Supplemental File

Arroyo toad field Surveys and data analysis

Using field data (2003–2018) collected by the U.S. Geological Survey (USGS), we identified factors that influence breeding habitat occupancy and colonization-extinction dynamics of arroyo toad in three major drainages in San Diego County on Marine Corp Base Camp Pendleton: Santa Margarita River (39 km); San Mateo Creek (32.3 km); (Swift et al., 2016) and San Onofre Creek (18 km). The USGS divided each drainage into n = 60 linear 1.5 km blocks and conducted field surveys annually in one randomly selected 250 m reach within each block. Surveys focused on locating egg strings and tadpoles of arroyo toad during the breeding season because both are readily observable during the day, easy to distinguish from other amphibian eggs and larvae, and directly indicate the presence of reproductive adults.

After confirmation of breeding activity, the USGS conducted a minimum of two surveys for each 250 m reach, and up to four surveys in sixteen additional reaches depending on the presence surface water. The following data were recorded during each survey: presence of egg strings and tadpoles of arroyo toad; presence and identification of all other aquatic animal species (native and non-native); presence and identification of non-native aquatic plants. Environmental variables hypothesized to affect occupancy, colonization, and/or extinction probabilities of arroyo toad across years were also recorded (Table S1).

We used the software PRESENCE (MacKenzie et al. 2002, 2003, & 2018) to estimate the probability of site occupancy by arroyo toad. We used Akaike's Information Criterion (AIC) and model selection procedures described by Burnham and Anderson (2002) to rank and compare models, assembling and comparing models in a stepwise manner. To reduce model complexity, we initially removed correlated variables by category (water, aquatic vegetation, etc.; Table S1) based on Pearson and Spearman rank tests (Bonferroni adjusted $p < 0.05$ and $r/\pi > 0.25$; Bonett and Wright 2000). If certain correlated variables were of particular interest (e.g., NNI score, specific non-native taxa, etc.), we tested them in separate models. We ran multi-season occupancy models, where occupancy status was allowed to shift between seasons, using presence/absence data for arroyo toad in a multi-state format (MacKenzie et al. 2002, 2003, 2011). Three states were possible: habitat dry and unoccupied, habitat wet and unoccupied, and habitat wet and occupied. Some transition parameters were fixed to 0 if certain states were not possible (i.e. dry and tadpoles present) or set equal to one another to estimate the following parameters: 1) the probability that habitat was dry/wet during breeding season, and if wet, 2) the probability of occupancy (tadpoles) by arroyo toad, 3) probability of colonization (tadpoles detected when no tadpoles detected the previous year) and 4) probability of extinction (no tadpoles detected when tadpoles detected the previous year).

For multi-season models, we initially focused on modeling first year occupancy probabilities. We then selected the top ranked models from that analysis for stepwise modeling of colonization and extinction probabilities. If more than one covariate resulted in model AIC values that were substantially lower than the null model (> 2 AIC), those models were evaluated together. Models with covariates exhibiting evidence of poor fit (i.e., no convergence reached, variance-covariance matrix unable to be produced, and standard error of a parameter estimate being greater than the parameter estimate value) were not evaluated.

To further evaluate the relationship between the non-native species index (NNI) and beaver dam presence, we performed two sets of analyses using Bayesian multilevel models in the R package brms (Bürkner 2017). First, we fit a Poisson generalized linear mixed effects model (GLM), which included a fixed intercept, fixed effect of beaver presence, and a random effect for year to account for repeated measures (Duarte et al. 2018). We evaluated model fit by ensuring that all model parameters had Gelman-Rubin values <1.1, by visually inspecting the posterior samples for convergence, and by generating posterior predictive plots to measure within-sample predictive performance. We specified default priors and ran the model across 4 chains for 2000 iterations, with a warmup of 1000 iterations, and a thinning rate of 1, totaling 4000 post-warmup samples. This model showed that the estimated NNI was nearly three times greater (mean = 2.9; 95%CI = 2.1–3.9) at sites where dams were present (mean = 1.9, 95%CI = 1.3–2.6) compared to sites where they were absent yet still contained water (mean = 0.7, 95%CI= 0.5–0.8).

We also performed a categorical regression treating NNI as a discrete state variable (Congdon 2005), with NNI modeled as a function of an intercept and beaver dam presence. We included year as a random effect, and specified default priors for the intercepts at each NNI level and the effect of beaver dams on NNI. We evaluated model fit and performed the analysis using the same run specifications as described above. Default priors used for these analyses are viewable in the model object after it is run in R. This analysis confirmed that a higher NNI score was more probable when a beaver dam was present (Fig 2B, main text).

