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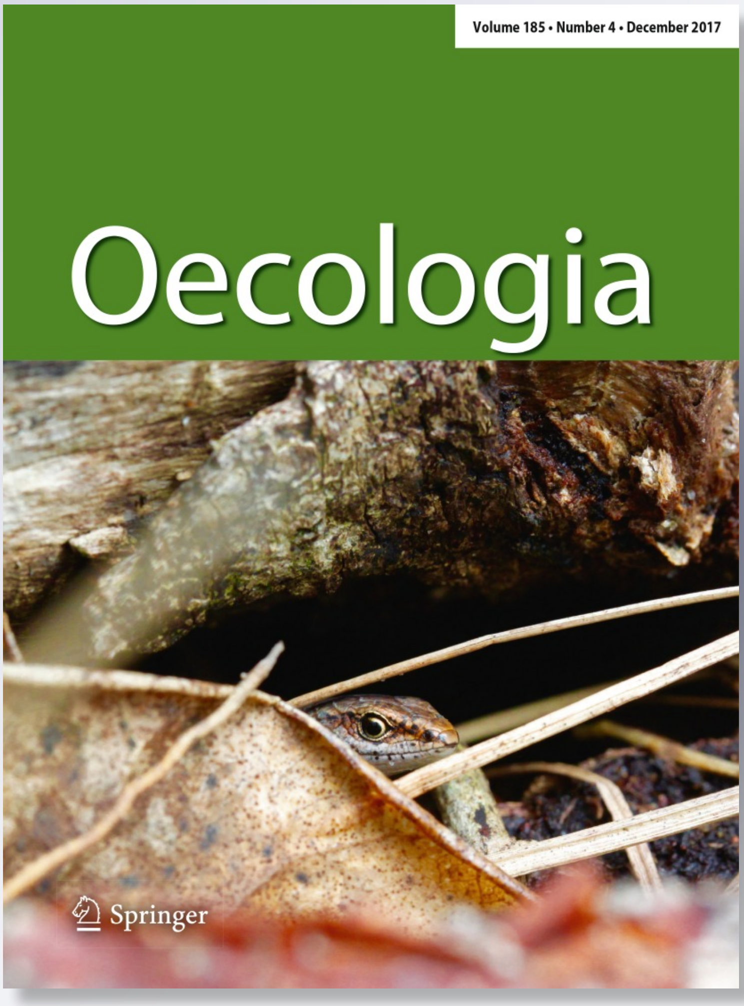

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BEHAVIORAL ECOLOGY – ORIGINAL RESEARCH

Desert amphibian selection of arid land breeding habitat undermines reproductive effort

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Abstract Understanding how animals select habitat is important for understanding how to better conserve those species. As droughts become more frequent and water availability declines in many systems, understanding selection of water sources becomes even more important for conservation. Tinajas and anthropogenic catchments are critical ephemeral breeding sites for Sonoran Desert anurans. Tadpoles have been documented in both water types even though anthropogenic catchments can contain very high concentrations of ammonia. We currently do not know how amphibians are selecting breeding habitat. We tested three hypotheses of habitat selection based on resource quality, resource quality and territoriality, and proximity of water site to other water sites. Male *Anaxyrus punctatus* called from all sites regardless of habitat quality or male quality; however, they were found more often at sites within 2 km of other sites. This suggests that male desert anurans are selecting close breeding habitat regardless of quality for breeding, indicating ammoniated sites are likely either population sinks or ecological traps. Consequently, adding anthropogenic water sites, without managing to reduce ammonia, will provide low quality habitat that could cause long-term declines in desert anuran populations.

Keywords Habitat selection · Ecological trap · Ephemeral wetlands · Desert anurans · Ammonia

Introduction

Selecting appropriate habitat is critical for individual fitness and population persistence, and an understanding of selection is important for the conservation of a species (Caughley 1994; Jones 2001). Much work on habitat selection assumes animals select habitat based on the quality of resources or the quality of resources modified by interference competition (Fretwell and Lucas 1970), and understanding the factors that drive habitat selection should then give managers insights into how to better support wildlife populations. Unfortunately, managers are often faced with a paucity of information about habitat preference on which to base decisions. This is becoming more of an issue as climate change alters community and ecosystem structure and function (Walther 2010), potentially affecting how species are making choices about habitat. Managers attempt to mitigate climate affects through a number of mechanisms including management of habitat based on uncertainty and incomplete information (Scarlett 2010). An example of management based on ambiguity is the establishment of anthropogenic water sites in the desert to provide wildlife water. There is controversy over whether these sites actually help native species (Broyles 1995; Griffis-Kyle et al. 2014), although for some species there is evidence these sites may be important (Calvert 2015). It is essential that we understand the criteria that organisms are using to select these sites for use in order to more efficiently manage our natural resources.

