The influence of predators, competitors, and habitat on the use of water sources by a small desert carnivore

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Abstract. Free water can influence the ecology of desert species. While the use of free water is influenced by physiological factors (e.g., species-specific water requirements, moisture in forage, temperature), non-physiological factors, such as habitat characteristics and interspecific interactions, are also important. In fact, for species of concern, interspecific interactions and habitat can be important factors influencing their spatial and temporal use of the landscape and its resources. The kit fox (Vulpes macrotis) is a small carnivore considered to be a species of concern over much of its range, and two of the most important conservation challenges it faces are related to (1) habitat and (2) predation/competition by intraguild species. Our objective was to determine the influence of habitat characteristics, predators (bobcats [Lynx rufus], coyotes [Canis latrans]), and potential competitors (badgers [Taxidea taxus], gray foxes [Urocyon cinereoargenteus]) on the use of water by kit foxes. From June to September 2010–2012, we used remote cameras to monitor carnivores at 63 water sources in the Mojave Desert. We used zero-inflated mixed-effects models and a two-stage model selection analysis to evaluate the influence of habitat, predators, and competitors on spatial visits to water by kit foxes. We also assessed temporal avoidance of intraguild predators and competitors by kit foxes at water sources using a coefficient of overlap. We found that visual obscurity, overhead canopy cover, badgers, and coyotes influenced spatial visits of kit foxes. In addition, kit foxes exhibited strong temporal overlap with badgers and bobcats, moderate temporal overlap with gray foxes, and weak temporal overlap with coyotes. Taken together, our study demonstrates that the spatial and temporal use of water sources by kit foxes is dynamic, depending on habitat characteristics and the activity of intraguild predators and competitors.

Key words: badger; bobcat; camera; coyote; gray fox; intraguild predation; kit fox.

INTRODUCTION

Free water can have a disproportionate influence on patterns of desert life relative to its scarce abundance (Noy-Meir 1973). Free water is generally most scarce during hot and dry times, when it is also in greatest physiological demand by many desert species. This high demand during physiologically challenging times often leads to water sources being focal points of activity on desert landscapes for multiple species (Weir and Davidson 1965, DeStefano et al. 2000, O’Brien et al. 2006). While the use of free water is influenced by physiological factors (e.g., species-specific water requirements, moisture in forage, temperature), other factors, such as interspecific interactions and habitat characteristics, are also important. For example, the communal use of
water sources can lead to interspecific interactions, such as competition (Valeix et al. 2007, Atwood et al. 2011, Hall et al. 2018) and predation (Valeix et al. 2009, 2010, de Boer et al. 2010). Understanding how habitat characteristics and interspecific interactions influence the spatial and temporal use of limiting resources is imperative to conservation efforts, particularly for species of concern.

The kit fox (Vulpes macrotis) is a small, desert carnivore considered to be a species of concern (Kluever et al. 2013) for two reasons, the first of which is related to habitat specialization (Arjo et al. 2007). Kit foxes are known to inhabit a narrow set of habitat characteristics covering three broad categories including topography, soil, and vegetation. Kit foxes occupy (1) areas of relatively low elevation (e.g., valley bottoms) with little topographic relief and ruggedness (McGrew 1979, Arjo et al. 2003), (2) areas with loose soils suitable for burrowing as they rely on dens for reproduction, thermoregulation, and cover (Egoscue 1956, 1962), and (3) open areas with sparse vegetation thought to maximize visibility and perception of potential threats (Egoscue 1956, McGrew 1979). While habitat specialization can be an effective strategy, it can leave populations vulnerable to changes in the habitat, as apparent with kit foxes throughout parts of their range (Arjo et al. 2007).

The second reason for which kit foxes are a species of concern is due to competition and predation from larger, more competitively dominant species of the carnivore guild (Moehrenschlager et al. 2007, Nelson et al. 2007, Kozlowski et al. 2008). Because kit foxes are at or near the bottom of the dominance hierarchy in desert carnivore guilds, they often use the landscape dynamically to maximize foraging opportunities while minimizing hazardous interactions with other carnivores. To minimize the risk of potentially lethal interactions, kit foxes employ strategies to avoid risky foraging locations where other carnivores are most active (Kozlowski et al. 2008, 2012, Robinson et al. 2014, Lonsinger et al. 2017). However, while there is information about the partitioning of foraging locations between kit foxes and their intraguild competitors and predators, we have a poor understanding about partitioning of water sources. Because water sources are scarce, geographically fixed, and communal in nature (known locations to predators/competitors; DeStefano et al. 2000, Valeix et al. 2010, Atwood et al. 2011), it may be difficult for kit foxes to successfully partition water sources with intraguild competitors and predators (Edwards et al. 2015). Furthermore, it is likely that any partitioning would be related to the habitat characteristics (Lonsinger et al. 2017) at individual water sources.

