportions of visits to scent stations in wet or dry areas by coyotes or kit foxes at either study area. There was no negative correlation between visits to scent stations by coyotes and kit foxes. Visitation to water sources was not different for coyotes between study areas, but kit foxes visited water sources more in Mojave than Great Basin. The intense visitation to water developments by kit foxes in Mojave challenges the commonly held

view that this species does not readily drink free water. Our results did not support the IEWH in the Great Basin or Mojave Deserts for these two canids.

INTRODUCTION

Anthropogenic manipulations to landscapes or resources that are designed to benefit wildlife may have negative indirect effects on communities. For example, anthropogenic provisioning of food is common practice for sustaining and enhancing populations of target species for economic (e.g., sport hunting, wildlife-based tourism) or conservation purposes (Orams 2002, Putman and Staines 2004, Moreno-Opo et al. 2012). However, the supplementation of a concentrated resource, such as food, may unintentionally attract generalist predators that in turn, prey on species targeted by the supplementation (Boutin et al. 1986, Dunn and Tessaglia 1994, Cooper et al. 2012). In addition, supplemental feeding may indirectly increase predation on other non-target species of the community (Cooper and Ginnett 2000, Hamilton et al. 2002, Martinson and Flaspohler 2003). Indirect effects from anthropogenic manipulation of landscapes are likely most pronounced when alteration influences resources that are limiting.

In arid regions, water available for drinking (hereafter free water) is a limiting resource for some species that is often manipulated to increase distribution or density of animals (Vallentine 1980, Rautenstrauch and Krausman 1989, Bleich et al. 2006, Cain III et al. 2006). Despite the widespread and long-term manipulation of free water (e.g., water developments for wildlife and livestock), there is little supporting information and much controversy concerning how this anthropogenic manipulation influences native species (Broyles 1995, Rosenstock et al. 1999, Krausman et al. 2006). Water developments may be beneficial for some native species

(Hervert and Krausman 1986, Owen-Smith 1996, Cutler and Morrison 1998). For example, water developments sustained suitable habitat for bighorn sheep (*Ovis canadensis*) where natural sources of free water were in decline (Longshore et al. 2009). However, manipulating a limiting resource, such as free water, may impose negative indirect effects on native species that have adapted to minimal availability of that resource.

The manipulation of free water in arid landscapes (i.e., addition of water developments) potentially weakens the advantages that arid-adapted species have accrued to minimize interspecific competition and predation from species that are water-dependent. In the Great Basin Desert, for example, it has been argued that water developments remove the limitation of arid systems to coyotes (*Canis latrans*) which compete with kit foxes (*Vulpes macrotis*) for habitat, space, and food (Arjo et al. 2007, Nelson et al. 2007, Kozlowski et al. 2008). This association is largely based on the differential physiological demand of free water by coyotes and kit foxes. To obtain enough preformed water (available in prey items) to survive in the absence of free water, both coyotes and kit foxes need to consume more prey than required to meet energetic demands (Golightly Jr. and Ohmart 1984). However, coyotes need to consume twice the amount of prey per unit of mass relative to kit foxes to acquire sufficient preformed water to survive without free water creating an advantage for kit foxes in arid landscapes (Golightly Jr. and Ohmart 1984). Furthermore, coyotes depend on evaporative cooling to expel heat and therefore have higher rates of water loss compared to kit foxes that rely on thermal conductance which reduces water loss (Golightly Jr. and Ohmart 1983). Kit foxes also adhere more strictly than coyotes to behavioral adaptations that minimize water loss such as subterranean living and nocturnal activity (Golightly Jr. and Ohmart 1984, O'Brien et al. 2006). Thus, it is less energetically feasible for coyotes to inhabit areas that lack free water relative to kit foxes. Water developments may, therefore, indirectly affect the arid-adapted kit fox by enabling the water-dependent coyote to occupy an otherwise inhospitable system and exert asymmetric interspecific competition on kit foxes (i.e., indirect effect of water hypothesis (IEWH); Arjo et al. 2007, Kozlowski et al. 2008).

The IEWH is comprised of two testable predictions: 1) water-dependent competitors will occur more frequently in areas near free water and 2) will spatially displace subordinate competitors. The predictions of the IEWH, however, have not been formally evaluated for canid communities and it is unclear whether this hypothesis is broadly applicable in arid systems. Our objective was to test the IEWH in the Great Basin and Mojave Deserts using coyotes and kit foxes as a model community. Specifically, we 1) evaluated support for the two predictions of the IEWH and 2) assessed relative use of free water by coyotes and kit foxes. This information will provide new insight into how anthropogenic modification of landscapes and resources may influence interspecific interactions and community dynamics.

METHODS

Study areas

This study was conducted at sites in both the Great Basin and Mojave Deserts. The Great Basin Desert study area consisted of 915 km^2 of private land managed by the United States Department of Defense, United States Army Dugway Proving Ground in west-central Utah (Fig. 1). The terrain was typical of Lake Bonneville lakebed characterized by dune systems and alkaline flats that were dominated by black greasewood (*Sarcobatus vermiculatus*). Where wildfires had occurred along the foothills, cheatgrass (*Bromus tectorum*) was common within communities of big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus* spp.), and juniper (*Juniperus osteosperma*) (Arjo et al. 2007). Elevations across the study area ranged from approximately 1300 to 1800 m. Annual weather consisted of mean air temperatures of 12.69° C (range: -20.02 to 40.58° C) and mean precipitation of 150 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). The US Army Dugway Proving Ground has not been grazed by domestic livestock for the last 60 years (Kozlowski et al. 2008). In this study area, we identified 22 water sources consisting of 11 water developments for wildlife (i.e., guzzlers), six natural springs, and five man-made ponds.

The Mojave Desert study area consisted of 1,064 km^2 of public land managed by the United States Department of the Interior, Bureau of Land Management in extreme southwestern Utah, northwestern Arizona, and southeastern Nevada (Fig. 1). This study area was characterized by an alternating landscape of rolling hills/ridges and dry desert washes radiating from the Beaver Dam Mountains and emptying into the Beaver Dam Wash to the southwest near the intersection of the Utah-Nevada-Arizona state borders (Hall et al. 2013). In areas that burned within the last decade, red brome (*B. rubens*) was well established among surviving creosote (*Larrea divaricata*), Joshua-tree (*Yucca brevifolia*), and black-brush (*Coleogyne ramosissima*) communities (Horn et al. 2012). Along the foothills, the vegetation primarily consisted of sagebrush and juniper, transitioning to pinyon pine (*Pinus edulis*) at higher elevations. Elevations across the Mojave study area ranged from approximately 800 to 2000 m. Annual weather consisted of mean air temperatures of 19.18° C (range: -10.04 to 41.70° C) and mean precipitation of 113 mm (MesoWest, Bureau of Land Management & Boise Interagency Fire Center). The Mojave study area was grazed by livestock from October to May. We identified

66 water sources in this study area consisting of 35 water developments for wildlife, 18 water troughs/tanks for livestock, 11 natural springs, and two man-made ponds.

Experimental design and sampling

To verify if presence of coyotes was greater in areas with free water (hereafter wet) compared to areas without (hereafter dry), we first established wet and dry areas in both study areas. Using ArcGIS (version 10.0, Environmental Systems Research Institute, Redlands, California), we created a uniform pattern of sample points with a distance of 4 km apart for both study areas. Each of these sample points was buffered with a 2 km radius based on the diameter of a core home range for coyotes (Springer 1982). If free water was located within a buffer zone for a given sample area, we considered it a wet area. We identified water sources using databases with geospatial information for springs and water developments provided by the US Army Dugway Proving Ground and the Utah Division of Wildlife Resources. In addition, we consulted with local ranchers concerning water sources for livestock that were not in our databases. We were confident in our efforts to identify all known water sources in both study areas.

We established 32 scent stations in 2011 and 39 in 2012 and monitored stations for two-week periods during July to August (hottest part of the year; Table 1). Approximately half of the scent stations were located in wet areas and the other half in dry areas (Table 1). Scent stations in dry areas were approximately 2.5 km farther from a known water source compared to scent stations in wet areas (Table 1). At each scent station, we placed a scent lure (2011: fatty acid scented disc [Pocatello Supply Depot, Pocatello, Idaho, USA]; 2012: liquid scent [Murray’s Lures, Walker, West Virginia, USA]) on the ground and an infrared-triggered camera (PC 900, Reconyx©, Holmen, Wisconsin) approximately two meters from the scent either directly north or south to avoid false camera triggers by the sun.

To evaluate relative rates of visitation to water sources by canids, we monitored all known water sources at the Great Basin and Mojave study areas. From May to October, 2010 to 2012, we used infrared-triggered cameras to photograph canids visiting water sources. We randomly sampled water sources with cameras at both study areas for approximately two-week periods for a total of 78 weeks. To determine which water sources to sample for a given period, we generated random points within each study area using ArcMap. We then identified the nearest water source to a random point and camera-sampled as many water sources as possible (in 2010, we used six cameras in each study area for sampling compared to 15 cameras in 2011-2012). We attached cameras to metal posts and placed them approximately two meters from the edge of water where animals gained access to drink. At water sources with multiple locations of drinking access (e.g., paired tanks of water, ponds), we placed cameras at a minimum of two locations where animals could drink. We considered proximity to trails and recent sign to determine the location of cameras at ponds and large springs (Atwood et al. 2011). Our estimates of visitation by canids at large water sources were likely conservative due to the inability to monitor all potential locations where canids could access water. We assumed, however, that any potential bias was similar at large water sources from both study areas.

