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Increased bat activity at urban water sources: implications for cross-species transmission of bat rabies to mesocarnivores

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Abstract

We examined the potential for urban water sources, specifically golf course ponds, to act as centers for rabies transmission from bats to mesocarnivores in the arid southwestern United States where surface water is often limited. Because residential housing can act as den and roost sites for both mesocarnivores and bats, we also examined the effect of housing density around water sources on activity. Using ultrasonic acoustic recorders to assess bat activity and camera traps to estimate mesocarnivore activity, we compared 14 pairs of wet and dry locations over two years by surveying twice during the summer, once prior to summer monsoons and once during the monsoon season, when surface waters were more available. Number of calls for all bat species combined were greater at wet sites compared to dry sites and calls of two bat species often associated with rabies, big brown bat (*Eptesicus fuscus*) and silver-haired bat (*Lasionycteris noctivagans*), were recorded more at wet sites than dry sites in the monsoon season. In both years, raccoons (*Procyon lotor*) were photographed more often at wet sites while striped skunks (*Mephitis mephitis*) and gray foxes (*Urocyon cinereoargenteus*) were less likely to be detected at wet sites. Bat, fox and raccoon activity was not associated with housing density while striped skunks showed a positive correlation. Finally, we examined potential for contact between mesocarnivores and big brown bats, a species implicated in cross-species rabies transmission in our area, by combining call activity of this bat species and photo detections of mesocarnivores during individual hours of the night into a Potential Contact Index (PCI) and found no significant effect of season (pre-monsoon vs. monsoon), species, or treatment (dry versus wet) but did find a significant species by treatment interaction, with raccoon PCI 3–30 times higher at wet sites and no effect on the other two mesocarnivores' PCI. Overall, we found higher activity of bats at urban waters could increase potential for cross-species transmission of rabies from bats to raccoons but not for gray foxes and striped skunks.

Keywords Big brown bat · Bat activity · Housing density · Mesocarnivores · Rabies · Urban water source

Introduction

The rabies virus is a zoonotic disease that threatens human health on a global scale. Although most human fatalities worldwide occur due to exposure from rabid dogs, in North America, canine rabies has been nearly eliminated due to effective vaccination programs and the major rabies reservoirs are now bats and mesocarnivores (Gilbert 2018; Velasco-Villa et al. 2017). Rabies virus variants typically circulate within reservoir populations, with cross-species transmission to non-reservoir species during outbreaks. Cross-species transmission typically leads to dead-end infections, but more rarely host-shift events may occur in which the virus adapts to the new host and is maintained in that host through time (Badrane and Tordo 2001). For example, three independent host-shifts occurred between 2001 and 2009 and again in 2021–2023 in Flagstaff, Arizona, when striped skunks (*Mephitis mephitis*) and gray foxes (*Urocyon cinereoargenteus*) became infected with rabies variants associated with the big brown bat (*Eptesicus fuscus*) (Leslie et al. 2006; Kuzmin et al. 2012). Cross-species

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transmission is a concern because with every transmission, the rabies virus has an opportunity to adapt to a new reservoir host, potentially undermining rabies management programs and threatening public health (Wallace et al. 2014). Therefore, it is important to identify the environmental factors that may promote interspecies interactions and increase the potential for transmission between species.

Cross-species transmission is typically detected by identifying genetic variants of rabies unique to one species present in another species, but the route of transmission has rarely been documented. Although bat-to- mesocarnivore transmission has often been assumed to occur either from mesocarnivores hunting or scavenging dead or dying infected bats at roost sites (Shankar et al. 2005; Theimer et al. 2017b), unprovoked attacks by rabid bats away from roosts is an alternate pathway. Attacks by rabid bats on humans are often associated with humans attempting to handle infected bats, but several cases of unprovoked attacks have also been documented (Kough 1954; Baer and Adams 1970). Observations of cross-species transmission among bat species are likewise rare, but Bell (1980) documented a hoary bat attacking individuals of three other bat species and later captured a hoary bat with blood on its face in net set over a swimming pool that subsequently tested positive for rabies. Likewise, Sasse et al. (2014) reported an adult female eastern red bat (*Lasiurus borealis*) and an adult female evening bat (*Nycticeius humeralis*) locked in an aggressive interaction with the red bat later testing positive for rabies. We know of no published observations of bats attacking wild mesocarnivores, but, taken together, the limited evidence available suggests that unprovoked attacks could occur whenever a rabid bat encounters another species. If that is the case, the probability of cross-species transmission via unprovoked attacks would be proportional to the number of contacts between bats and mesocarnivores and environmental factors that increase the potential for bats and mesocarnivores to come into proximity could increase the probability of cross -species transmission via unprovoked attacks by rabid bats on mesocarnivores.