Ephemeral water sites in the Sonoran Desert provide critical habitat for many wildlife species (O'Brien et al. 2006), and will become more important as climate continues to change. Air temperatures are increasing, and water availability is declining, leading to longer droughts and shorter hydroperiods in ephemeral wetlands (Seager et al. 2007; Intergovernmental Panel on Climate Change [IPCC]

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2014). This is especially challenging for desert anurans living in environments like the Sonoran Desert that already experience extreme summer maximum temperatures that exceed 40 °C, and annual precipitation that averages 17 cm (1981–2010s; NOAA National Climate Data; Gila Bend, AZ, downloaded 08 March 2015). Many desert anurans are explosive breeders, more active during the warmer summer months when monsoon storms cue them to emerge from their underground shelters to breed in ephemeral rain-filled pools (Creusere and Withford 1976; Sullivan 1989). Because of these desert species' dependence on ephemeral sites for reproduction, short hydroperiods can cause catastrophic losses of entire cohorts of tadpoles reducing lifetime fitness of adults (Newman 1987, 1989). As water availability declines in the future, fewer cohorts will make it successfully through metamorphosis, potentially leading to desert amphibian population declines.

Some summer breeding amphibian species in desert regions use ephemeral waters for reproduction. In the Sonoran Desert, these waters are generally tinajas and anthropogenic catchments. Tinajas are natural rock depressions, created by erosion and filled by rain, that serve as natural water sources for many wildlife species (O'Brien et al. 2006; Jocque et al. 2010). Land managers have also constructed artificial catchments to supplement water for wildlife in arid regions (Rosenstock et al. 2004; O'Brien et al. 2006). These anthropogenic catchments, designed to minimize evaporation and maximize the holding capacity of the site, funnel rainfall into a reservoir which is connected downslope to a trough that allows wildlife safe access to the water. However, the ammonia concentrations found in some of the anthropogenic catchments are much greater than those in tinajas (Hermosillo 2013; Griffis-Kyle et al. 2014), exceed the US Environmental Protection Agency's guidelines for freshwater aquatic life (US EPA 2013), and are known to cause mortality in amphibians and invertebrates tested (Camargo and Alonso 2006). Ammonia likely builds up in these anthropogenic catchments, because they are structurally different so that rains are not able to wash away decaying organic matter as happens in tinajas (Griffis-Kyle et al. 2014).

Water availability is declining in arid environments, so natural resource managers are likely to supplement water by establishing more anthropogenic catchments, hence the large concentrations of ammonia in these waters is of great concern. Since the ammonia levels found in some of these catchments are high enough to cause mortality in aquatic organisms like amphibians (Camargo and Alonso 2006), it is possible that those anthropogenic catchments function as ecological traps, attracting adults to breeding habitat, but having a negative effect on population growth (Pulliam 1988; Battin 2004). We must first determine how frequently adult anurans use these ammoniated waters as breeding sites before we can address whether they function as population sinks or ecological traps.

Adult desert amphibians are selecting breeding habitat based on unknown criteria. Selection could be based solely on habitat quality (ideal free selection: Fretwell and Lucas 1970), territoriality may modify their selection (ideal despotic selection: Fretwell and Lucas 1970), or they may simply choose the water site closest for breeding (proximal selection). We tested hypotheses of amphibian habitat selection including (1) males are more prevalent at habitats of higher quality and less prevalent at low quality sites with no detectable difference in male quality between sites (ideal free habitat selection); (2) males of higher quality are present at high quality breeding sites and male of lower quality are present at low quality breeding sites (ideal despotic habitat selection); (3) no sign of selection in terms of presence or male quality and animals found more often at more closely spaced water sites (proximate habitat selection).