Statistical analyses

We used *z*-tests (Zar 1999) to compare the proportion of scent stations in wet and dry areas visited by canids at both study areas. To determine if there was spatial segregation between kit foxes and coyotes we used Kendall's *Tau-b* correlation analyses to compare visits to scent stations. Kendall's *Tau-b* correlation accounted for ties that occurred because of zero visit data due to only one species of canid primarily visiting a given station (Kendall 1962). We excluded all stations that were not visited by at least one species of canid from analyses.

We used Mann-Whitney *U*-tests to compare the mean daily visitation rates (# of visits / # of operable camera trap days) of canids to water sources between study areas. We defined a visit as all photo captures of a species occurring within 30 min. Thus, photo captures occurring more than 30 min apart were considered independent (Michalski and Peres 2007). We performed all analyses using Program R (R Development Core Team 2011). We set the level of significance for all statistical tests at $\alpha = 0.05$. We used Bonferroni corrections for series of statistical tests and adjusted α-levels accordingly.

RESULTS

We detected coyotes and kit foxes at scent stations in Great Basin and Mojave Deserts (Fig. 2). In Great Basin, we detected coyotes at more stations than kit foxes, but in Mojave we found the opposite relationship (Fig. 3). There was no difference between the proportion of stations visited by coyotes in Great Basin or Mojave (2011: $z = 0.47$, $P = 0.64$; 2012: $z = 1.77$, $P = 0.08$; Fig. 3). Conversely, the proportion of stations visited by kit foxes in Mojave was greater than in Great Basin (2011: $z = 4.04$, $P < 0.01$; 2012: $z = 3.52$, $P < 0.01$; Fig. 3). There was no difference in the proportions of visits to wet and dry stations by coyotes or kit foxes in 2011 (Great Basin coyotes: $z = 1.44$, $P = 0.15$; Great Basin kit foxes: $z = 1.01$, $P = 0.31$; Mojave coyotes: $z = 0.59$, $P = 0.55$; Mojave kit foxes: $z = 0.89$, $P = 0.37$; Fig. 4) or 2012 (Great Basin coyotes: $z = 0.00$, $P = 1.00$; Great Basin kit foxes: $z = 0.00$, $P = 1.00$; Mojave coyotes: $z = 1.03$, $P = 0.30$; Mojave kit foxes: $z = 1.07$, $P = 0.29$; Fig. 5). We detected coyotes and kit foxes at scent stations relatively close to and far from free water and did not observe a clear pattern between visitation and distance to free water (Fig. 6).

For correlation analyses, there were too few visits by canids to scent stations in Great Basin during 2011 for statistical correlation. We did not observe a negative correlation between visits of coyotes and kit foxes to scent stations at Great Basin in 2012 (*Tau-b* = -0.68, $P = 0.02$ (Bonferroni adjusted $P = 0.01$), $df = 11$, $N = 13$). Similarly, in Mojave we did not observe a negative correlation between visits of both canid species during 2011 (*Tau-b* = -0.27, $P = 0.26$, $df = 15$, $N = 17$) or 2012 (*Tau-b* = -0.23, $P = 0.29$, $df = 17$, $N = 19$).

We observed coyotes and kit foxes at water sources in both deserts (Fig. 2). In 6,476 camera trap days at water sources in Great Basin, we observed 924 coyote visits and four kit fox visits. In 4,803 camera trap days at water sources in Mojave, we observed 353 coyote visits and 1,530 kit fox visits. In Great Basin, coyotes visited 19 of the 22 available water sources whereas kit foxes only visited two. In Mojave, coyotes visited 38 of the 66 available water sources and kit foxes visited 25. There was no difference between mean daily visitation rates for coyotes across study areas (Mann-Whitney $U = 490.00$, $P = 0.07$; Fig. 7). Alternatively, mean daily visitation rate was higher for kit foxes in Mojave than kit foxes in Great Basin (Mann-Whitney $U = 471.50$, $P < 0.01$; Fig. 7).

DISCUSSION

Our study was the first to evaluate the potential indirect effect that anthropogenic water developments may have on canid communities in two deserts. We tested the two predictions of the IEWH in the Great Basin and Mojave Deserts. We did not find any support for the first prediction since we detected coyotes equally in wet and dry areas in both deserts (and likewise for kit foxes). Also, we did not find support for the second prediction due to lack of spatial segregation between coyotes and kit foxes in both study areas. Our data indicated that factor(s) other than the presence or distribution of free water were associated with occurrence of coyotes.

Although kit foxes have been observed to spatially avoid coyotes, results from our scent station experiment did not reveal spatial avoidance (Cypher and Spencer 1998, Warrick and Cypher 1998, Nelson et al. 2007). Similar to our observations, other studies have documented kit foxes coexisting with coyotes without spatial avoidance (White et al. 1994, White et al. 1995). Observations with other carnivore communities have demonstrated that subordinate competitors can coexist with larger, dominant competitors. For example, coyotes (subordinate) did not spatially adjust their use of habitat to avoid wolves (*C. lupus*), rather coyotes altered behaviors near wolf-killed carcasses (Atwood and Gese 2010). Likewise, gray foxes (*Urocyon cinereoargenteus*; subordinate) were able to coexist with coyotes and bobcats (*Lynx rufus*) by temporally partitioning the use of free water with these larger competitors (Atwood et al. 2011). For kit foxes, the availability of resources and refuges (i.e., burrows) likely plays a role in how they partition space with coyotes (White et al. 1995, Moehrenschlager et al. 2007).

Our data indicated that kit foxes were less abundant in Great Basin than Mojave, supporting previous reports of reduced populations in Great Basin (Arjo et al. 2007). However, abundance of coyotes appeared to be similar in both deserts, based on visits to scent stations and water sources. We suggest that coyotes may not solely regulate populations of kit foxes, though they can account for high rates of mortality (Warrick et al. 1999, Cypher et al. 2000). Previous work has demonstrated that removal of coyotes did not influence survival of kit foxes, indicating that coyote-induced mortality may be compensatory and that other factors affect population dynamics of kit foxes, such as prey availability (Cypher and Scrivner 1992, White et al. 1996, Dennis and Otten 2000).

Historical variation in availability and distribution of free water in western North America may provide, in part, explanation for the lack of support for the IEWH in the Great Basin and Mojave Deserts. Western North America has experienced dramatic fluctuations in climate (and associated availability of water) over the last several thousand years. For example, 12,000 y BP much of Great Basin and Mojave was a wetland environment with large lakes (Broecker and Kaufman 1965, Currey 1990). Since that time, this region has alternated between levels of extreme drought and wet conditions (Cook et al. 2004). The relatively recent addition of free water (i.e., water developments) in western North America, therefore, may not be novel to species inhabiting this region as both coyotes and kit foxes have experienced these conditions in their evolutionary histories. This natural variation in availability of free water over time has rarely been considered in controversies surrounding anthropogenic modification of water availability (Larsen et al. 2012).

Kit foxes have been perceived to be independent of free water based on physiological and behavioral adaptations (Golightly Jr. and Ohmart 1983;1984). Moreover, historical distributions of kit foxes typically include areas located far from known sources of water, further supporting the notion that this species of canid can exist without free water (Egoscue 1956). Nonetheless, published accounts have reported sporadic use of free water by kit foxes (O’Farrell 1999, O'Brien et al. 2006). Our study revealed an extreme rate of visitation to water developments by kit foxes in Mojave not previously reported in other areas of western North America. In Mojave, kit foxes were the most photographed carnivore at water developments and one of the most commonly photographed mammals (Hall et al. 2013). The intensity of visitation to water developments by kit foxes in Mojave challenges the commonly held view that this species seldom drinks free water.

The difference between visitation rates of kit foxes to free water between deserts may be due to at least two factors. First, according to our scent station data, there are likely more kit foxes in Mojave than Great Basin, resulting in an increased probability of detection at free water. Second, nighttime temperatures at Great Basin (mean = 14.42° C, SE = 0.09) were on average 8.70° C cooler than Mojave (mean = 23.12° C, SE = 0.08) although maximum daytime temperatures at both study areas were similar (~41° C). Relatively warmer nighttime temperatures in Mojave likely resulted in a reduced thermal gradient for kit foxes to dissipate heat from nocturnal activities which may have resulted in higher rates of water loss (Golightly Jr. and Ohmart 1983) compared to kit foxes in Great Basin. Relatively warmer nights and subsequent higher rates of water loss likely created a greater physiological demand for free water by kit foxes in Mojave compared to Great Basin.

Drinking free water may alleviate physiological stresses and improve survival even for species that are adapted to arid climates (Brawata and Neeman 2011). For kit foxes to persist without free water they need to consume nearly twice as much prey per day than what is solely required for energetic demands (Golightly Jr. and Ohmart 1984). By drinking free water, kit foxes may reduce energy and time associated with securing additional prey items to satisfy water demand. Less time spent foraging and less distance traveled in search of prey also reduces the likelihood of encounters with other competitors and potential predators (Moehrenschlager et al. 2007). Furthermore, drinking free water may benefit female kit foxes during lactation due to additional loss of water via production of milk (Cain III et al. 2006). The frequent visitation to free water by kit foxes in Mojave indicates that water developments may be beneficial to this arid-adapted species (Simpson et al. 2011).