One environmental factor that could affect the probability of cross-species interaction and disease transmission is creation of artificial waters in urban landscapes, especially in water-limited environments like the arid southwestern USA. Heightened levels of bat activity around surface waters are well documented (Anderson et al. 2006; Lisón and Calvo 2011) and likely driven both by need of bats to drink and higher levels of insect prey near water (Salvarina et al. 2018). Water availability is also critical for lactation (Mclean and Speakman 1999), as demonstrated by the tendency of many bat species to establish maternity colonies near standing water (Walker et al. 2020; Adams and Thibault 2006). Free water is a fundamental requirement for terrestrial mammals as well (Leopold 1933, Nagy 2004) especially for wildlife in arid landscapes (Rosenstock et al. 1999). Proximity to water has been positively associated with occupancy and space use by mesocarnivores (Dias et al. 2019; Kluever et al. 2017) and anthropogenic water sources are commonly used to benefit wildlife in arid water-limited landscapes (Krausman et al. 2006). In urban areas in the arid southwest, the ponds and lakes associated with golf courses often provide surface water in areas otherwise lacking permanent natural water sources, and the plentiful green space and anthropogenic structures associated with golf courses are attractive habitat features for wildlife. Mesocarnivores such as coyotes and raccoons respond positively to golf courses relative to other urban habitats (Gallo et al. 2017) and because of their relatively large size relative to other urban green spaces, golf courses may be especially important in maintaining bat diversity in urban areas (Threlfall et al. 2016).

In addition to water, there are several factors associated with urban environments that can affect bat activity. Artificial lighting can negatively impact even light-tolerant bat species (Pauwels et al. 2019) as well as decrease abundance and disrupt activity for others (Mariton et al. 1987). Anthropogenic noise also may impact bats ability to successfully forage for insect prey (Bunkley et al. 2015). One factor likely especially important for rabies cross-species transmission from bats to mesocarnivores is housing density. Mesocarnivores like skunks, foxes, and raccoons (*Procyon lotor*) often reach higher population densities in urban and suburban areas than in rural areas (Bateman and Fleming 2012) and often use anthropogenic structures as den sites (Hadidian et al. 1991; Theimer et al. 2017a). Bat responses to urbanization and housing density vary, but several species, including big brown bats, commonly roost in buildings (Agosta 2002; Neubaum et al. 2007; Fagan et al. 2018; Walker et al. 2020) while others may roost in large, non-native trees planted by humans in urban areas (Evelyn et al. 2004; Kubista and Bruckner 2015).

In this study, we examined the potential for artificial waters (urban golf course ponds) and housing density to influence the activity levels of bats and mesocarnivores in a water-limited, urban landscape. We predicted that bat activity and mesocarnivore detections would increase around artificial water sources due to physiological demands of water and higher abundance of aquatic insect prey. We also predicted activity would increase with increasing housing density in the relatively low-density urban areas we studied, as these structures increase sites for bat roosts and mesocarnivore dens. In addition, we focused on a subset of bat calls associated with big brown bats (*Eptesicus fuscus*) to determine whether the potential for bat-mesocarnivore interactions at water and non-water sites was similar across mesocarnivore species and whether the potential for interaction increased during a dry period versus a wet period of the year. We focused on calls of big brown bats because (1) it is a widespread and common North American species that commonly roosts in homes and buildings (Kunz and Reynolds 2003), (2) it is the species most commonly reported with rabies, with estimates of 6–17% of those tested being positive for rabies (Mondul et al. 2003; Shankar et al. 2005) and (3) cross-species transmission from big brown bats to striped skunks and gray foxes has occurred repeatedly in the area we studied (Leslie et al. 2006; Kuzmin et al. 2012), but the route of that transmission remains unknown.

Study areas

Between 5 June and 5 August of 2018 and 2019 we collected bat acoustic recordings and trail camera images of mesocarnivores in three cities in northern Arizona USA: Williams, (35.2495°N, 112.1910° W), population = 3,200, elevation = 2061 m; Flagstaff (35.1853°N, -111.6519°W), population = 73,964, elevation 2105 m; and Pinetop-Lakeside (34.1425°N, 109.9604°W), population = 4,433, elevation = 2073 m. All three cities lie within extensive ponderosa pine (*Pinus ponderosa*) forests and experience a monsoonal rainfall pattern during summer, in which the month of June is typically dry while monsoonal rains begin in July.