Materials and methods

Study area

We sampled both tinajas and anthropogenic catchments at the Barry M. Goldwater Range East, located in the southwestern portion of Arizona, USA, in and around seven mountain ranges (BMGR East, Department of Defense, US Air Force) (Fig. 1). The BMGR East is in the Sonoran Desert, and is approximately 4250 km^2 ranging in elevation from 210 to 1097 m. Water availability for summer breeding anurans in the Sonoran Desert is controlled by summer monsoon rains. The average summer maximum temperatures in the Sonoran Desert reach 40 °C, and individual days can be much hotter. We sampled from July through October 2012 (total monthly precipitation were 2.9, 1.0, 0.8, and 0, respectively; mean maximum monthly air temperatures were 45.5 °C, 46.6, 42.2, and 40.5 °C, respectively—NOAA National Climate Data Center, July–October 2012, Gila Bend, AZ, USA, download: 08 March 2015).

Both tinajas and anthropogenic catchments are widely distributed across the seven mountain ranges. These water pools vary greatly in hydroperiod due to sporadic rainfall, fast evaporation rate, and reservoir size and design. For this study, we chose seven replicate tinajas and six replicate anthropogenic catchments (Fig. 1), that paired between a larger project (Griffis-Kyle et al. 2014) and sites with game cameras established by the US Department of Defense and US Fish and Wildlife Service.

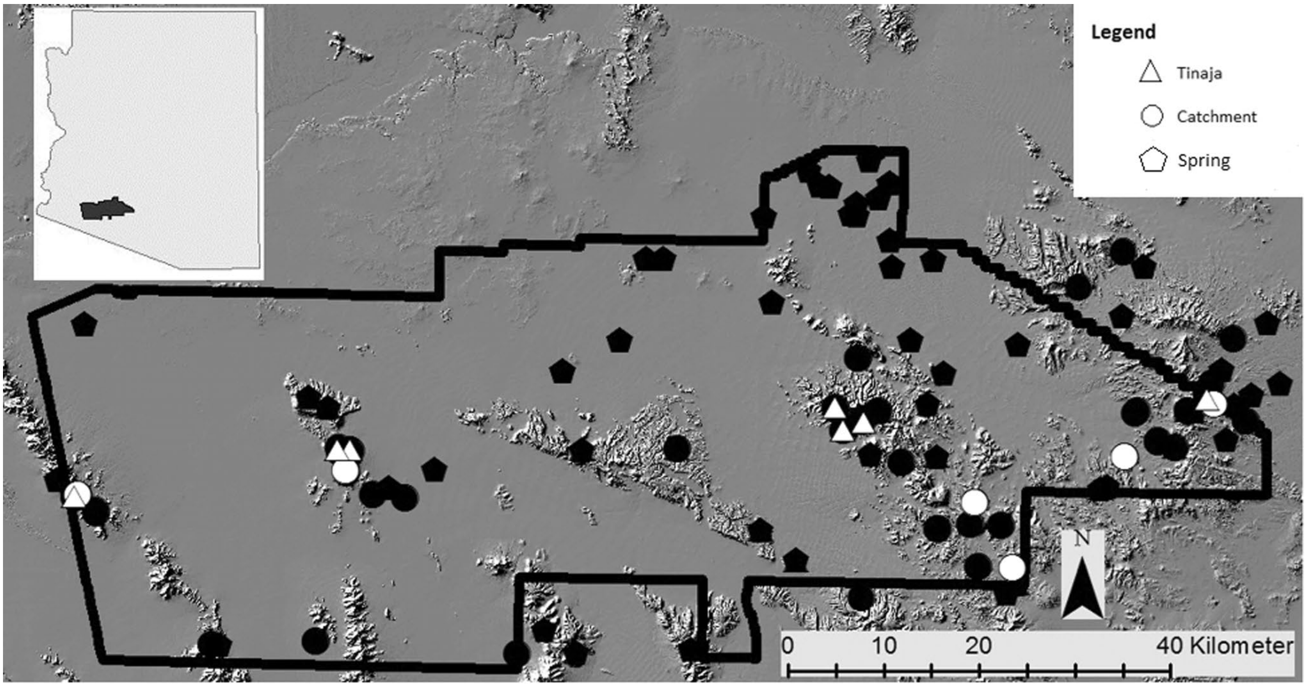

Fig. 1 Map of all water locations at the Barry M. Goldwater Range East in the Sonoran desert. White symbols represent the 13 water sites where we installed audio loggers for the study period from July to October 2012

Study species

We recorded three desert anuran species during their breeding period from July to October 2012: red-spotted toad (*Anaxyrus punctatus*), Couch's spadefoot toad (*Scaphiopus couchii*), and Sonoran Desert toad (*Incilius alvarius*). However, *S. couchii* and *I. alvarius* were scarce and did not provide enough data for this analysis, so we focused on *A. punctatus*. *Anaxyrus punctatus* is an explosive breeder (Degenhardt et al. 1996), cued to breed during hot summer months in this area by summer monsoonal rains that start in July. These seasonal summer monsoons fill the tinajas and anthropogenic catchments with water, in which female amphibians deposit their eggs after mating with calling males (Woodward and Mitchell 1991). *Anaxyrus punctatus* make identifiable advertisement calls during reproduction, which can be used to clearly distinguish them from other desert anuran species.