Our results did not provide support for the indirect effect of water hypothesis at Great Basin or Mojave Deserts. The apparent high abundance of kit foxes that we observed in Mojave, an arid landscape with many water developments, created a paradox based on the logic that water developments indirectly influence these canids via increased distribution of coyotes (Arjo et al. 2007, Kozlowski et al. 2008). We did not find any support for the assertion that free water played a negative indirect role on kit foxes. Furthermore, our data did not indicate that space use of coyotes and kit foxes was negatively correlated. We reject the IEWH as operational in our study areas during our study years. The ultimate factor(s) that influence the distribution of coyotes and kit foxes in these two deserts are unknown and warrant further study.

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LITERATURE CITED

Arjo, W. M., E. M. Gese, T. J. Bennett, and A. J. Kozlowski. 2007. Changes in kit fox-coyote-prey relationships in the Great Basin Desert, Utah. Western North American Naturalist 67:389-401.

Atwood, T. C., T. L. Fry, and B. R. Leland. 2011. Partitioning of anthropogenic watering sites by desert carnivores. Journal of Wildlife Management 75:1609-1615.

Atwood, T. C., and E. M. Gese. 2010. Importance of resource selection and social behavior to partitioning of hostile space by sympatric canids. Journal of Mammalogy 91:490-499.

Bleich, V. C., N. G. Andrew, M. J. Martin, G. P. Mulcahy, A. M. Pauli, and S. S. Rosenstock. 2006. Quality of water available to wildlife in desert environments: comparisons among anthropogenic and natural sources. Wildlife Society Bulletin 34:627-632.

Boutin, S., C. J. Krebs, A. R. E. Sinclair, and J. N. M. Smith. 1986. Proximate causes of losses in a snowshoe hare population. Canadian Journal of Zoology 64:606-610.

Brawata, R. L., and T. Neeman. 2011. Is water the key? Dingo management, intraguild interactions and predator distribution around water points in arid Australia. Wildlife Research 38:426-436.

Broecker, W. S., and A. Kaufman. 1965. Radiocarbon chronology of Lake Lahontan and Lake Bonneville II, Great Basin. Geological Society of America Bulletin 76:537-566.

Broyles, B. 1995. Desert wildlife water developments: questioning use in the southwest. Wildlife Society Bulletin 23:663-675.

Cain III, J. W., P. R. Krausman, S. S. Rosenstock, and J. C. Turner. 2006. Mechanisms of thermoregulation and water balance in desert ungulates. Wildlife Society Bulletin 34:570-581.

Cook, E. R., C. A. Woodhouse, C. M. Eakin, D. M. Meko, and D. W. Stahle. 2004. Long-term aridity changes in the western United States. Science 306:1015-1018.

Cooper, C. B., K. A. T. Loyd, T. Murante, M. Savoca, and J. Dickinson. 2012. Natural history traits associated with detecting mortality within residential bird communities: can citizen science provide insights? Environmental Management 50:11-20.

Cooper, S. M., and T. F. Ginnett. 2000. Potential effects of supplemental feeding of deer on nest predation. Wildlife Society Bulletin 28:660-666.

Currey, D. R. 1990. Quaternary paleolakes in the evolution of semidesert basins, with special emphasis on Lake Bonneville and the Great Basin, U.S.A. Palaeogeography Palaeoclimatology Palaeoecology 76:189-214.

Cutler, T. L., and M. L. Morrison. 1998. Habitat use by small vertebrates at two water developments in southwestern Arizona. Southwestern Naturalist 43:155-162.

Cypher, B. L., and J. H. Scrivner. 1992. Coyote control to protect endangered San Joaquin kit foxes at the Naval Petroleum Reserves, California. Proceedings of the Vertebrate Pest Conference 15:42-47.

Cypher, B. L., and K. A. Spencer. 1998. Competitive Interactions between coyotes and San Joaquin kit foxes. Journal of Mammalogy 79:204-214.

Cypher, B. L., G. D. Warrick, M. R. M. Otten, T. P. O'Farrell, W. H. Berry, C. E. Harris, T. T. Kato, P. M. McCue, J. H. Scrivner, and B. W. Zoellick. 2000. Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. Wildlife Monographs 145:1-43.

Dennis, B., and M. R. M. Otten. 2000. Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. Journal of Wildlife Management 64:388-400.

Dunn, E. H., and D. L. Tessaglia. 1994. Predation of birds at feeders in Winter. Journal of Field Ornithology 65:8-16.

Egoscue, H. J. 1956. Preliminary studies of the kit fox in Utah. Journal of Mammalogy 37:351-357.

Golightly Jr., R. T., and R. D. Ohmart. 1983. Metabolism and body temperature of two desert canids: coyotes and kit foxes. Journal of Mammalogy 64:624-635.

_____. 1984. Water economy of two desert canids: coyote and kit fox. Journal of Mammalogy 65:51-58.

Hall, L. K., C. C. Day, M. D. Westover, R. J. Edgel, R. T. Larsen, R. N. Knight, and B. R. McMillan. 2013. Vigilance of kit foxes at water sources: a test of competing hypotheses for a solitary carnivore subject to predation. Behavioural Processes:In press. http://dx.doi.org/10.1016/j.beproc.2012.1012.1007.

Hamilton, A. M., A. H. Freedman, and R. Franz. 2002. Effects of deer feeders, habitat and sensory cues on predation rates on artificial turtle nests. American Midland Naturalist 147:123-134.

Hervert, J., and P. R. Krausman. 1986. Desert mule deer use of water developments in Arizona. Journal of Wildlife Management 50:670-676.

Horn, K. J., B. R. McMillan, and S. B. St Clair. 2012. Expansive fire in Mojave Desert shrubland reduces abundance and species diversity of small mammals. Journal of Arid Environments 77:54-58.

Kendall, M. G. 1962. Rank correlation methods. Third edition. Hodder Arnold, London.

Kozlowski, A. J., E. M. Gese, and W. M. Arjo. 2008. Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. American Midland Naturalist 160:191-208.

Krausman, P. R., S. S. Rosenstock, and J. W. Cain III. 2006. Developed waters for wildlife: science, perception, values, and controversy. Wildlife Society Bulletin 34:563-569.

Larsen, R. T., J. A. Bissonette, J. T. Flinders, and J. C. Whiting. 2012. Framework for understanding the influences of wildlife water developments in the western United States. California Fish and Game 98:148-163.

Longshore, K. M., C. Lowrey, and D. B. Thompson. 2009. Compensating for diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. Journal of Arid Environments 73:280-286.

Martinson, T. J., and D. J. Flaspohler. 2003. Winter bird feeding and localized predation on simulated bark-dwelling arthropods. Wildlife Society Bulletin 31:510-516.

Michalski, F., and C. A. Peres. 2007. Disturbance-mediated mammal persistence and abundance-area relationships in Amazonian forest fragments. Conservation Biology 21:1626-1640.

Moehrenschlager, A., R. List, and D. W. Macdonald. 2007. Escaping intraguild predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift foxes. Journal of Mammalogy 88:1029-1039.

Moreno-Opo, R., A. Margalida, F. García, Á. Arredondo, C. Rodríguez, and L. M. González. 2012. Linking sanitary and ecological requirements in the management of avian scavengers: effectiveness of fencing against mammals in supplementary feeding sites. Biodiversity and Conservation 21:1673-1685.

Nelson, J. L., B. L. Cypher, C. D. Bjurlin, and S. Creel. 2007. Effects of habitat on competition between kit foxes and coyotes. Journal of Wildlife Management 71:1467-1475.

O'Brien, C. S., R. B. Waddell, S. S. Rosenstock, and M. J. Rabe. 2006. Wildlife use of water catchments in southwestern Arizona. Wildlife Society Bulletin 34:582-591.

O'Farrell, T. P. 1999. Kit Fox. Pages 422-431 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Queen's Printer for Ontario, Ontario.

Orams, M. B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. Tourism Management 23:281-293.

Owen-Smith, N. 1996. Ecological guidelines for watering points in extensive protected areas. South African Journal of Wildlife Research 26:107-112.

Putman, R. J., and B. W. Staines. 2004. Supplementary winter feeding of wild red deer Cervus elaphus in Europe and North America: justifications, feeding practice and effectiveness. Mammal Review 34:285-306.

R Development Core Team. 2011. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, ISBN 3-900051-07-0. http://www.R-project.org.

Rautenstrauch, K. R., and P. R. Krausman. 1989. Influence of water availability and rainfall on movements of desert mule deer. Journal of Mammalogy 70:197-201.

Rosenstock, S. S., W. B. Ballard, and J. C. Devos Jr. 1999. Viewpoint: benefits and impacts of wildlife water developments. Journal of Range Management 52:302-311.

Simpson, N. S., K. M. Stewart, and V. C. Bleich. 2011. What have we learned about water developments for wildlife? Not enough! California Fish and Game 97:190-209.

Springer, J. T. 1982. Movement patterns of coyotes in south central Washington. Journal of Wildlife Management 46:191-200.

Vallentine, J. F. 1980. Range development and improvements. Second edition. Brigham Young University Press, Provo.

Warrick, G. D., and B. L. Cypher. 1998. Factors affecting the spatial distribution of San Joaquin kit foxes. Journal of Wildlife Management 62:707-717.