Until relatively recently, it was presumed that kit foxes rarely used water for drinking. This presumption was based on kit foxes denning far from known water sources (Egoscue 1956), drinking seldom in the wild (O’Farrell 1999, O’Brien et al. 2006), and acquiring metabolic and preformed water (Golightly Jr. and Ohmart 1984). However, kit foxes not only frequently drank from water sources in the Mojave Desert, but they were the most commonly photographed carnivore at water sources (Hall et al. 2013a, b). Similar to other arid-adapted species (e.g., Sonoran pronghorn [Antilocapra americana sonoriensis]), drinking water may play a larger role in the ecology of kit foxes during times of physiological stress (particularly in hot deserts) than previously understood (Morgart et al. 2005). Despite the frequent use of water by kit foxes previously observed in the Mojave Desert, our understanding of the influence of habitat, competitors, and predators on the use of water by these small carnivores is lacking.

Our objective was to determine the influence of predators, competitors, and habitat characteristics on the use of water sources by a small carnivore species in a hot and arid desert. To achieve our objective, we used remote cameras to monitor visitation of kit foxes and their predators and competitors to water sources in the Mojave Desert from 2010 to 2012 and we conducted habitat surveys at these water sources. If intraguild predators and competitors were the primary influences on visitation to water by kit foxes, we predicted that kit foxes would avoid locations and times (i.e., strong negative association between visits of kit foxes and intraguild predators and competitors) where these species were most active. If habitat characteristics were the primary influence on the spatial use of water by kit foxes, we predicted that these features would be associated with visitation to water by kit foxes regardless of the presence of intraguild predators and competitors. If the use of water by kit foxes was
influenced by a combination of habitat characteristics, predators, and competitors, we expected that each would exhibit the predicted associations with visits to water by kit foxes as described above. Understanding the influences on the use of limiting resources, such as water, by species of concern can better inform conservation efforts and management of these species and the resources that they use.

**METHODS**

**Study area**

The Mojave Desert study area consisted of 400 km$^2$ of public land managed by the Bureau of Land Management located in extreme southwestern Utah (Fig. 1). Common vegetation at lower elevations included creosote (*Larrea tridentata*), Joshua tree (*Yucca brevifolia*), blackbrush (*Coleogyne ramosissima*), and red brome (*Bromus rubens*). Along the foothills, the vegetation primarily consisted of sagebrush (*Artemisia* spp.) and juniper (*Juniperus osteosperma*), transitioning to pinyon pine (*Pinus edulis*) at higher elevations. Elevations across the Mojave study area ranged from approximately 800 to 2000 m. Annual mean air temperatures were 17°C, with a low of 1°C in December and February, and a high of 37°C in July and August. Annual mean precipitation was

![Fig. 1. Distribution of water sources with visits by different species of carnivores. We monitored water sources with infrared-triggered cameras in the Mojave Desert in southwestern Utah, USA, from 2010 to 2012.](image-url)
230 mm with the majority occurring in the winter months (PRISM Climate Group 2019).