In each city, we used a paired study design, with paired sites consisting of a dry and wet site. Dry sites lacked water bodies; no water sources were within 500 m. Wet sites included artificial water bodies, ranging from 0.02 to 1.59 hectares in size. Within each pair, wet and dry sites were ≥ 500 m but ≤ 1000 m apart. We chose these distances based on our previous experience radio-tracking and camera-trapping bats and mesocarnivores in these areas (Theimer et al. 2017a, b; Walker et al. 2020). We chose a minimum distance of 500 m to reduce the chance that attraction of bats and mesocarnivores to water would influence our measurements of activity away from water. We chose a maximum distance of 1000 m because beyond that distance housing density, tree density and other environmental factors varied more between wet and dry sites. Nine pairs were located in and around Flagstaff, two pairs were in Williams and three pairs were in Pinetop. All fourteen pairs (28 sites) were located on golf courses within a suburban matrix. To control for the lack of tree canopy caused by the presence of water at wet sites, we chose dry sites that had open canopy areas of similar size.

Methods

To monitor bat activity, we deployed SM3BAT bioacoustics recorders (Wildlife Acoustics, Maynard, Massachusetts, USA) paired with an omnidirectional U1 ultrasonic microphone for six consecutive nights at each site. Each site was sampled once in June and once in July in both years to allow us to test for the effect of the monsoon (July) and pre-monsoon conditions (June). To account for spatial variation in bat activity, we moved our detectors every two nights, surveying each site at three survey points. The three survey points were spaced evenly around each site (Fig. 1). We mounted microphones to the top of 12.7 mm conduit tubing measuring 2.5 m tall. We chose this height for cameras

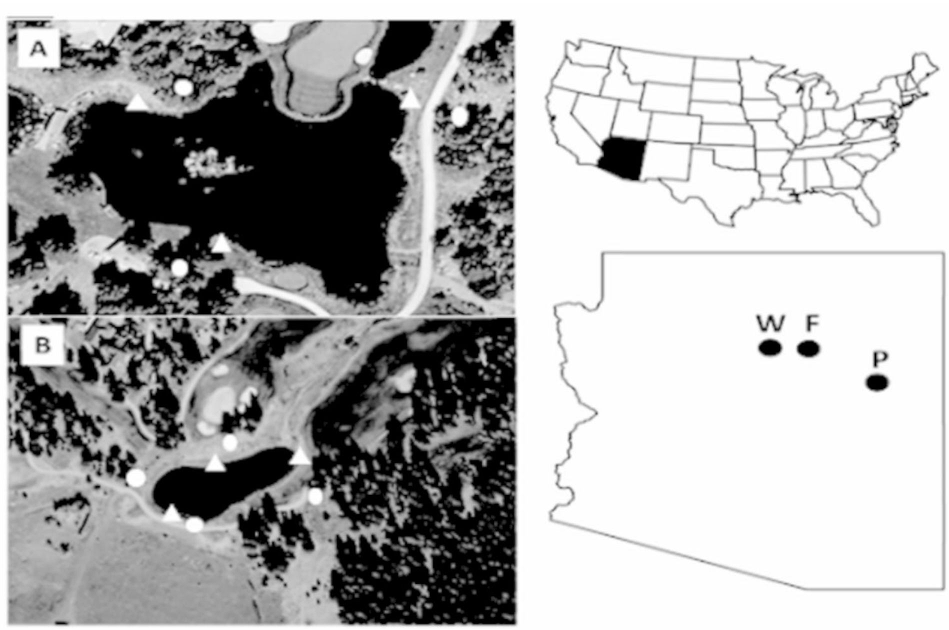

Fig. 1 **A**. Locations of the acoustic bat detectors (white triangles) and mesocarnivore cameras (white circles) placed at a wet site in 2018. A single camera was moved from one location to another every 2 nights. **B**. Locations at a wet site in 2019 when 4 cameras were placed in a fixed location for all 6 nights. Golf courses were monitored in Flagstaff, Pinetop, and Williams, Arizona USA in June and July 2018–2019

based on manufacturer recommendations to decrease interference from the ground. The recorders were programmed to initiate recording 30 min prior to sunset and cease recording 30 min after sunrise.

To monitor mesocarnivores, we deployed Reconyx HyperFire HC500 and Bushnell Trophy Cam HD trail cameras for 6 nights at each site concurrent with bat monitoring. We placed cameras in steel boxes mounted on trees approximately 0.5 m above ground. During the 2018 field season, we used a single camera at each site, which we moved to a new location every two nights. During the 2019 field season, we used four cameras at each site and the cameras remained in a fixed position for all six nights.