Warrick, G. D., J. H. Scrivner, and T. P. O'Farrell. 1999. Demographic responses of kit foxes to supplemental feeding. Southwestern Naturalist 44:367-374.

White, P. J., K. Ralls, and R. A. Garrott. 1994. Coyote - kit fox interactions as revealed by telemetry. Canadian Journal of Zoology 72:1831-1836.

White, P. J., K. Ralls, and C. A. V. White. 1995. Overlap in habitat and food use between coyotes and San Joaquin kit foxes. Southwestern Naturalist 40:342-349.

White, P. J., C. A. V. White, and K. Ralls. 1996. Functional and numerical responses of kit foxes to a short-term decline in mammalian prey. Journal of Mammalogy 77:370-376.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentis-Hall, New Jersey.

Table 1. Distances from scent stations to nearest known source of free water in wet and dry areas. We collected data from 2011 to 2012 in the Great Basin and Mojave Deserts, Utah, USA.

		Stations in wet areas		Stations in dry areas	
Study area	Year	Mean distance km (±SE)	*N*	Mean distance km (±SE)	*N*
Great Basin	2011	1.25 (±0.18)	16	3.71 (±0.38)	16
	2012	1.31 (±0.12)	20	3.87 (±0.31)	19
Mojave	2011	0.77 (±0.11)	18	3.20 (±0.33)	14
	2012	0.62 (±0.11)	21	3.32 (±0.28)	18

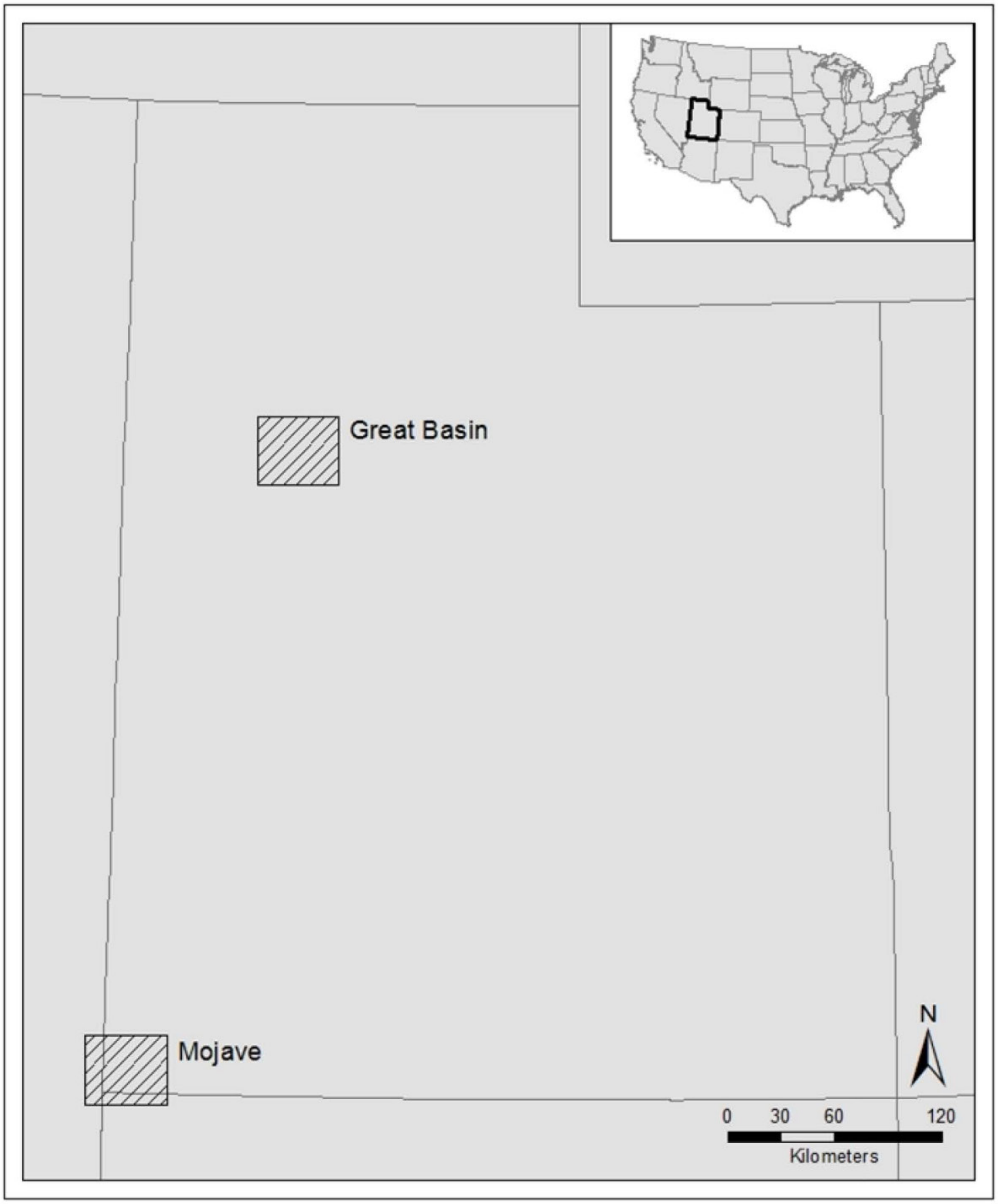

Figure 1. Locations of study areas in the Great Basin and Mojave Deserts, USA.

Figure 2. Photo captures of canids from infrared-triggered cameras. Clockwise from top left: kit fox (*Vulpes macrotis*) at a scent station, coyote (*Canis latrans*) at a scent station, coyote at a water development, and kit fox at a water development. Data were collected in the Great Basin and Mojave Deserts, USA, 2011 to 2012.

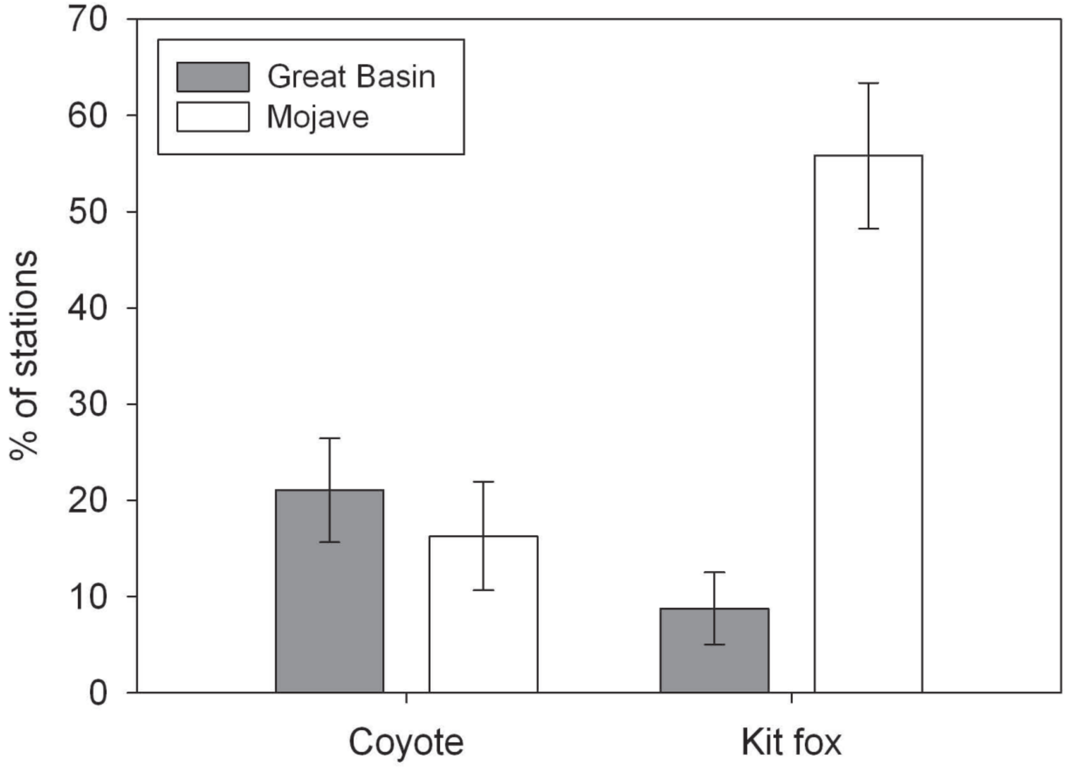

Figure 3. Overall proportions (±SE) of scent stations visited by canids. Data were collected on coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) in the Great Basin and Mojave Deserts, USA, 2011 to 2012.