**Data collection**

We monitored all known water sources in our study area to evaluate the use of water by kit foxes and other carnivores during the hot and dry months (June–September) of 2010–2012 (Fig. 1). This time frame allowed us to focus on water when it was likely in greatest demand, while also avoiding the potential exclusion by livestock at some of the water sources (livestock in our study area was grazed in the fall through spring). We identified 63 permanent water sources consisting of 33 water developments for wildlife (i.e., guzzlers), 17 water troughs/tanks for livestock, 11 natural springs, and two man-made ponds. We selected water sources to monitor using a clustered sampling scheme within a geographic information system in ArcGIS (ArcMap, version 10; Environmental Systems Research Institute, Redlands, California, USA). In this scheme, we first created a random point in our study area and then located the nearest known water source to that random point. From that water source, we monitored as many neighboring water sources as possible with the number of cameras we had available (range: 6–15 cameras per cluster). For each cluster sample, we monitored water sources for approximately two-week periods with Reconyx (PC900 HyperFire model; Holmen, Wisconsin, USA) and Cuddeback (Attack IR model; De Pere, Wisconsin, USA) cameras. We attached cameras to metal posts and placed them approximately 2 m from water sources. Cameras were programmed to trigger upon both heat and motion and take one photograph every 30 s. We used date and time stamps associated with photographs from the cameras to generate visits of carnivores at water sources. We defined two separate visits as two consecutive images of a single species separated by at least 30 min, and we treated visits as independent events (Michalski and Peres 2007, Atwood et al. 2011, Hall et al. 2013b). To determine the influence of intraguild predators and competitors on the use of water sources by kit foxes, we screened photographs for other species of carnivores at water sources. We classified species as predators of kit foxes based on documented evidence of predation from the literature; however, this classification was not intended to imply that predators of kit foxes were solely predators and not also potential competitors. We reserved our classification of competitors to those species that do not have corresponding direct evidence of predation on kit foxes, but exhibit overlap in the use of resources (e.g., prey, habitat). We included the number of visits to water by predators and competitors of kit foxes as a model variable. We also used the timestamps from photographs to determine diel timing of visits to assess whether kit foxes were visiting water sources at different times of the day compared with predators and competitors.

To determine the influence of habitat characteristics on the occurrence of kit foxes at water sources, we measured several vegetative, visibility, and topographical variables around each water source. We included four different measurements of vegetative cover. First, we classified the primary type of vegetation for each water source as either woodland shrub or creosote using the statewide dominant vegetation layer from the Utah Division of Wildlife Resources (http://gis.utah.gov/data). Second, because nearly two-thirds of our study area has been affected by wildfires over the last two decades (Horn et al. 2012), we used a GIS to categorize water sources as burned or unburned if the water source fell within a burn zone. Third, we estimated cover of vegetation and, fourth, height of vegetation at water sources using the Random T-Square sampling approach along 30-m transects in all cardinal directions (Krebs 1999).

We included eight variables related to site visibility of and access to water sources. We used a Robel pole (Robel et al. 1970) to measure horizontal visual obscurity along transects at 5-, 10-, 15-, 20-, 50-, 75-, and 100-m intervals radiating away from the water source in all four cardinal directions (Hall et al. 2013a). At nearly a third of the water sources that we sampled, there was...
structural roof cover over the water to serve as a rain catchment and to minimize evaporation. Due to the low-profile nature of catchment canopies, these structures often served as vertical obstructions to visibility for species using these water sources, potentially influencing their behaviors (Hall et al. 2013a). Thus, we accounted for this variation by considering water sources as either covered or uncovered.

We also measured four topographical characteristics at water sources. We used ArcGIS to calculate terrain ruggedness around water sources up to 90 m using a 30-m resolution digital elevation model (Sappington et al. 2007, Atwood et al. 2011). We included a surrogate metric of terrain ruggedness by measuring the distance from a water source to the nearest rocky outcrop or cliff. We also recorded the elevation (m) of each water source, since kit foxes typically occur at lower elevations (List and Cypher 2004). Lastly, since kit foxes rely on the year-round use of dens/burrows (White et al. 1995, Moehrenschlager et al. 2007), we included soil type at each water source and considered sandy and loamy soils to be suitable for burrowing (soil layer from the U.S. Department of Agriculture, Natural Resources Conservation Service; http://gis.utah.gov/data).

Statistical analyses

Photo-counts from remote cameras can result in some sites not detecting the focal species, producing data with zero counts. The inability to detect species at all sites is particularly evident for desert carnivores that already occur at relatively low densities. To deal with the issues that arise from excess zeroes in photo-count data, we used generalized linear mixed-effects models with a zero-inflated negative binomial distribution. Zero-inflated models allowed us to simultaneously assess the influence of explanatory variables on photo-counts and the probability of a zero count (Larsen et al. 2011).