To process bat recordings, we first used Sonobat Batch Scrubber 5.4 (Sonobat ™, Arcata, CA, USA) to eliminate any non-bat vocalizations and then used Sonobat version 3.2.1 U.S. West (SonoBat™, Arcata, CA, USA) to classify bat calls to species level when possible. Calls were defined by classifying an entire sequence (bat pass). In examining how bat activity varied with the presence of water and housing density, we examined both total bat calls and the subset of calls identified as either big brown bats or silver-haired bats (*Lasionycteris noctivagans*). The calls of these two species are difficult to distinguish from each other consistently due to similarities in call structure and frequency (Betts 1998). Therefore, we lumped calls identified as either species into a single category hereafter referred to as "Epfu/Lano" calls. Mist-netting of bats in previous years at several of the sites used in this study by one of the authors (C. Chambers) recorded that out of a total of 130 captures of big brown bats and silver-haired bats, 98% were big brown bats, suggesting that the majority of Epfu/Lano calls in our acoustic monitoring data could be attributed to big brown bats. We focused on this subset of calls because both species are often associated with rabies virus in North America (Finnegan et al. 2002), but more importantly because several independent cross-species transmissions from big brown bats to striped skunks and gray foxes have been documented in our study area between 2001 and 2023. For all of our analyses, we utilized the recommended default Sonobat settings: setting maximum number of calls per file to 8, acceptable call quality to 0.80, acceptable quality to tally passes of 0.20, and a decision threshold of 0.90. Additionally, a total of 560 "Epfu/Lano" calls in 2018 and 880 calls in 2019 were randomly selected across water and dry sites and months and manually vetted against reference calls to check the auto-classifiers accuracy.

To estimate housing density around each site, we downloaded aerial imagery for the state of Arizona from the National Agriculture Imagery Program (NAIP) and used proximity tools in ArcMap 10.6.1 (ESRI, Redlands, CA) to create 1 km buffers around each study site. We determined housing density by counting the number of structures that we could distinguish within each buffer area. Garages and sheds that were separate from houses were counted as individual structures since they could be used for dens and roosts (Agosta 2002; Neubaum et al. 2007; Theimer et al. 2017a).

Statistical analysis

We compared activity (measured as rate of calls per hour) between wet and dry sites using (1) calls of all bats combined and (2) the subset of calls identified as either *Eptesicus fuscus* or *Lasionycteris noctivagans* (Epfu/Lano). We used linear mixed modeling to predict activity of all bat species combined and Epfu/Lano separately. We considered "water", "monsoon" and "housing density" to be fixed effects. "Water" was a categorical variable that indicated if a site had water present or not. "Monsoon" was a categorical variable that indicated if the data were collected in pre-monsoon (June) or monsoon conditions (July). "Housing density" was a numerical variable that reflected the number of structures within 1 km of each site. We included the random effects Site and Year since we expected site-to-site variation (e.g., bat populations are not evenly distributed throughout the landscape). Year accounted for some of the year-to-year variation in environmental conditions such as strength of the annual monsoon. Models were constructed and compared with Akaike information criterion (AIC) (Akaike 1973). Because distributions for both of our response variables were heavily skewed, consistent with a lack of homoscedasticity, we log-transformed our response variables. We then used pair-wise contrasts to test for differences between wet and dry sites in total bat calls or Epfu/Lano calls.

Mesocarnivore data were analyzed at the species level using logistic regression. We constructed separate models for skunks, raccoons, and foxes. The dependent variable for each model was converted into a discrete variable (0, 1) with detection equal to 1 and no detection equal to 0. The models were constructed with the independent variables: water, monsoon and housing density. Competing models were again compared based on Akaike information criterion. A pair-wise comparison between wet and dry sites allowed us to determine the probability for detection for each mesocarnivore species. All analyses were conducted with R (R Core Team. (2016). *R: A Language and Environment for Statistical Computing*. Vienna, Austria).

To assess the potential for cross-species transmission between big brown bats and mesocarnivoes, we assumed that the probability of rabies transmission from bats to mesocarnivores was a random event dependent upon the relative number of times bats and mesocarnivores came in contact. In our system, this would depend upon the level of