Habitat sampling

We measured water chemistry a minimum of twice during the sampling period, including: pH, temperature, and conductivity using hand held probes (MP-6p Portable Meter, Hach, Loveland Colorado, USA) and nitrate + nitrite and ammonia + ammonium using a hand held colorimeter on site (DR/890 Portable Colorimeter, Loveland Colorado, USA). We sampled other site variables including elevation, aspect, surface area of each pool, and shading. Elevation and aspect of each water site were calculated in ArcGIS 10.1 from a USGS National Elevation Dataset layer of roughly 10 m × 10 m resolution (1/3 arc second). The surface area ($area = \pi \times a \times b$) and volume $\left(\text{volume} = \left[\left(\frac{4}{3}\right) \times \pi \times a \times b \times c\right]/2\right)$ of each pool was approximated for an ellipsoid from measures of long and short diameters and water depth (meters). Shading of the water was estimated with a spherical densitometer (average of readings from water edge in cardinal directions). We recorded air temperature and relative humidity using data loggers (ibuttons—Dallas Semiconductor, Maxim, TX) placed in the shade, under vegetation slightly above ground level, at each water site, which sampled every 30 min from mid August to mid October 2012. For some of the measurements, we sampled only at the 13 water sites where audio loggers have been installed; however, ammonia concentration, surface area, and tadpoles were sampled at all 27 water sites that were visited. We used least-cost paths between water sites for our measure of isolation (calculated in Griffis-Kyle and Jenness 2013).

Amphibian survey

To quantify amphibian presence, activity, and quality, we used tadpole surveys at 27 water sites and audio data loggers to record amphibian vocalization at 13 water sites (Song

Meter SM2 Rev C by Wildlife Acoustic Inc.). We used up to 20 dip net sweeps to sample the water column for tadpoles once within 8 days of a rain and once within 15 days of a rain to catch both fast and relatively slower developing species. Lower frequency amphibian calls are correlated with large body size (e.g. Forester and Czarnowsky 1985; Ryan 1980; Márquez 1995) and overall male fitness (Howard 1978; Wilbur et al. 1978; Robertson 1986). The audio loggers recorded daily during the sampling period from 2200 to 0400 MST for 5 min intervals every 30 min with a rate of 32,000 samples per second. For analysis purposes 2200 was time zero and each hour was split into 100 divisions. We used Julian date for analysis. The recordings of the amphibian calls were saved as WAV audio files on external SD cards that were then transferred to a computer via a card-reader unit.

Audio file processing

We recorded calling males in order to assess male presence and male quality at each of the water sites. To review the sampled recordings and detect the amphibian calls, we used Song Scope Bioacoustics Software (Version 4.0 Wildlife Acoustics, Concord Massachusetts, USA). Song Scope is an automatic vocalization recognition software that identifies species using recognizers based on classification algorithms created from recorded calls and training data (Agranat 2009). To create recognizers, we used clear amphibian vocalizations of *A. punctatus* from our field recordings. To reduce background noise such as wind or rain, we used the freeware Audacity 2.0.6 (http://audacity-beta.en.softonic.com/#). We then categorized abundance of calling individuals using a standard index (0 = No detections; 1 = Individuals can be counted, spaces between calls; 2 = Call of individuals can be distinguished; some overlapping of calls; 3 = Full chorus, calls are constant, continuous, and overlapping) (Weir and Mossman 2005).

To test classification validity of Song Scope Software, we compared files in which Song Scope detected amphibian calls to random files in which Song Scope detected no calls. We randomly chose 50 files (250 min) of field detections via a pseudo-random number generator (Microsoft Excel 2013) and listened to them, identifying true positives (*A. punctatus* was present and detected by Song Scope), and false positives (*A. punctatus* was absent, but identified as present by the software). Then, we sampled 50 randomly chosen field recordings (250 min) with no Song Scope detections and identified true negatives (no *A. punctatus* calling and none detected by Song Scope), and false negatives (*A. punctatus* calling that was not detected by Song Scope).