We used a two-stage modeling approach (Carpenter et al. 2010, Hall et al. 2013a) to determine the influence of predators, competitors, and habitat characteristics on patterns of water use by kit foxes. In the first stage, we wanted to identify the most informative variables in the habitat category and the predator–competitor category that we could advance to stage 2 of model comparison (i.e., combining top habitat, predator, and competitor models). To help us determine the top models, we first conducted correlation analyses to identify multicollinearity between variables. When explanatory variables were correlated (|r| > 0.3; Atwood et al. 2011), we used the variable that had the lowest Akaike’s information criterion corrected for small samples (AICc) score. We then used our refined subset of variables to create simple models (no more than two fixed effects) in the habitat category and the predator–competitor category and allowed these to compete within their respective categories. In addition, we created weather models including temperature and precipitation variables from study area-wide climate models (PRISM Climate Group 2019) and allowed these models to compete. To account for the variation between camera types, cluster samples (i.e., two-week sample periods where multiple water sources were simultaneously monitored), years, and water sources, we included these variables as random effects in our models. Because we sampled with replacement, water sources were often sampled more than once. By including water source as a random effect, we accounted for the potential dependency between samples. The cluster sample and site (i.e., water source) variables also helped account for any potential lack of independence between neighboring samples due to individual kit foxes visiting more than one water source in a single two-week period. We evaluated top models within categories by assessing ΔAICc scores (Burnham and Anderson 2002) and considered models to be competing if they were within two ΔAICc points of each other. Top models included those that (1) were within two ΔAICc points of the model with the lowest AICc score and (2) exceeded the AICc value of the null model (intercept and random effects only). After the first stage, we advanced the top models to the second stage of model analysis.

In stage 2 of model selection, we combined the top models from all categories. Using the top models, we created all possible combinations of composite models, including additive and interaction terms, and allowed these models to compete. Using ΔAICc scores and model weights, we ranked the top models in order of model support (Burnham and Anderson 2002). We then evaluated both the log-likelihood and AICc values associated with these models to identify whether
certain variables enhanced model fit or were uninformative parameters. We considered parameters to be uninformative when little to no improvement in log-likelihood and AICc values was evident (Burnham and Anderson 2002, Anderson 2008, Arnold 2010). We also evaluated β-estimates from these models to verify whether variables of interest (e.g., habitat characteristics, predator, or competitor activity) behaved in accordance with our predictions. We used the glmmTMB package (Brooks et al. 2017) to run generalized linear mixed models in Program R (R Development Core Team 2015).

To determine whether kit foxes used water sources at different times of the day compared with predators and competitors, we calculated coefficients of temporal overlap using the package overlap in Program R. Overlap uses kernel density estimation and an overlap coefficient, Δ, to determine temporal overlap between species (Linkie and Ridout 2011). The overlap coefficient ranges from 0 to 1, where 0 is indicative of no overlap, >0.8 represents strong overlap, and 1 represents complete overlap of the area under the activity curve (Linkie and Ridout 2011). Because we had a relatively large sample size of visits, we used the Δ4 estimate, which has been recommended for large sample sizes (Linkie and Ridout 2011). We calculated confidence intervals (CIs) using 1000 bootstrap samples. We performed all analyses using Program R (R Development Core Team 2015).

RESULTS

In 3262 camera days from 2010 to 2012, we recorded 2022 independent visits of mammalian carnivores, of which 1242 were of kit foxes (Fig. 2). We detected kit foxes at only 40% of our sampled water sources, which resulted in many of our sites (and resampled sites) with zero visits. We also photographed visits of American badgers (Taxidea taxus), bobcats (Lynx rufus), coyotes (Canis latrans), cougars (Puma concolor), gray foxes (Urocyon cinereoargenteus), northern raccoons (Procyon lotor), striped skunks (Mephitis mephitis), and western spotted skunks (Spilogale gracilis; Fig. 2). We included bobcats and coyotes as intraguild predators (Cypher et al. 2000, Kluever and Gese 2017) of kit foxes and badgers and gray foxes as potential competitors (Long 1973, Fritzell and Haroldson 1982, Clark et al. 2015) in our analyses but did not include the remaining species in analyses as their visits were rare (Fig. 2). We detected focal predators and competitors at water sources where kit foxes were present and absent (Fig. 3).

In stage 1 of our model selection process, we identified top models representing habitat, predators, and competitors. For our habitat variables, visual obscurity at 20 m from the water source and overhead canopy cover were the top competing models (Table 1). For our predator and competitor models, activity of badgers and the combined effect of activity of badgers and coyotes were the top competing models (Table 1). Models containing activity of bobcats or gray foxes were not considered competing models as their ΔAICc values were not within two AICc points of the top model (Table 1). Similarly, temperature or days since rainfall did not outcompete the null model. The following nine habitat variables were not considered for model selection as they were correlated with more informative variables (|r| > 0.3) that performed better: distance to outcrop, elevation, soil type, and visual obscurity measured at 5, 10, 15, 50, 75, and 100 m.
From the results of stage 2 of model selection, we found two top competing models (Table 2). The best model, however, accounted for nearly three times the model weight as the second-best model (Table 2). Both models were similar in that they included visual obscurity at 20 m, overhead canopy cover, activity of badgers, and activity of coyotes; however, the best model included a badger $\times$ coyote interaction term and the second-best model included a canopy cover $\times$ visual obscurity at 20 m interaction term. Coefficients from the best model showed that visual obscurity at 20 m and coyote activity had strong negative associations (CIs did not overlap zero) with visitation to water by kit foxes (Table 3). Overhead canopy cover and the activity of badgers had strong positive associations with kit fox visits to water (Table 3). The badger $\times$ coyote interaction had a strong positive association with kit foxes (Table 3). The coefficients from the other competing model were of the same direction (i.e., positive, negative) as the coefficients of the top model, but the CIs of the estimates for badger, coyote, and canopy cover overlapped zero; the CIs for visual obscurity at 20 m did not overlap zero.