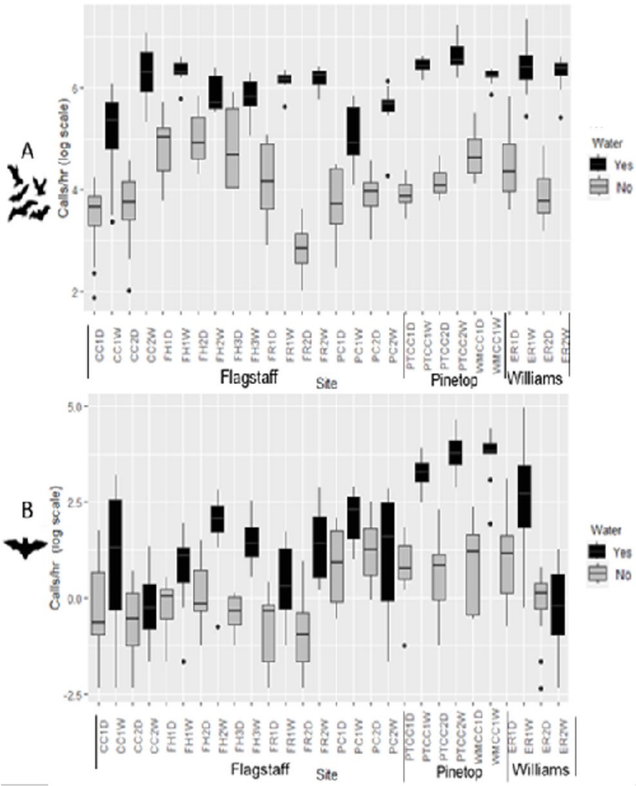

Fig. 2 Variation in call rates across 14 pairs of wet (blue) and dry (red) sites at Flagstaff, Pinetop, and Williams, Arizona USA in June and July 2018–2019 for all bats combined (**A**) and big brown bat/silver-haired bat (*Eptesicus fuscus* / *Lasionycteris noctivagans*) subgroup (**B**). Sites are grouped by city, wet and dry pairs are plotted next to each other. Five number summary data is displayed for each site

bat activity whenever a mesocarnivore was present. Given that the level of both bat and mesocarnivore activity may vary across the hours of the night, we estimated probability of big brown bat to mesocarnivore transmission based on a Potential Contact Index (PCI) calculated by multiplying the number of detections of each mesocarnivore species in each hour of the night multiplied by the activity of bat calls identified as big brown bat or silver-haired bat recorded at that hour. We then calculated an overall mean PCI across all sites for each mesocarnivore in both June and July of 2018 and 2019. For this analysis, we focused on calls classified as big brown bat/silver haired bat rather than all bats, as big brown bats were the species implicated in cross-species transmission at our study sites. Likewise, we focused this analysis on the three mesocarnivores most common at our sites, striped skunks, raccoons and gray foxes. Using the mean PCI across all hours of the night at each site in each year as replicates, we then tested effect of month (June vs. July), effect of treatment (wet versus dry) and effect of species using one-way AOV separately for 2018 and 2019. We did not combine years into one analysis because the number of cameras used to detect mesocarnivores varied between years. We hypothesized that (1) PCI would be higher for all mesocarnivores in June rather than July because both bats and mesocarnivores would be more concentrated at permanent water during the dry, pre-monsoon season, (2) PCI would differ among mesocarnivore species due to differences in relative abundance, with raccoons and striped skunks more abundant and therefore having higher PCI than gray fox, and (3) PCI for all three mesocarnivores would be higher at wet rather than dry sites because of higher bat activity at wet sites and greater visitation of wet sites by mesocarnivores.

Results

We recorded 1,070,724 acoustic bat passes over 432 survey nights at 28 study sites. When pooled across all bat species, the mean call rate (±SE) at wet sites (430±85/hr) was significantly higher ($P < 0.0001$, $\alpha = 0.05$) than dry sites (63±12/hr) (Fig. 2). We did not detect an effect of month ($F = 0.49$, $P = 0.48$) or housing density ($F = 0.12$, $P = 0.73$) (Table 1). We recorded 40,856 Epfu/Lano passes. The number of Epfu/Lano passes recorded was significantly higher ($P < 0.0003$, $\alpha = 0.05$) at wet sites (4.5±2/hr) than dry sites (1±0.5/hr) and activity for the Epfu/Lano group was higher during the monsoon (July) than during pre-monsoon conditions (June) (Table 1). The Epfu/Lano call rate during the monsoon (July) at wet sites was (6±3/hr) and (3±2/hr) at wet sites during Pre-monsoon. (June). We did not detect an effect of housing density on Epfu/Lano call rate ($F = 0.04$, $P = 0.84$).

Water and housing density had a significant effect on skunk detections with the odds of detecting a skunk decreasing by 47% near water and increasing by 0 0.7% for each unit increase in housing density. Raccoons showed a positive response to water with the odds of detecting a raccoon increasing by 13% near water. Foxes showed a negative

Table 1 Model summary statistics for all bat species model (top) and Epfu/ Lano group (bottom)

Group	Variable	Estimate	SE	P	Group	Variance	SD
All bats	Intercept	4.68496	0.5541	7.9E-9	Site	0.2673	0.5170
	Water	1.94327	0.20594	9.8E-10	Year	0.0359	0.1895
Epfu/Lano	Intercept	-0.3382	0.508	0.584177	Site	0.8610	0.9279
	Water	1.5191	0.3657	0.000313	Year	0.3772	0.6142
	Monsoon	0.6700	0.1011	1.38E-10			