To test if the external factors air temperature and relative humidity influence calling audio frequencies (Hz) of *A. punctatus*, we extracted calling events of *A. punctatus* from all field recordings. When determining the presence of *A. punctatus* all calls were considered. When assessing advertisement calls as indicator for male quality, we excluded calling events with calling index of 0 or 1. A calling index of 1 indicates that only single individuals called so no interference competition likely occurred, which means detecting assortment of males based on male quality was not possible. For each of these calling events of *A. punctatus*, we took the minimum and maximum of the high energy band (dominant frequency), in which the power spectrum was the strongest, of each audio file, and calculated the midpoints.

Analysis

We tested classification accuracy of Song Scope Software for *A. punctatus* using contingency table analyses and calculating likelihood ratios (true/false positives/negatives) (SPSS Version 22). To test for validity of Song Scope Software performance for *A. punctatus*, we calculated sensitivity and specificity. The sensitivity of this test refers to the ability of Song Scope Software to correctly identify the species that vocalized during the study period. The specificity of this test refers to the ability of Song Scope Software to correctly identify nights without calling events. To test for accuracy, we calculated the F1 scores. The F1 score is the harmonic mean of precision and sensitivity and estimates the accuracy of the test results, with 1 as best score and 0 as worst score (Fielding and Bell 1997; Powers 2011).

To identify differences in habitat quality between types of sites, we tested for five different site quality variables that varied between sites (ammonia concentration, surface area, elevation, aspect, and shading), and performed a Bonferroni correction on the alpha ($\alpha = 0.01$). Other site and water quality attributes did not vary between the different water types. We identified site attributes that were significantly different (ammonia concentration, and surface area). These variables were used as measures of habitat quality and were applied in an Analysis of Variance (ANOVA) for categorical predictors and regression methods for continuous variables (SPSS Version 22). The residuals were visually assessed and approximated normality.

To test if there was a difference in amphibian presence, absence, and calling activity of *A. punctatus* related to habitat quality, we performed a binary logistic regression for presence and ordinal logistic regression for calling activity. We performed a Bonferroni correction on the alpha ($\alpha = 0.025$) since we tested the two independent habitat quality variables: ammonia concentration and pool surface area.

To test if male quality differed between tinajas and anthropogenic catchments, we looked at calling frequency variables (Hz) of the calling males, and performed an ANCOVA to test if calling frequency variables (calling minimum, calling maximum, and calling midpoint) varied between these two site types. We found no relationship with relative humidity, but a positive correlation between air temperature calling frequencies, so we used temperature as a covariate with ammonia concentration and surface area in our analyses.

To test if distance of another tinaja would affect the presence of *A. punctatus* at water sites, we performed a binary logistic regression to evaluate presence and absence of *A. punctatus* related to least-cost-path distance (Griffis-Kyle and Jenness 2013). The number of sites we had audio loggers at was relatively few, so we used data from the larger project on *A. punctatus* tadpole locations for 27 sites. To decrease the probability of making a type 2 error, we used an alpha of 0.10.

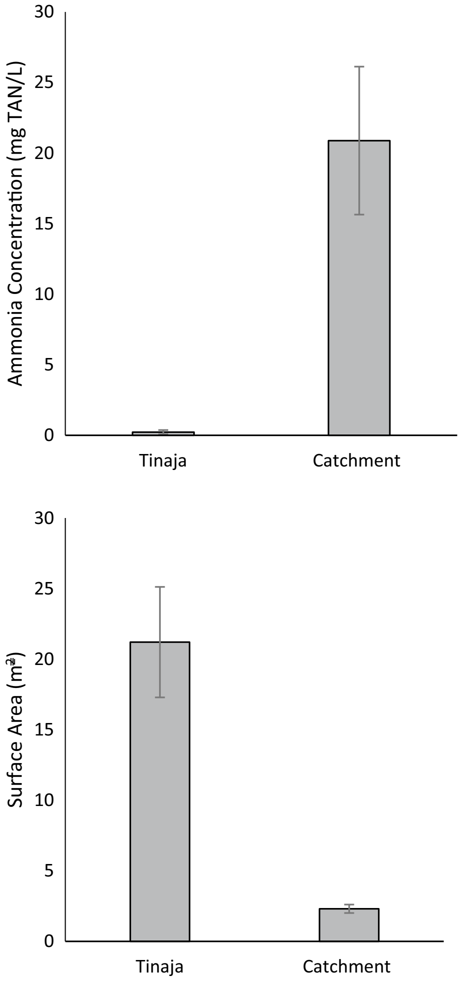

Fig. 2 Ammonia concentration was much greater in anthropogenic catchments ($n = 17$) than in tinajas ($n = 9$) (top graph). Surface area in tinajas ($n = 8$) was much greater than in anthropogenic catchments ($n = 16$) (bottom graph). Error bars on graphs represent standard errors

Results

In total, we recorded 15,099 audio files and a total of 1258.25 h from July to October 2012 at 13 water sites. *A. punctatus* occurred at every study site except one (Arizona Game and Fish Wildlife Water #636).