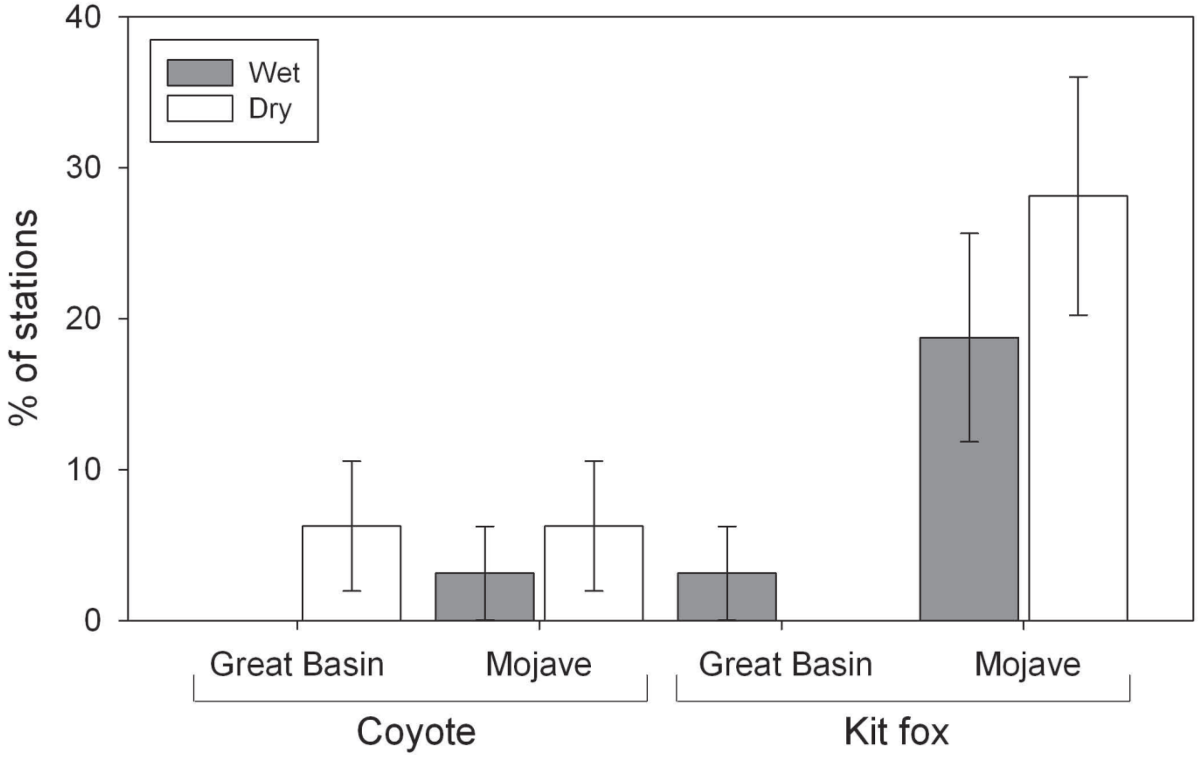

Figure 4. Proportions (±SE) of scent stations visited by canids in wet and dry areas in 2011. Stations in wet areas were ≤ 2 km from free water (mean = 1.01 km) whereas stations in dry areas were ≥ 2 km from free water (mean = 3.46 km). Data were collected on coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) in the Great Basin and Mojave Deserts, USA.

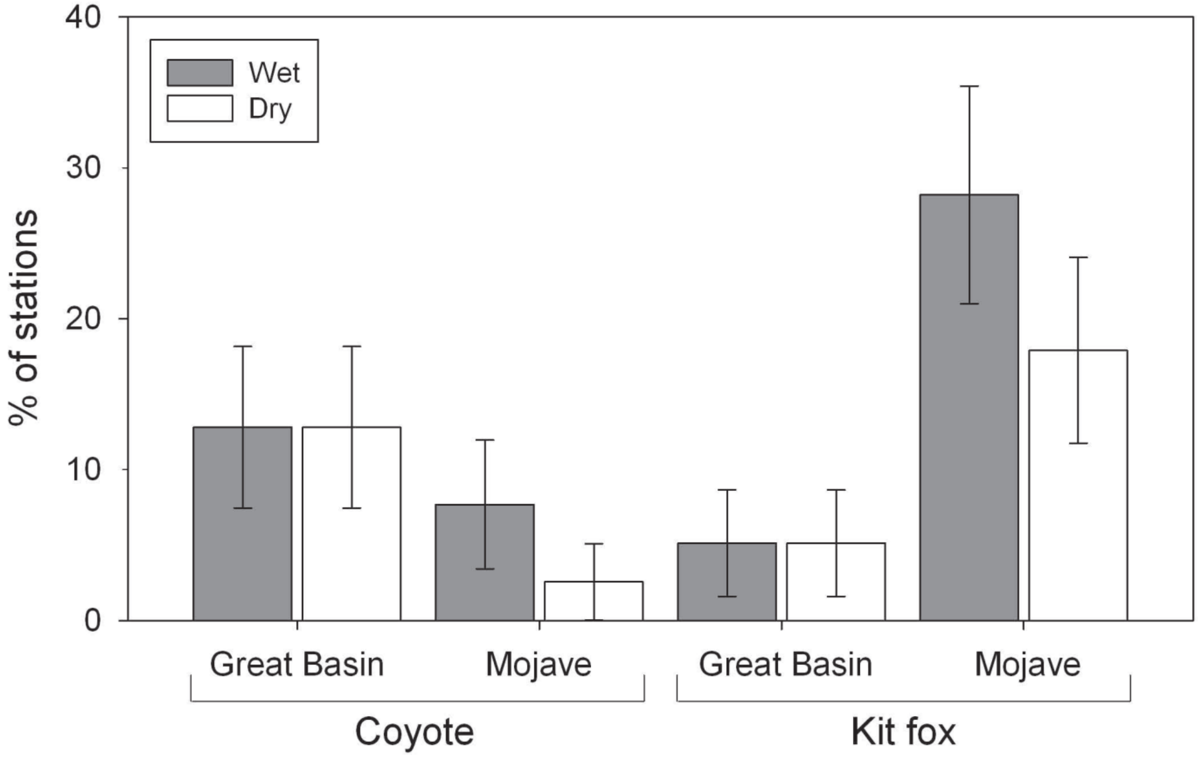

Figure 5. Proportions (±SE) of scent stations visited by canids in wet and dry areas in 2012. Stations in wet areas were ≤ 2 km from free water (mean = 0.97 km) whereas stations in dry areas were ≥ 2 km from free water (mean = 3.59 km). Data were collected on coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) in the Great Basin and Mojave Deserts, USA.

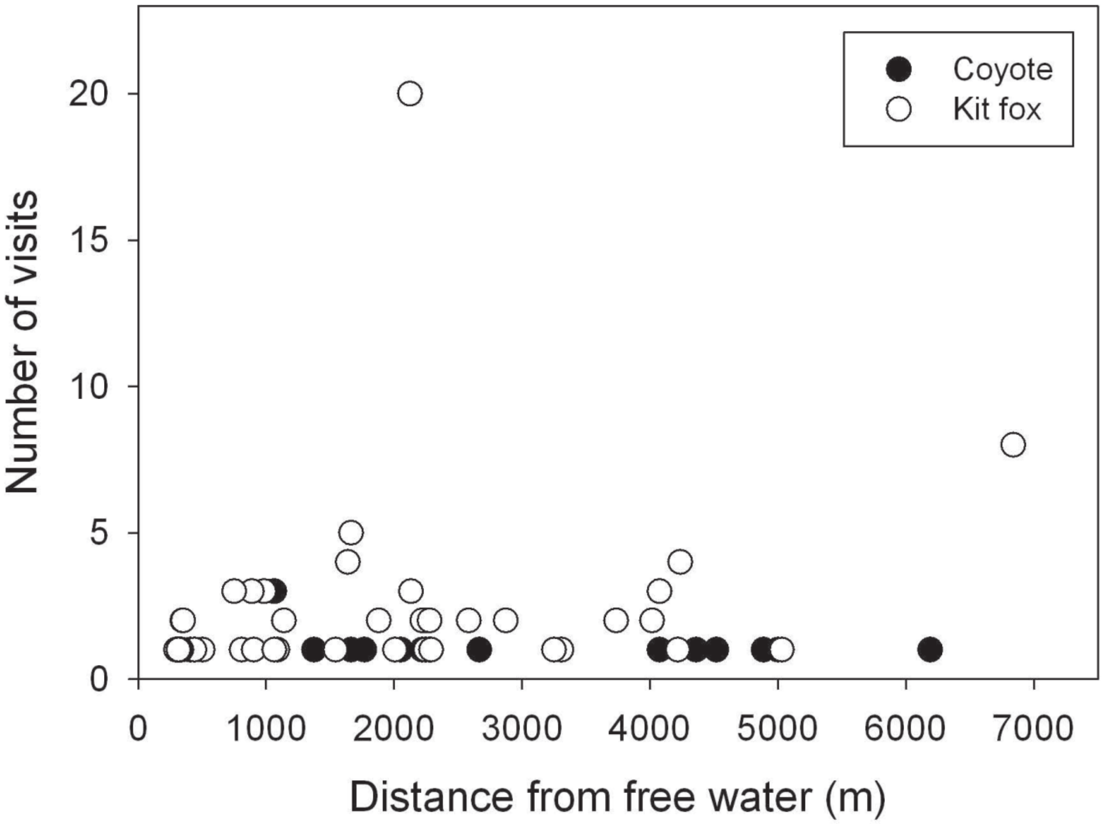

Figure 6. Visitation by canids to scent stations in relation to distance from free water. We defined a visit as all photo captures of a species occurring within 30 min. Data were collected on coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) in the Great Basin and Mojave Deserts, USA, 2011 to 2012.