Table 2 Model summary statistics for final skunk model (top), fox model (middle) and raccoon model (bottom) at golf courses in Flagstaff , Pinetop, and Williams Arizona USA in June and July 2018-2019

Species	Variable	Estimate	SE	P
Skunk	Intercept	-3.21332	0.357028	2.00E-16
	Water	-0.73686	0.343326	0.0319
	Housing density	0.007439	0.001286	7.29E-09
Fox	Intercept	-1.8095	0.2039	2.00E-16
	Water	-1.8334	0.4968	0.000224
Raccoon	Intercept	0.13065	0.02777	3.54E-06
	Water	0.12955	0.03943	0.00111

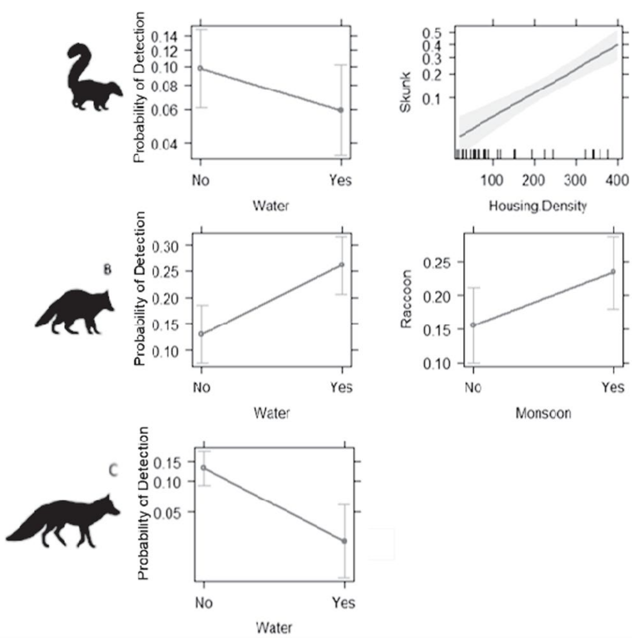

Fig. 3 Main effects of models examining the relationship between the probability of mesocarnivore detection and presence of water and housing density for striped skunk (*Mephitis mephitis)* (**A**), raccoon (*Procyon lotor)* (**B**) and gray fox (*Urocyon cinereoargenteus)* (**C**) summarized across 14 pairs of wet and dry sites at Flagstaff, Pinetop, and Williams, Arizona, USA in June and July 2018–2019

response to water with the odds of detecting a fox decreasing by 16% near water (Table 2; Fig. 3).

Our test of the effect of month, species and presence of water on the Potential Contact Index between big brown bats and mesocarnivores showed similar results in 2018 and 2019 (Table 3). In 2018, there was no significant effect of month ($F_{35,1}$ = 0.001, p = 0.975), species ($F_{35,2}$ = 1.263, p = 0.295) or treatment (dry versus wet) ($F_{35,1}$ = 0.332, p = 0.568), but there was a significant treatment x species interaction ($F_{35,2}$ = 3.456, p = 0.043), with PCI of raccoons increasing 3 to 30-fold in June and July respectively at wet sites compared to dry sites while PCI of skunks remained low at both dry and wet sites in both months while foxes were not recorded at wet sites in either month. Results in 2019 were similar, with again no significant effect of month ($F_{35,1}$ = 0.970, p = 0.757) or treatment ($F_{64,1}$ = 2.874, p = 0.095), a marginal significant effect of species ($F_{64,2}$ = 3.305, p = 0.043) and a significant treatment x species interaction ($F_{64,2}$ = 3.676, p = 0.031), with PCI of raccoons increasing 18-28-fold at wet sites compared to dry sites while again PCI of skunks remained low at both and foxes were not recorded at wet sites in July.

Discussion

Cross-species transmission of rabies from bats to carnivores has been important in the evolution of the rabies virus, as rabies variants now established in several mesocarnivore reservoirs independently evolved from bat variants (Badrane and Tordo 2001) and more recent host-shifts are evidence these transmissions are still occurring (Leslie et al. 2006; Kuzmin et al. 2012). The specific routes by which transmissions occur, whether by bites during unprovoked attacks by bats or hunting or scavenging bats by mesocarnivores, remains undocumented, but the probability of those cross-species transmissions is dependent on the prevalence of the virus in bat populations and the contact rate between bats and mesocarnivores. Prevalence has most often been estimated either as the proportion of bats turned into health agencies for testing that test positive for rabies virus in the brain or brain stem, or by testing wild populations for presence of rabies antibodies in the blood (seroprevalence). The former estimates indicate roughly 6% of bats turned in for testing in the United States test positive for rabies (Mondul et al. 2003; Patyk et al. 2012) with the caveat that bats submitted for testing

Table 3 Mean ± SE Potential Contact Index (PCI) between big brown bats and three mesocarnivores and total number of detections of mesocarnivores (in parenthesis) at golf course ponds (Wet) and paired sites without a pond (Dry) in June (pre-monsoon) and July (monsoon) in 2018 and 2019 at 14 different sites in northern Arizona, USA.