Our temporal overlap analyses revealed differences in diel patterns and temporal overlap between kit foxes and their predators and competitors. Kit foxes, badgers, and bobcats were primarily nocturnal when visiting water sources, whereas coyotes were active at water sources throughout the day with minor peaks at dawn and dusk (Fig. 4). Kit foxes had strong temporal overlap with badgers ($\Delta_t = 0.85, 95\% \text{ CI } \pm 0.03$) and bobcats ($\Delta_t = 0.83, 95\% \text{ CI } \pm 0.05$), moderate temporal overlap with gray foxes ($\Delta_t = 0.76, 95\% \text{ CI } \pm 0.07$), and weak temporal overlap with coyotes ($\Delta_t = 0.51, 95\% \text{ CI } \pm 0.04$; Fig. 4).

**DISCUSSION**

The spatial and temporal use of limiting resources by subordinate species can be complex as they navigate heterogeneous landscapes occupied by intraguild predators and competitors. Our results echo this statement, showing that the spatial and temporal use of water by kit foxes was best explained by a combination of habitat characteristics, predators, and competitors. Variables from our top spatial model (comprising most of the model weight) also exhibited strong associations with visits of kit foxes, further supporting the importance of these variables to the spatial use of water by kit foxes. We also found evidence of temporal avoidance of predators by kit foxes (1) in our temporal overlap analyses; and (2) because we did not detect a single direct encounter between kit foxes and their predators. Combined with our temporal results, our findings provide support that predators and competitors, in addition to habitat characteristics, influenced the use of water by kit foxes.

Badgers were classified as competitors in our analysis and were one of two species in our top spatial models. The spatial and temporal activity of badgers, however, almost completely overlapped the spatial and temporal activity of kit foxes. Our work corroborates previous studies indicating that both badgers and kit foxes can coexist with minimal to no antagonistic interactions (Clark et al. 2015). Badgers were the only species with which we recorded five instances of direct encounters with kit foxes; some of these
encounters were recorded with brief videos as part of another study (Hall et al. 2013a). All these encounters were nonantagonistic and usually depicted a badger drinking at the water source, while a kit fox was in the background seemingly waiting for the water source to become available. One encounter showed a kit fox leaving a water source, and within a few seconds, a badger entered the frame and started drinking; in this encounter, neither species was confrontational toward the other. Despite the apparent overlap in diet and habitat reported for badgers and kit foxes (Long 1973, McGrew 1979), our study did not provide evidence that kit foxes spatially or temporally avoided badgers, suggesting that competition may not be a factor underlying the spatial and temporal use of the landscape by kit foxes. Rather, the positive association between badgers and kit foxes in our study may be the result of one or both species receiving a benefit from the presence of the other species, similar to what has been observed between badgers and coyotes in other studies (Robinson and Cummings 1947, Minta et al. 1992).

Coyotes were the other species in our top spatial models and were classified as predators in our analysis but are also documented competitors of kit foxes (White et al. 1995, Nelson et al. 2007, Kozlowski et al. 2008). In the top model comprising most of the model weight, coyotes

### Table 1. Stage 1 model selection results for zero-inflated negative binomial models of kit fox (*Vulpes macrotis*) visits.