Song Scope Software 4.0 was able to correctly identify the presence and absence of *A. punctatus* (Contingency table analysis: $\chi^2 = 789.0$, $df = 1$, $p < 0.0005$). The sensitivity of the Song Scope Software to correctly identify vocalizations for *A. punctatus* was 66%. The 34% incorrectly classified were storms where rainfall masked all other sounds to the human ear or conversely, sounds that were too faint and the software missed. The specificity of the software to identify files without vocalizations was 99%. The F1 score, a measure of accuracy including precision and sensitivity, for *A. punctatus* was 0.79.

Ammonia concentration was significantly greater in anthropogenic catchments than in tinajas (ANOVA $F = 8.1$, $df = 25$, $p = 0.009$) (Table 1, Fig. 2). Pool surface area of tinajas was significantly larger than for anthropogenic catchments (ANOVA $F = 47.6$, $df = 25$, $p < 0.0005$) (Fig. 2). All other site descriptors did not vary significantly by site type (in all cases $F < 3.7$, $p > 0.05$ with a Bonferroni alpha of 0.01).

Neither site quality attributes, ammonia concentration or pool surface area, were significantly related to species

Table 1 Average, standard error (SE) and maximum for ammonia concentrations reported as concentrations in mg or total ammonia nitrogen per l, collected from water sites located at the Barry M. Goldwater Range East Modified from Griffis-Kyle and Jenness (2013)

	Anthropogenic catchment			Tinaja		
	Average	SE	Range	Average	SE	Range
pH	8.2	0.3	(6.3, 10.2)	7.7	0.3	(6.6, 9.9)
Ammonia[a]	22.2	5.3	(0, 55)	0.3	0.2	(0, 1.0)

Barry M. Goldwater Range East during the anuran breeding season July to October 2012 in the Sonoran desert. Toxicity of ammonia is dependent on pH, so pH is included in the table

[a] Maximum detection limit for test was 50 mg l^{-1} N-NH_3

presence (in all cases: $\chi^2 < 8$, $df = 1$, $p > 0.5$) (Fig. 3) or abundance during the nights recordings from July to October 2012 (in all cases $\chi^2 < 4$, df $= 1$, $p > 0.07$). None of the measured calling frequency variables, minimum, maximum, or midpoint, varied significantly by site type (in all cases $F < 2.6$, $df = 8$, $p > 0.2$). Tadpoles were present more often in waters with closer neighbors including ammonia concentration and pool surface area as covariates (Fig. 4) ($\chi^2 = 12.8$, $df = 3$, $p = 0.06$).

Discussion

We show the desert anuran, *A. punctatus*, does not assess habitat quality when selecting breeding sites and thus does not follow ideal free or ideal despotic models of habitat selection. Hence, habitat selection in this system does not equate with habitat quality. Our results show adult males select the closest habitats with water—proximal habitat selection. Proximal selection is caused by passive density-independent dispersal where individuals are dispersing from good breeding habitats without respect to resource availability (Delibes et al. 2001). As individuals disperse across the desert landscape, experiencing high temperatures and low water availability, any evidence of water may be a reasonable cue for staying. The opportunity to breed is potentially so limiting that populations may have evolved to take advantage of any available water for reproduction, regardless of its quality. Hence landscape level patterns of population extent may mimic patterns of diffusion rather than active selection (Delibes et al. 2001; Griffis-Kyle et al. 2011). Additionally, this pattern likely applies to other desert anurans as they tend to use any water available for breeding including very small puddles and potholes in roads (Griffis-Kyle unpublished data).