2018	June Dry	June Wet	July Dry	July Wet
Striped Skunk	3.0 ± 1.9 (17)	3.0 ± 3.0 (3)	3.7 ± 2.0 (6)	1.8 ± 1.2 (10)
Raccoon	1.0 ± 1.1 (2)	35.1 ± 20.4 (23)	6.2 ± 4.5 (17)	18.7 ± 9.4 (21)
Gray Fox	2.9 ± 12.4 (7)	0 (0)	11.4 ± 4.5 (17)	0 (0)
2019				
Striped Skunk	11.3 ± 6.3 (43)	8.9 ± 4.1 (24)	21.6 ± 13.0 (48)	18.0 ± 11.1 (14)
Raccoon	16.9 ± 6.3 (47)	301.0 ± 155.9 (164)	17.6 ± 9.3 (19)	421.3 ± 184.1 (139)
Gray Fox	7.9 ± 4.1 (26)	23.5 ± 19.6 (5)	10.5 ± 17.9 (12)	0 (0)

are unlikely to represent an unbiased sample. The number of studies estimating seroprevalence in wild populations of bats are limited, but they indicate seroprevalence can vary widely across populations and across time, with seropositive proportions in some populations as high as 20% in some big brown bat populations (O'Shea et al. 2011) to 50% in some Brazilian free-tailed bat (*Tadarida brasiliensis*) roosts (Turmelle et al. 2010). Importantly, seroprevalence indicates past exposure to rabies virus but does not necessarily indicate animals are or would actively transmit the disease, as some wild seropositive animals brought into captivity failed to develop the disease while some seronegative bats did (Davis et al. 2012) and long-term monitoring of seroprevalence in marked individuals showed that wild bats could gain and lose seroprevalence through time (O'Shea et al. 2014). Contact rates are likewise difficult to assess, and in our study we assumed environmental factors, like water, that increased activity of bats or mesocarnivores would increase the probability of encounter and thereby the probability of cross-species transmission.

Our finding of higher bat activity around wet sites, for both all bat species combined and the Epfu/Lano subset, is consistent with previous studies examining overall bat responses to water (Loumassine et al. 2020; Monadjem and Reside 2008) and the responses of *Eptesicus fuscus* specifically (Li and Wilkins 2014; Gallo et al. 2018). Bats primarily use water in two ways, as a drinking source and as foraging habitat (Campbell 2009). High energetic costs associated with flight (Voigt et al. 2010) and large wing membranes that result in higher surface area to volume ratios (Herreid and Schmidt-Neilsen 1966) make bats more susceptible to water loss through evaporation. In addition to meeting water demands, the increased availability of aquatic insect prey makes water sources valuable foraging grounds for insectivorous bats (Salvarina et al. 2018). Water availability may be especially important for bats in the water-limited landscape of the desert southwest USA (Loumassine et al. 2020), and in these areas, artificial waters such as those on golf courses may be especially important.

Given the significant positive effect of water on bat activity, we were surprised that monsoon was not a significant predictor, as we expected bat use of our water sources would decline once monsoons increased water availability across the landscape, at least during our first study year (2018). The higher call rates in the monsoon season for the Epfu/Lano group was likewise unexpected. The limited monsoon activity during our second (2019) field season (5.3 cm of rainfall compared to 25.1 cm during 2018 in Flagstaff), may have contributed to our failure to see differences in total bat activity between pre-monsoon and monsoon conditions in that year, but cannot explain the lack of response in 2018 or the increase in activity of the Lano/Epfu subset during July. Instead, we hypothesize that stable or increasing activity in July was driven by increased use of waters by lactating females combined with overall higher population sizes due to recruitment of newly-independent juvenile bats that become volant in July and August (Christian 1956). Water may be especially important for females during lactation (Adams 2010) with lactating females visiting water 13 times more often compared to non-reproductive females in one study (Adams and Hayes 2008).