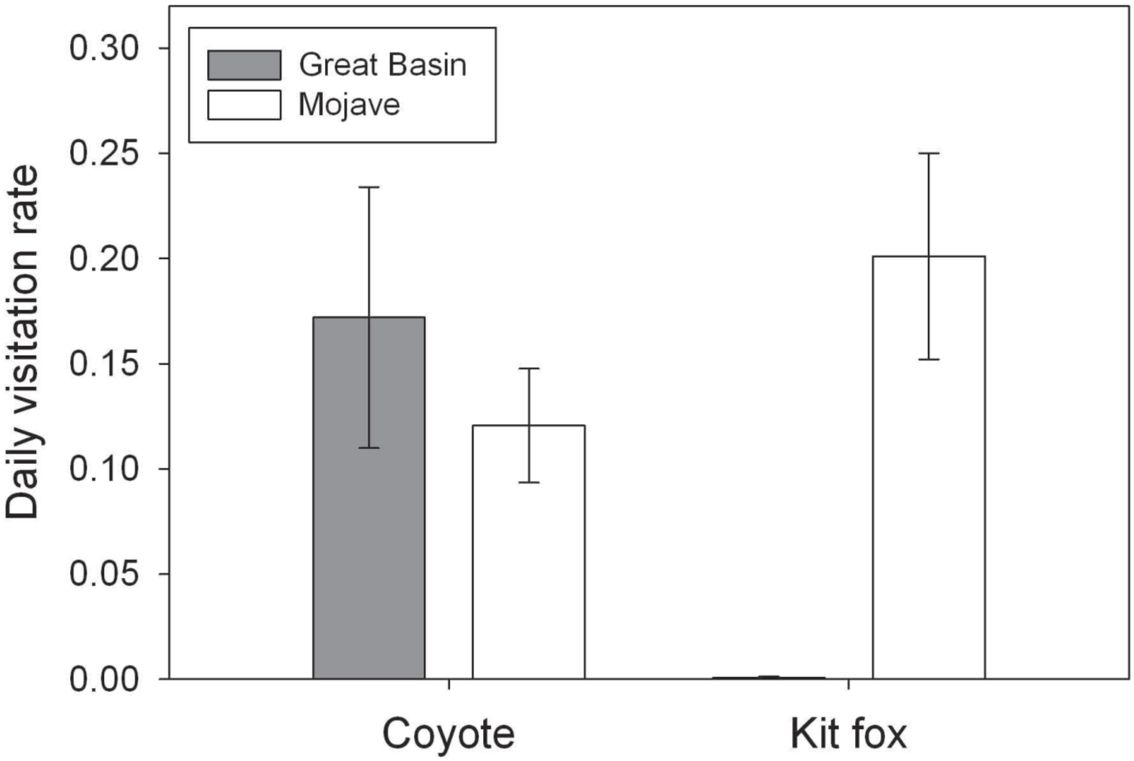

Figure 7. Mean daily visitation rates (±SE) of canids to sources of free water. We defined daily visitation rate as the number of species visits / the number of operable camera trap days per water source. Data were collected on coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) in the Great Basin and Mojave Deserts, USA, 2010 to 2012.

CHAPTER 2

VIGILANCE OF KIT FOXES AT WATER SOURCES: A TEST OF COMPETING HYPOTHESES FOR A SOLITARY CARNIVORE SUBJECT TO PREDATION

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 (PPH) proposes that prey increase vigilance where there is evidence of predators. The visibility-vigilance hypothesis (VVH) suggests that prey increase vigilance where visibility is obstructed. The refuge-vigilance hypothesis (RVH) 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 RVH 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 PVH and VVH 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.

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 (PVH) 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 (Hauser and Caffrey 1994, Zuberbuhler et al. 1997, Jones 1998, Laundré et al. 2001, Wolff and Van Horn 2003, Rainey et al. 2004, Adams et al. 2006, Parsons and Blumstein 2010). The visibility-vigilance hypothesis (VVH) 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 (Underwood 1982, Metcalfe 1984, Goldsmith 1990, Martella et al. 1995, Arenz and Leger 1997, Whittingham et al. 2004, Hernández et al. 2005, Bednekoff and Blumstein 2009, Barri et al. 2012). Alternatively, the refuge-vigilance hypothesis (RVH) proposes that prey may perceive areas with low visibility (greater cover) as refuges (Lima et al. 1987, Lima 1990, Kotler et al. 2002) 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 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 (Creel and Creel 1996, Kitchen et al. 1999, Brawata and Neeman 2011). 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 (Fortin et al. 2004, Baker et al. 2011). 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 (Valeix et al. 2010, Brawata and Neeman 2011). 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 (PVH; 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 (VVH; Burger 2001). Alternatively, if concealing cover provides refuge (RVH; Lima et al. 1987), we expect vigilance to decrease at water sources where visibility is obstructed.

METHODS

Study area

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 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.

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 d per sample) and each water source was sampled ≥ 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, California). 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 to 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 ≥ 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 ≥ 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.

Predator data

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

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).

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 ΔAICc 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 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 (ω_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 (Burnham and Anderson 2002, Anderson 2008, Arnold 2010). 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 2011).

RESULTS

In 4,222 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 2,116 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 (*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 ΔAICc 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 ΔAICc 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, ΔAICc = 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 (Burnham and Anderson 2002, Anderson 2008, Arnold 2010). 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).

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 RVH (Lima et al. 1987, Lima 1990, Kotler et al. 2002) 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 demonstrated decreased vigilance under cover (reduced visibility) include baboons (*Papio cynocephalus ursinus*) (Cowlishaw 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 (Kotler et al. 1991, Embar et al. 2011). 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 (Tchabovsky et al. 2001, Boinski et al. 2003). 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, Moehrenschlager 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 PVH 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^2) than that of northwestern Zimbabwe (0.004 water sources/km^2) 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 PVH 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 (Pusenius and Ostfeld 2002, Orrock et al. 2004, Fanson 2010). 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 RVH 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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LITERATURE CITED

Adams, J. L., K. W. Camelio, M. J. Orique, and D. T. Blumstein. 2006. Does information of predators influence general wariness? Behavioral Ecology and Sociobiology 60:742-747.

Anderson, D. R. 2008. Model-based inference in the life sciences: a primer on evidence. Springer, New York.

Arenz, C. L., and D. W. Leger. 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. Journal of Wildlife Management 74:1175-1178.

Baker, D. J., R. A. Stillman, S. L. Smart, J. M. Bullock, and K. J. Norris. 2011. Are the costs of routine vigilance avoided by granivorous foragers? Functional Ecology 25:617-627.

Barri, F. R., N. Roldan, J. L. Navarro, and M. B. Martella. 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., and D. T. Blumstein. 2009. Peripheral obstructions influence marmot vigilance: integrating observational and experimental results. Behavioral Ecology 20:1111-1117.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76:1075-1085.

Boinski, S., L. Kauffman, A. Westoll, C. M. Stickler, S. Cropp, and E. Ehmke. 2003. Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). Behaviour 140:1421-1467.

Brawata, R. L., and T. Neeman. 2011. Is water the key? Dingo management, intraguild interactions and predator distribution around water points in arid Australia. Wildlife Research 38:426-436.

Bridges, A. S., and A. J. Noss. 2011. Behavior and activity patterns. Pages 57-69 *in* A. F. O'Connell, J. D. Nichols, and K. U. Karanth, editors. 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 Bulletin 104:357-359.

_____. 2001. Visibility, group size, vigilance, and drinking behavior in coati (*Nasua narica*) and white-faced capuchins (*Cebus capucinus*): experimental evidence. Acta Ethologica 3:111-119.

Burnham, K. P., and D. A. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. second edition. Springer, New York.

Caro, T. M., and C. J. Stoner. 2003. The potential for interspecific competition among African carnivores. Biological Conservation 110:67-75.

Carpenter, J., C. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806-1814.

Clark, H. O., Jr. 2007. Hypothetical relationships between the San Joaquin kit fox, California grizzly bear, and gray wolf on the Pre-European California landscape. Endangered Species Update 24:14-19.

Coonan, T. J., C. A. Schwemm, G. W. Roemer, D. K. Garcelon, and L. Munson. 2005. Decline of an island fox subspecies to near extinction. Southwestern Naturalist 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., and N. M. Creel. 1996. Limitation of African wild dogs by competition with larger carnivores. Conservation Biology 10:526-538.

Cypher, B. L., G. D. Warrick, M. R. M. Otten, T. P. O'Farrell, W. H. Berry, C. E. Harris, T. T. Kato, P. M. McCue, J. H. Scrivner, and B. W. Zoellick. 2000. Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. Wildlife Monographs 145:1-43.

de Boer, W. F., M. J. P. Vis, H. J. de Knegt, C. Rowles, E. M. Kohi, F. van Langevelde, M. Peel, Y. Pretorius, A. K. Skidmore, and R. Slotow. 2010. Spatial distribution of lion kills determined by the water dependency of prey species. Journal of Mammalogy 91:1280-1286.

Egoscue, H. J. 1956. Preliminary studies of the kit fox in Utah. Journal of Mammalogy 37:351-357.

_____. 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. Biological Review 64:13-33.

Embar, K., B. P. Kotler, and S. Mukherjee. 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*). Northeastern Naturalist 17:19-28.

Fortin, D., M. S. Boyce, E. H. Merrill, and J. M. Fryxell. 2004. Foraging costs of vigilance in large mammalian herbivores. Oikos 107:172-180.

Frank, L. G., and R. Woodroffe. 2001. Behaviour of carnivores in exploited and controlled populations. Pages 419-442 *in* J. L. Gittleman, S. M. Funk, D. W. Macdonald, and R. K. Wayne, editors. Carnivore Conservation. Cambridge University Press, London.

Goldsmith, A. E. 1990. Vigilance behavior of pronghorns in different habitats. Journal of Mammalogy 71:460-462.