Neither presence nor abundance of *A. punctatus* were related to water type, physical structure or chemical attributes of the sites, suggesting male breeding site selection is not modeled appropriately by the ideal free model of habitat selection (i.e. pick the best until it is filled) (Fretwell and Lucas 1970). Other studies focused on larger scale habitat differences find patterns of selection based on factors such as surrounding vegetation (Boeing et al. 2014), soil properties (Dayton et al. 2004), and elevation and latitude (Bradford et al. 2003), but none have identified attributes of the water site itself as important in breeding site selection. This may be a function of natural selection in that it is more important for a desert anuran to take advantage of any available water for breeding rather than passing up the possibility to breed. If even a few individuals are successful, the trait to take advantage of any site would be retained in the population.

Better quality males are not excluding lower quality males from these small high quality water sites, as measured

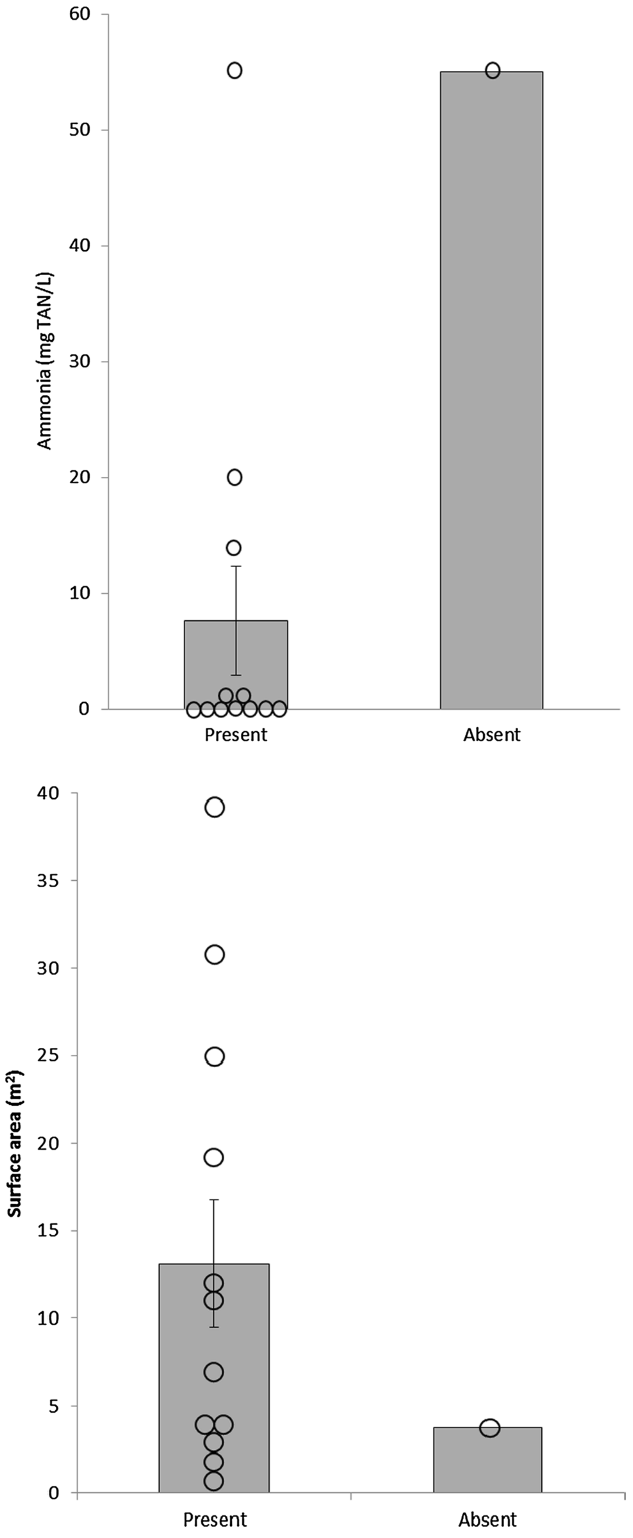

Fig. 3 The two habitat variables, ammonia concentration (top graph), and surface area (bottom graph) were not significantly related to *Anaxyrys punctatus* calling male presence. Circles represent data points; error bars represent standard errors. Calling males were only absent at one site (calling index 0; Arizona Game and Fish Wildlife Water #636); therefore, there are no error bars for the absent bars