We also expected all three terrestrial mammals to show a positive relationship with artificial water sources given the relative rarity of surface water in the surrounding urban matrix, but found a positive association only for raccoons, the species most often detected by our camera traps. Racoons often forage in wetland habitats (Beasley and Rhodes 2010) and diet items associated with aquatic habitats like fish, aquatic invertebrate adults and larvae, earthworms, crayfish and the eggs of ducks and coots (Greenwood 1982) were present at our urban golf course ponds. Striped skunks in non-urban studies showed variable responses to water. Distance to water was not a significant factor for striped skunks in den site selection in Canadian prairies (Lariviere et al. 2000) while Baldwin et al. (2004) observed both positive and negative associations between water and skunk trap success in deciduous forests in Tennessee and Schneider et al. (2019) observed positive associations with water in urban North Dakota. As with striped skunks, gray foxes were detected more frequently at dry sites. Given that gray foxes may partition their use of anthropogenic water sources to reduce interspecific conflict (Atwood et al. 2011), the high raccoon activity around wet sites in our study may have reduced use at those sites by foxes, and potentially by skunks as well.

Housing density has been shown to interact with presence and abundance of both bats (Hale et al. 2012; Caryl et al. 2016) and mesocarnivores (Riley 2006, Cervinka et al. 2014), but we found no effect of housing density on bat activity, or on fox and raccoon occurrence. We speculated that increasing housing density would benefit mesocarnivores by providing den locations and opportunities to exploit anthropogenic food sources, but only striped skunks showed a positive relationship with housing density. Other studies have documented that striped skunks respond positively to human modified landscapes (Salek et al. 2014, Allen et al. 2022) but may decline above an upper threshold of modification (Amspacher et al. 2021), but direct comparison to our response to housing density was not possible because these other studies either combined housing density into an overall index of human modification or reported other variables that were correlated with housing density. That said, our sites were characterized by houses built on relatively large, often unfenced lots set amid the Gambel oak-ponderosa pine forests that dominate the region, so likely would have fallen within moderate levels of human modification in these other studies. Although raccoons showed increased activity with increasing housing densities in other studies (Riley et al. 1998, Ordenana et al. 2010, Gross et al. 2012), we did not find an effect, perhaps, because the response to water in the arid southwest overshadowed any effects of housing density. Likewise, gray foxes showed no response to housing density, although several studies have suggested that they are tolerant of urbanization (Harrison 1997; Riley 2006). Spatial overlaps with other mesocarnivores in urban areas appear to negatively affect gray foxes (Parsons et al. 2019), and the high incidences of raccoons in our suburban sites may be the reason fox detections were low.

Overall, our data indicate that artificial urban water sources in northern Arizona, specifically those associated with golf courses, have the potential to increase the cross-species transmission of rabies between bats and racoons, while the probability of bat-contact is no greater for striped skunks and gray foxes at these waters than away from them, in part because activity of these two mesocarnivores was lower at water sites. Rabies in raccoons is not typically a concern in the southwestern USA (Ma et al. 2023), presumably because populations are much lower than those in urban and suburban areas of the eastern United States. However, if raccoon populations continue to grow as human-dominated landscapes spread in the southwestern United States, raccoons may become more important in rabies dynamics given the high levels of raccoon detections around artificial water sources on golf courses we documented. Given that several independent host shifts of rabies from big brown bats to striped skunks and gray foxes have been documented in our study area (Leslie et al. 2006; Kuzmin et al. 2012), our results suggest that those transmissions were more likely at sites away from water. Striped skunks are more likely to scavenge dead bats than either racoons or gray foxes in our study area (Theimer et al. 2017b) and scavenging of dead and dying bats may be one route of transmission away from water. Both big brown bats and striped skunks use human structures as roost or den sites (Agosta 2002; Neubaum et al. 2007; Theimer et al. 2017a), and scavenging of bats or unprovoked attacks by bats may be more likely at these sites. Given the relatively low rate of scavenging of bats by gray foxes in our area (Theimer et al. 2017b), the route of transmission from bats to foxes may be more likely through incidental contacts via unprovoked attacks, most likely away from water. That said, although visitation by foxes at water was rare, when it did occur the potential contact index (PCI) was relatively high because the amount of bat activity at those waters was very high at the time foxes visited. Thus, even rare visits to waters by foxes could increase their potential for bat contact and disease transmission. Finally, maternity roosts of big brown bats are often within 1 km of open water (Walker et al. 2020), so proximity to water may be important in increasing the probability of cross-species transmission to skunks and foxes but at a broader spatial scale rather than at the waters themselves. Overall, our results suggest that artificial waters, specifically those associated with golf courses, have the potential to increase cross-species transmission of rabies in arid, water-limited communities in the southwestern USA but that effect may be influenced by species-specific responses to water among mesocarnivores and the inter-specific interactions among those mesocarnivores.

Author contributions The co-authors contributed to the research in the following ways. Lias Hastings and Tad Theimer designed the study with input from Carol Chambers and David Bergman. Critical field equipment and support was furnished by David Bergman and Carol Chambers. Lias Hastings conducted the field work, data summary and analysis and wrote the initial draft with input from Tad Theimer and Carol Chambers. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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