| Model† | K‡ | LL§ | ΔAICc¶ | Weight# |
|--------|----|-----|--------|----------|
| Habitat | | | | |
| Canopy + Robel20 | 9 | −533.53 | 0.00 | 0.53 |
| Robel20 | 8 | −535.55 | 1.88 | 0.21 |
| Rugged + Robel20 | 9 | −535.22 | 3.36 | 0.10 |
| ShrubHeight + Robel20 | 9 | −535.30 | 3.53 | 0.09 |
| ShrubCover + Robel20 | 9 | −535.47 | 3.88 | 0.08 |
| Rugged + Canopy | 9 | −545.45 | 23.83 | 0.00 |
| Rugged + Burn | 9 | −546.19 | 25.31 | 0.00 |
| Canopy | 8 | −547.28 | 25.34 | 0.00 |
| Canopy + ShrubCover | 9 | −546.21 | 25.36 | 0.00 |
| Burn + ShrubHeight | 9 | −546.87 | 26.67 | 0.00 |
| Canopy + ShrubHeight | 9 | −547.15 | 27.22 | 0.00 |
| Burn | 8 | −548.76 | 28.31 | 0.00 |
| Rugged | 8 | −548.83 | 28.44 | 0.00 |
| Rugged + ShrubCover | 9 | −548.07 | 29.08 | 0.00 |
| Rugged + ShrubHeight | 9 | −548.16 | 29.25 | 0.00 |
| Burn + ShrubCover | 9 | −548.47 | 29.88 | 0.00 |
| Null | 7 | −551.23 | 31.11 | 0.00 |
| Predators and competitors | | | | |
| Badger | 8 | −549.74 | 0.00 | 0.22 |
| Coyote + Badger | 9 | −548.77 | 0.20 | 0.20 |
| Null | 7 | −551.23 | 0.85 | 0.14 |

Notes: Models composed of variables from two categories (i.e., habitat, predators, and competitors) were compared within their respective categories. Only models that outperformed the null model were listed. We advanced competing models (within two AICc values of the top model) to stage 2 of model selection analysis. Data were collected in the Mojave Desert in southwestern Utah, USA, from 2010 to 2012.

† Null, intercept and random-effects model; burn, whether the area immediately surrounding the water source had been recently burned (within last decade); rugged, ruggedness metric calculated within a 100-m radius using a 10-xsm resolution digital elevation model; Robel20, visibility measured (height of visual obstructions, e.g., vegetation, rocks) at a distance of 20 m; canopy, presence of structural roof cover over water sources; badger, number of American badger (*Taxidea taxus*) visits; coyote, number of coyote (*Canis latrans*) visits; year, cluster sample (two-week sample period where multiple water sources were simultaneously monitored), camera type, and site were included in each model as random effects; a conditional intercept, a zero-inflated intercept, and an overdispersion parameter were also included in each model.

‡ Number of parameters.

§ Model log-likelihood.

¶ Change in AICc (Akaike’s information criterion corrected for small samples) value compared with top model.

# AICc weight.
Table 2. Stage 2 model selection results for zero-inflated negative binomial models of kit fox (*Vulpes macrotis*) visits as a function of top variables from stage 1 of model selection.

| Model†                   | K‡ | LL§ | ΔAICc¶ | Weight# |
|-------------------------|----|-----|--------|---------|
| Canopy + Robel20 + Badger + Coyote + Badger × Coyote | 12 | −527.86 | 0.00 | 0.32 |
| Badger + Coyote + Canopy + Robel20 + Canopy × Robel20 | 12 | −528.81 | 1.89 | 0.12 |
| Badger + Coyote + Robel20 + Badger × Coyote | 11 | −530.30 | 2.68 | 0.08 |
| Canopy + Robel20 + Canopy × Robel20 | 10 | −531.47 | 2.81 | 0.08 |
| Badger + Canopy + Coyote + Robel20 + Badger × Canopy | 12 | −529.53 | 3.33 | 0.06 |
| Badger + Coyote + Canopy + Robel20 | 11 | −530.75 | 3.58 | 0.05 |
| Badger + Canopy + Robel20 | 10 | −532.01 | 3.89 | 0.05 |
| Badger + Canopy + Robel20 + Badger × Canopy | 11 | −530.96 | 3.99 | 0.04 |
| Badger + Robel20 + Canopy + Coyote + Badger × Robel20 | 12 | −530.05 | 4.39 | 0.04 |
| Canopy + Robel20 | 9 | −533.53 | 4.78 | 0.03 |
| Badger + Robel20 + Canopy + Badger × Robel20 | 11 | −531.50 | 5.07 | 0.03 |
| Coyote + Canopy + Badger + Robel20 + Coyote × Canopy | 12 | −530.59 | 5.47 | 0.02 |
| Coyote + Robel20 + Badger + Canopy + Coyote × Robel20 | 12 | −530.75 | 5.78 | 0.02 |
| Badger + Coyote + Robel20 | 10 | −533.00 | 5.88 | 0.02 |
| Badger + Robel20 | 9 | −534.21 | 6.12 | 0.01 |
| Robel20 | 8 | −535.55 | 6.65 | 0.01 |
| Badger + Robel20 + Coyote + Badger × Robel20 | 11 | −532.56 | 7.18 | 0.01 |
| Badger + Robel20 + Badger × Robel20 | 10 | −533.90 | 7.68 | 0.01 |
| Coyote + Robel20 + Badger + Coyote × Robel20 | 11 | −533.00 | 8.07 | 0.01 |
| Badger + Coyote + Badger × Coyote | 10 | −544.79 | 29.45 | 0.00 |
| Badger | 8 | −549.74 | 35.04 | 0.00 |
| Badger + Coyote | 9 | −548.77 | 35.24 | 0.00 |
| Null | 7 | −551.23 | 35.89 | 0.00 |