Griesser, M., and M. Nystrand. 2009. Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. Behavioral Ecology 20:709-715.

Hannon, M. J., S. H. Jenkins, R. L. Crabtree, and A. K. Swanson. 2006. Visibility and vigilance: behavior and population ecology of Uinta ground squirrels (*Spermophilus armatus*) in different habitats. Journal of Mammalogy 87:287-295.

Hauser, M. D., and C. Caffrey. 1994. Anti-predator response to raptor calls in wild crows, *Corvus brachyrhynchos hesperis*. Animal Behaviour 48:1469-1471.

Hernández, L., J. W. Laundré, and M. Gurung. 2005. Use of camera traps to measure predation risk in a puma-mule deer system. Wildlife Society Bulletin 33:353-358.

Jones, M. E. 1998. The function of vigilance in sympatric marsupial carnivores: the eastern quoll and the Tasmanian devil. Animal Behaviour 56:1279-1284.

Kitchen, A. M., E. M. Gese, and E. R. Schauster. 1999. Resource partitioning between coyotes and swift foxes: space, time, and diet. Canadian Journal of Zoology 77:1645-1656.

Kotler, B. P., J. S. Brown, S. R. X. Dall, S. Gresser, D. Ganey, and A. Bouskila. 2002. Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. Evolutionary Ecology Research 4:495-518.

Kotler, B. P., J. S. Brown, and O. Hasson. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249-2260.

Kozlowski, A. J., E. M. Gese, and W. M. Arjo. 2008. Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin Desert of western Utah. American Midland Naturalist 160:191-208.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. Canadian Journal of Zoology 79:1401-1409.

Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal 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., K. L. Wiebe, and L. M. Dill. 1987. Protective cover and the use of space by finches: is closer better? Oikos 50:225-230.

Martella, M. B., D. Renison, and J. L. Navarro. 1995. Vigilance in the greater rhea: effects of vegetation height and group size. Journal of Field Ornithology 66:215-220.

Mech, L. D. 1974. *Canis lupus*. Mammalian Species 37:1-6.

Metcalfe, N. B. 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? Animal Behaviour 32:981-985.

Michalski, F., and C. A. Peres. 2007. Disturbance-mediated mammal persistence and abundance-area relationships in Amazonian forest fragments. Conservation Biology 21:1626-1640.

Moehrenschlager, A., R. List, and D. W. Macdonald. 2007. Escaping intraguild predation: Mexican kit foxes survive while coyotes and golden eagles kill Canadian swift foxes. Journal of Mammalogy 88:1029-1039.

Nersesian, C. L., P. B. Banks, and C. McArthur. 2012. Behavioural responses to indirect and direct predator cues by a mammalian herbivore, the common brushtail possum. Behavioral Ecology and Sociobiology 66:47-55.

Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behavioral Ecology 15:433-437.

Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153:492-508.

Parsons, M. H., and D. T. Blumstein. 2010. Feeling vulnerable? Indirect risk cues differently influence how two marsupials respond to novel dingo urine. Ethology 116:972-980.

Periquet, S., M. Valeix, A. J. Loveridge, H. Madzikanda, D. W. Macdonald, and H. Fritz. 2010. Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. Animal Behaviour 79:665-671.

Pusenius, J., and R. S. Ostfeld. 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 Oecologica 11:801-818.

R Development Core Team. 2011. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, ISBN 3-900051-07-0. http://www.R-project.org.

Rainey, H. J., K. Zuberbühler, and P. J. B. Slater. 2004. Hornbills can distinguish between primate alarm calls. Proceedings of the Royal Society Biological Sciences Series B 271:755-759.

Robel, R. J., J. N. Briggs, A. D. Dayton, and L. C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Range Management 23:295-297.

Switalski, T. A. 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. Canadian Journal of Zoology 81:985-993.

Symonds, M., and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13-21.

Tchabovsky, A. V., B. Krasnov, I. S. Khokhlova, and G. I. Shenbrot. 2001. The effect of vegetation cover on vigilance and foraging tactics in the fat sand rat *Psammomys obesus*. Journal of Ethology 19:105-113.

Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. Behaviour 79:81-107.

Valeix, M., H. Fritz, A. J. Loveridge, Z. Davidson, J. Hunt, F. Murindagomo, and D. W. Macdonald. 2009. Does the risk of encountering lions influence African herbivore behaviour at waterholes? Behavioral Ecology and Sociobiology 63:1483-1494.

Valeix, M., A. Loveridge, Z. Davidson, H. Madzikanda, H. Fritz, and D. Macdonald. 2010. How key habitat features influence large terrestrial carnivore movements: waterholes and

African lions in a semi-arid savanna of north-western Zimbabwe. Landscape Ecology 25:337-351.

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457-464.

Whittingham, M. J., S. J. Butler, J. L. Quinn, and W. Cresswell. 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., and T. Van Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. Canadian Journal of Zoology 81:266-271.

Zoellick, B. W., C. E. Harris, B. T. Kelly, T. P. O'Farrell, T. T. Kato, and M. E. Koopman. 2002. Movements and home ranges of San Joaquin kit foxes (*Vulpes macrotis mutica*) relative to oil-field development. Western North American Naturalist 62:151-159.

Zuberbuhler, K., R. Noe, and R. M. Seyfarth. 1997. Diana monkey long-distance calls: messages for conspecifics and predators. Animal Behaviour 53:589-604.

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 (±SE) for visibility variables and mean frequency (±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
Visibility		
Structural roof cover[a]	0.41	0.11
Viewshed 25m radius[b]	0.00	0.00
Viewshed 50m radius	0.07	0.02
Viewshed 75m radius	0.18	0.02
Viewshed 100m radius	0.25	0.03
Viewshed 125m radius	0.35	0.03
Viewshed 150m radius	0.42	0.03
Vegetation height 25m radius[c]	0.34	0.04
Vegetation height 50m radius	0.62	0.05
Vegetation height 75m radius	0.75	0.04
Vegetation height 100m radius	0.79	0.04
Vegetation height 125m radius	0.83	0.04
Vegetation height 150m radius	0.86	0.04
Predators[d]		
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

[a] Presence (1) or absence (0) of roof cover
[b] Proportion of pixels visible around each water source
[c] Height of vegetation measured in all four cardinal directions around each water source
[d] Frequency of visitation based on photo-captures from infrared-triggered cameras

Table 2. AICc, ΔAICc, log likelihood (LL), number of parameters (*K*), and model weights (ω_i) for models of kit fox vigilance as a function of predator and visibility explanatory variables. We advanced competing models (within two ΔAICc values of the top model) to stage two of analysis. Vigilance behavior data were collected on kit foxes (*Vulpes macrotis*) in Utah, USA from May 2010 to January 2012.

Model	AICc	ΔAICc	LL	*K*	ω_i
Visibility models					
Structural roof cover	-30.64	0.00	18.63	2	0.76
Vegetation height 125m	-24.85	5.79	15.74	2	0.04
Vegetation height 100m	-24.10	6.54	15.36	2	0.03
Vegetation height 50m	-23.70	6.94	15.16	2	0.02
Viewshed 50m	-23.49	7.15	15.06	2	0.02
Viewshed 150m	-23.45	7.19	15.04	2	0.02
Viewshed 100m	-23.22	7.42	14.92	2	0.02
Vegetation height 150m	-23.09	7.55	14.86	2	0.02
Vegetation height 25m	-23.04	7.60	14.83	2	0.02
Viewshed 125m	-23.00	7.64	14.82	2	0.02
Vegetation height 75m	-22.85	7.79	14.74	2	0.02
Viewshed 75m	-22.69	7.95	14.66	2	0.01
Predator models					
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

Table 3. AICc, ΔAICc, log likelihood (LL), number of parameters (*K*), and model weights (ω_i) for combined (stage two) models of kit fox vigilance as a function of predator and visibility explanatory variables. Vigilance behavior data were collected on kit foxes (*Vulpes macrotis*) in Utah, USA from May 2010 to January 2012.