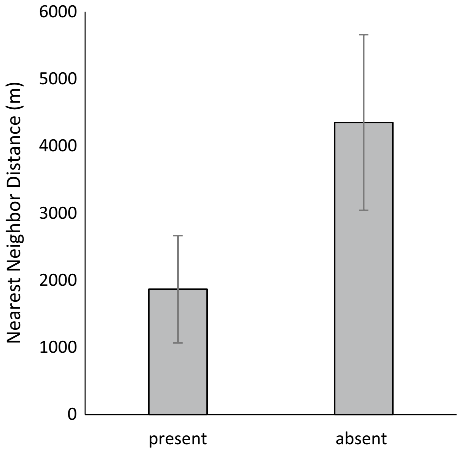

Fig. 4 Tadpoles of A*naxyrus punctatus* were present at tinajas that were located closer together, and absent from more isolated water ($n = 25$). Error bars on graphs represent standard errors

by calling frequency, either. Hence, this system does not approximate the ideal-despotic model of habitat selection (i.e. territoriality) (Fretwell and Lucas 1970; Van Horne 1983). This is not surprising, as most of the territorial behaviors in anurans at breeding pools are individuals protecting oviposition sites rather than excluding individuals from the water pool (Wells 2010). There has been work demonstrating competitive exclusion of species (e.g. Dayton and Fitzgerald 2001), but not exclusion of individuals within the same species.

It is disturbing that *A. punctatus* males are unable to assess habitat quality at ephemeral desert breeding sites. Many of the catchments contained ammonia concentrations known to cause mortality in aquatic organisms (Camargo and Alonso 2006). If females respond to the calling males at these low quality sites, embryos and larvae will be exposed to very high concentrations of ammonia (measured of > 14 mg TAN/L, pH Griffis-Kyle et al. 2014; background concentrations of 0.1 mg TAN/L, Mueller et al. 1992), greater than the US EPS's criteria for chronic concentrations for these warm waters (not to exceed 1.9 mg TAN/L at pH 7 and 20° C more than once in 3 years on average, US EPA 2013). We found tadpoles at some of the water sites with elevated ammonia. Large ammonia concentrations interrupt diffusion of substances across gills and cause the buildup of ammonia in the tissues of aquatic organisms (Russo 1985). This buildup of ammonia in tissues causes damage to gills (Lang et al. 1987) and interferes with behavior and physiological processes such as respiration, metabolism, and circulation, which leads to slowed growth and development, suppressed immune function, and death (Russo 1985; Jofre and Karasov 1999; Camargo and Alonso 2006; Griffis-Kyle and Ritchie 2007). We also detected two other species calling at anthropogenic catchments, *S. couchii* (Couch spadefoot toad), and *I. alvarius* (Sonoran toad), which were not included in our analyses due to insufficient data, but indicate that other amphibian species are also likely unable to sense the high ammonia concentrations.

We have shown that proximate selection is a better fit to the patterns of occurrence observed in the field, where individuals disperse and then use the closest water site for breeding. Because these sites can be low quality habitat, and there is evidence of reproduction in them (Griffis-Kyle et al. 2014), they likely function as population sinks (Pulliam 1988). Habitat sinks, such as these ammoniated catchments, may be difficult for amphibians to judge because they do not actually see the breeding failure; individuals are long gone from the water site when tadpoles hatch, develop, and go through metamorphosis (Delibes et al. 2001). Human-modified systems have been identified elsewhere as potential habitat sinks because the modifications humans make are difficult or impossible for organisms to assess (Tilton 1995; Delibes et al. 2001). However, before we can determine whether these sites are habitat sinks or ecological traps that are causing population declines (Battin 2004), we must assess female response to male calling at these sites and measure amphibian reproductive effort and success.

We demonstrated that the male *A. punctatus* are making what is likely a maladaptive choice by selecting low quality habitat instead of higher quality breeding sites. These sites may be even more problematic for the populations because in source-sink dynamics, habitat selection equates with habitat quality (Battin 2004). Attractive sinks, also called ecological traps, those sites in which animals cannot assess quality, lead to this maladaptive habitat selection (Delibes et al. 2001). So in a landscape with mainly natural waters, these ammoniated catchments may not have a large effect on population growth. However, the addition of anthropogenic water sites is likely to continue, especially as the Sonoran Desert is expected to warm with increasing temperatures and declining amounts of, and increasing variability in, rainfall (Weiss and Overpeck 2005; IPCC 2014). As more catchments are added, they will dilute the likelihood of a dispersing individual finding a natural source, and above some threshold of density may lead to population extinction (Delibes et al. 2001).

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Author contribution statement KGK designed the study, was awarded funding, created sampling protocols and supervised data collection, mentored graduate student, and contributed to and edited manuscripts. AK transcribed, processed, analyzed the audio-recording data, and wrote the manuscript.

Compliance with ethical standards All applicable institutional and national guidelines for the care and use of animals were followed.

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