Note: Data were collected in the Mojave Desert in southwestern Utah, USA, from 2010 to 2012.  † Null, intercept and random-effects model; Robel20, visibility measured (height of obstructions, e.g., vegetation, rocks) at a distance of 20 m; canopy, presence of structural roof cover over water sources; badger, number of American badger (*Taxidea taxus*) visits; coyote, number of coyote (*Canis latrans*) visits; year, cluster sample (two-week sample period where multiple water sources were simultaneously monitored), camera type, and site were included in each model as random effects; a conditional intercept, a zero-inflated intercept, and an overdispersion parameter were also included in each model.  ‡ Number of parameters.  § Model log-likelihood.  ¶ Change in AICc (Akaike’s information criterion corrected for small samples) value compared with top model.  # AICc weight.

Table 3. Coefficients, standard errors (SE), z-values, P-values, and upper (UCL) and lower (LCL) 95% confidence intervals from the top model comprising the majority of model weight assessing the influence of predators, competitors, and habitat characteristics on the visits of kit foxes (*Vulpes macrotis*) to water sources.

| Coefficient† | Estimate | SE | z | P | LCL | UCL |
|--------------|----------|----|---|---|-----|-----|
| Intercept    | 0.10     | 0.40 | 0.24 | 0.81 | −0.69 | 0.88 |
| Badger       | 0.26     | 0.10 | 2.53 | 0.01 | 0.06 | 0.46 |
| Coyote       | −0.77    | 0.31 | −2.48 | 0.01 | −1.38 | −0.16 |
| Canopy       | 0.58     | 0.26 | 2.21 | 0.03 | 0.07 | 1.09 |
| Robel20      | −1.45    | 0.35 | −4.16 | 0.00 | −2.14 | −0.77 |
| Badger × Coyote | 0.29 | 0.13 | 2.21 | 0.03 | 0.03 | 0.56 |

Note: Data were collected in the Mojave Desert in southwestern Utah, USA, from 2010 to 2012.  † Robel20, visibility measured (height of obstructions, e.g., vegetation, rocks) at a distance of 20 m; canopy, presence of structural roof cover over water sources; badger, number of American badger (*Taxidea taxus*) visits; coyote, number of coyote (*Canis latrans*) visits.

had a strong negative association with kit foxes that appeared to manifest in some level of partitioning of water sources between coyotes and kit foxes. Coyotes were present at approximately half of the water sources used by kit foxes, supporting similar patterns of spatial overlap between kit foxes and coyotes from other studies (White et al. 1994, 1995, Robinson et al. 2014).
The spatial overlap that occurred between kit foxes and coyotes in our study was evident around the margins of a narrow section of habitat (approximately 4 × 15 km; Fig. 1) that was commonly used by kit foxes. This observation aligns with what others have found demonstrating that kit foxes partition space with coyotes by using areas less frequented by coyotes (Kozlowski et al. 2012, Robinson et al. 2014, Lon-singer et al. 2017). In addition, our findings revealed a weak temporal overlap between kit foxes (nocturnal) and coyotes (active throughout the day), suggesting possible diel avoidance. However, this suggestion should be interpreted with caution. Kit foxes, like many other desert-adapted species, also use nocturnality to escape the heat and minimize evaporative water loss (Milton and Dean 2004). In addition, the golden eagle (Aquila chrysaetos) is an important predator of kit foxes (Kluever and Gese 2017, Cypher et al. 2019) and is diurnal. Determining whether the nocturnal behavior of kit foxes in our study was due to coyotes, golden eagles, or their own physiology is not entirely clear, but does show that in a world of trade-offs, a single behavior can sometimes have multiple benefits.