Model	AICc	ΔAICc	LL	*K*	ω_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

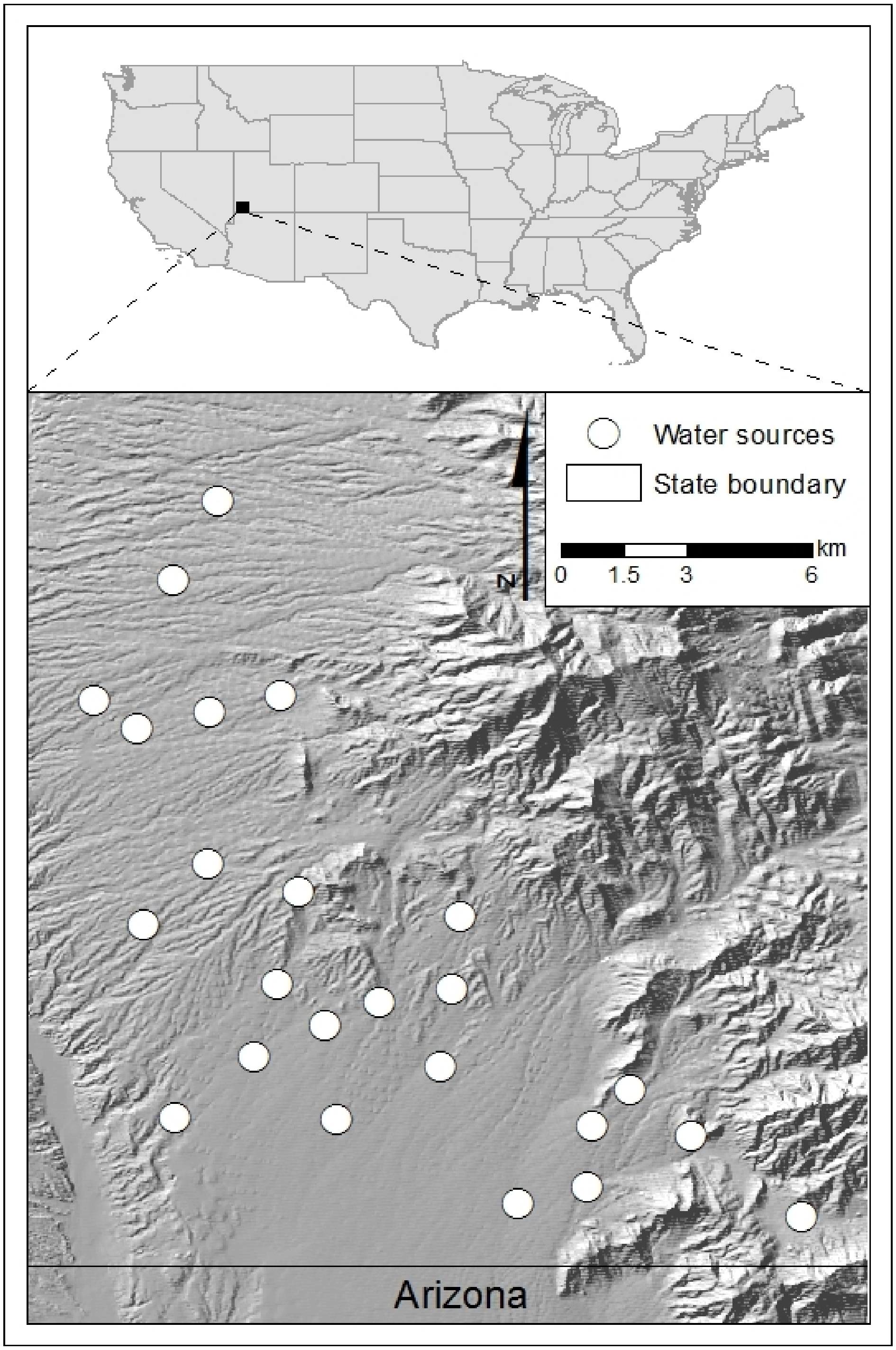

Figure 1. Study area in Mojave Desert, Utah, USA where we evaluated kit fox (*Vulpes macrotis*) vigilance from May 2010 to January 2012. White circles represent locations of water sources used by kit foxes during our sampling period.

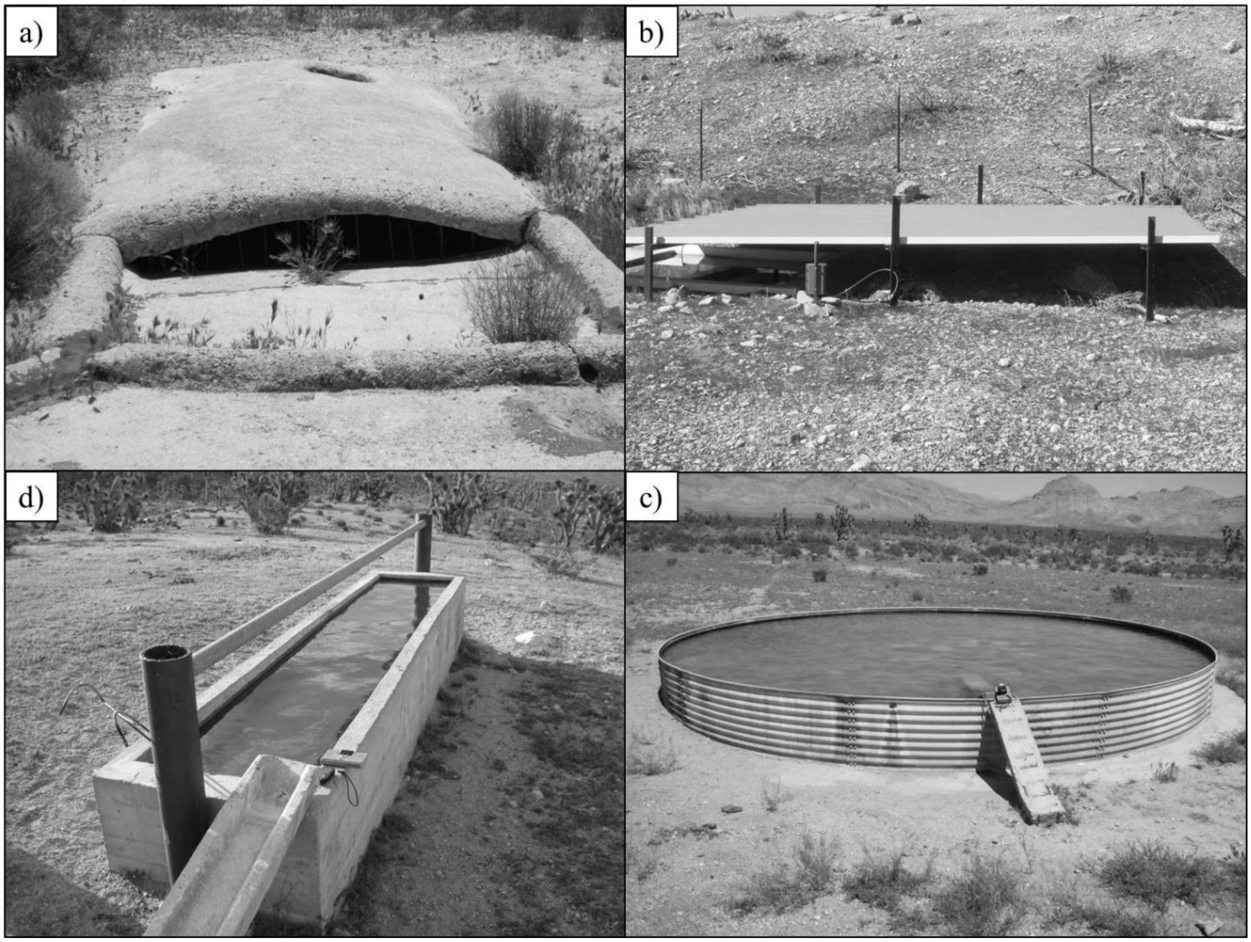

Figure 2. Different types of water sources used by kit foxes (*Vulpes macrotis*) in Utah, USA between May 2010 and January 2012. a) concrete earthen tank, b) fiberglass catchment with metal roof, c) metal water tank for livestock, and d) concrete drinking trough for livestock.

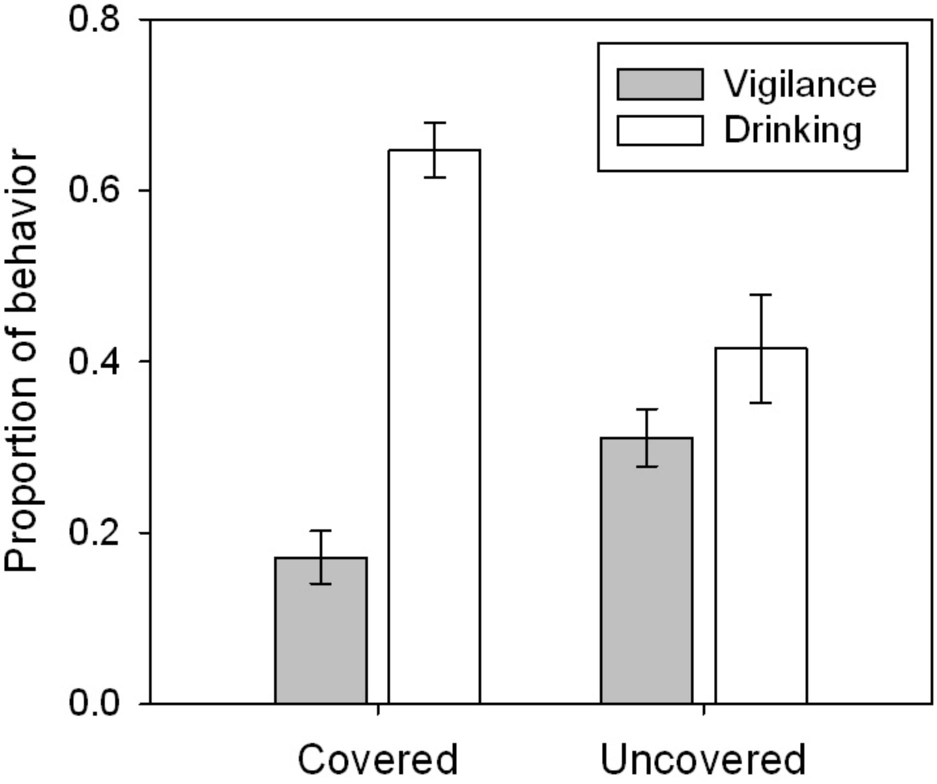

Figure 3. Proportions (±SE) of vigilance behavior and drinking by kit foxes (*Vulpes macrotis*) at water sources with (N = 9) and without (N = 13) structural roof cover from data collected in Utah, USA from May 2010 to January 2012.