Bobcats and gray foxes were not as important in our analyses as badgers and coyotes. Bobcats are known predators of kit foxes, but their contribution to significant mortality of kit foxes is uncommon. In our study, bobcats visited nearly two-thirds of the water sources that kit foxes also...
used (n = 16) and exhibited a strong temporal overlap with kit foxes. Our findings illustrated that kit foxes did not spatially or temporally avoid bobcats, a finding not completely uncommon among dominant and subordinate carnivores (Mattisson et al. 2011, Schuette et al. 2013, Lesmeister et al. 2015, Gompper et al. 2016). Our results suggest that bobcats may be uncommon or opportunistic predators of kit foxes. Similar to bobcats, gray foxes also had a weak negative association with kit foxes, but a moderate temporal overlap with kit foxes. Gray foxes differed from bobcats in that the overlap of sites with kit foxes was low (n = 3). While we did not specifically model the selection of water sources for gray foxes, this species generally was present at water sources higher in the foothills and characterized by increased ruggedness and dense vegetation. These habitat characteristics are likely important for gray foxes to escape predation and interspecific strife, as reported in other work (Atwood et al. 2011), but are contrastingly different than what kit foxes typically use (Egoscue 1956, McGrew 1979). While gray foxes and kit foxes have similarities in diet (McGrew 1979, Fritzell and Haroldson 1982), our results suggest that gray foxes and kit foxes partition resources based on differences in habitat and that gray foxes are not an important competitor of kit foxes.

Previous work has shown that habitat features play an important role in the spatial ecology of small carnivores (Gompper et al. 2016). One reason for this is to minimize perceived risk of predation (Smith et al. 2015); another reason is to maximize foraging opportunities (White et al. 2015; another reason is to maximize foraging opportunities (White et al. 1996, Dennis and Otten 2000). Both of these reasons may support our findings of kit foxes visiting water sources more frequently in open areas (Egoscue 1956, McGrew 1979) and that also provided (overhead) cover (Hall et al. 2013a). Our findings seem contradictory on the surface until we consider that kit foxes use burrows (increased cover) located in open areas (Egoscue 1956). Considering first the risk of predation perspective, by relying on burrows, kit foxes are accustomed to the close-quarter cover that a burrow offers and likely perceive burrow-like conditions (e.g., subterranean water sources or water sources with low overhead cover) as safe (Hall et al. 2013a). Alternatively, when a kit fox is outside the perceived safety of its burrow, it likely relies on the openness of its habitat to visually survey for potential threats (Egoscue 1956). Considering the foraging perspective, kangaroo rats (Dipodomys spp.) are a common prey species of kit foxes (McGrew 1979, Nelson et al. 2007), and these rodents occupy sparsely vegetated, open areas conducive to their locomotive abilities (Horn et al. 2012). Supporting this notion, we observed that kangaroo rats were more commonly detected at water sources where kit foxes visited as opposed to water sources where kit foxes were absent (L. Hall, unpublished data). We also found that at water sources with overhead canopy cover we detected desert wood rats (Neotoma lepida) more often compared to water sources without canopy cover (L. Hall, unpublished data). While it was not within the scope of this study to discern the underlying reason for which kit foxes selected certain features associated with water sources, our findings suggest that the use of water sources with canopy cover and in open areas may provide refuge and forage benefits for kit foxes.

Our study showed that the way in which kit foxes spatially and temporally access water sources is dynamic and not dependent upon a single factor. We recognize that our inferences are limited because we did not experimentally manipulate predators, competitors, or habitat characteristics, which would have allowed us to draw stronger conclusions about our findings. Yet, despite this, our extensive sampling effort over both space and time not only revealed insight into environmental relationships of kit foxes but also corroborated findings from related studies (Atwood et al. 2011, Edwards et al. 2015). Moreover, our study is the first of its kind to evaluate long-standing notions underlying the broad spatial and temporal use of water by kit foxes. Our results revealed that the use of water by kit foxes is complex and supported the hypothesis that their use of water is dependent upon the activity of heterospecifics and habitat characteristics that may minimize the risk of predation and offer foraging opportunities. Given the importance of understanding the drivers of resource acquisition by species of concern, our study provides novel information regarding the influence of predators, competitors, and habitat characteristics on the spatial and temporal use of water by kit foxes.
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