The data used to perform the occupancy analysis (Supplemental Data.xlsx) and R code for running the Poisson GLM and categorical regression (Supplemental R code.pdf) are downloadable form the journal website.

Table S1. Covariates used to estimate habitat occupancy for the arroyo toad. Data collection for *covariates began in 2004 and were evaluated for association with colonization/extinction probabilities from 2004-2018, but not for first year occupancy in 2003.

Covariate	Definition	Correlated Variables	Hypothesized effect
Detection probability			
Year	Year of survey	n/a	n/a
*Low flow shallow water index	Proportion of site containing low flow shallow water	Channel velocity, discharge, dissolved oxygen (DO_{sat})	Positive
*Aquatic vegetation cover index	Total cover of submergent, emergent, algae mat	Component variables correlated	Negative
Presence of predators and/or competitors (tested individually)	Western toad, beaver dams, crayfish, predatory fish, bullfrog, non-native species index (sum of last 3 species)	Non-native Index correlated to component variables	Negative
Initial Presence/ Absence (Ψ) and Colonization/Extinction (γ, ε)			
Year	Year of survey	n/a	n/a
*Entrenchment ratio	Confinement of channel: flood prone width ÷ bank width (lesser value = more confined)	Flood prone width, bank width	Negative
*Channel sand cover index	Proportion of channel with sand	Flood plain sand cover	Positive
*Aquatic vegetation index	Yearly estimates of total cover from vegetation	Aquatic submergent vegetation index, aquatic cover index	Negative

*Disturbance level index	Level of disturbance from training activities (artillery, troops, heavy equipment)	n/a	Negative
Hydroperiod	Ephemeral, perennial	n/a	Both
Presence of predators/ competitors and hydroperiod (tested individually)	Hydroperiod (ephemeral, perennial), western toad, beaver dams, crayfish, predatory fish, bullfrog, non-native index (sum of last 3 species)	see above	Negative

Native species of conservation concern

In addition to those provided in the main text, we provide examples of native aquatic species of conservation concern in the Southern California/Northern Baja California Coast Ecoregion that have potential to be negatively impacted by beaver-modified habitat. We present the federal and state listing statuses under the U.S. Endangered Species Act (ESA) and the State of California (CA), respectively (U.S. Fish and Wildlife Service, Environmental Conservation Online System, https://ecos.fws.gov: California Department of Fish and Wildlife (CDFW), California Natural Diversity Database. https://wildlife.ca.gov/Data/CNDDB).

For reptiles and amphibians, Thompson et al. (2016), an extension of the original work of Jennings and Hayes (1994), divide the species of special concern (SSC) into three priority categories based on the immediacy and severity of threats (Priority 1–3, with Priority 1 being the highest). All listed below are Priority 1 species, which are those anticipated to experience further decline or extirpation without any immediate management intervention. Moyle et al. (2015) divide the SSCs for fish into five status categories: extinct, critical, high, moderate, and low concern. Two listed below are of critical concern (high risk of extinction; range reduced or restricted in California; population abundance low or declining; threats projected to reduce remaining California habitat and populations in <10 generations), one is listed as high (high risk of becoming a critical concern; range and abundance reduced; existing habitat and populations continue to be vulnerable in <10 generations), and one is of moderate concern (declining, fragmented and/or small populations possibly subject to rapid status change; management actions needed to prevent increased conservation concern).

<u>Santa Ana speckled dace *Rhinichthys gabrielino*</u> (ESA not listed; CA SSC; Moyle et al. 2015, 2023) critical risk): The Santa Ana speckled dace is currently under review for protection under the U.S. Endangered Species Act (https://ecos.fws.gov/ecp/species/4124). The species is at high risk to extinction because remaining populations are small, fragmented, and increasingly subject to threats posed by fire, post-fire debris flows, water extraction, invasive species, pollution, and expanded urbanization. Populations survive in gravel-cobble riffles with overhanging riparian vegetation (Moyle et al. 2015). The streamlined body form is characteristic of species that inhabit flowing water (Moyle 2002), including pools in lower gradient streams (Feeney and Swift 2008; O'Brien et al. 2011), but not backwaters or standing water. Populations are now restricted to headwater areas in the Los Angeles, San Gabriel, and Santa Ana Rivers, including Cajon Creek in the Santa Ana River where beaver was recently discovered in 2020 (R.N. Fisher, pers. obs.), and historically in the headwaters of the San Jacinto River. Non-native predatory fish species are common throughout the species' range, including brown trout (*Salmo trutta*), hatchery-stocked rainbow trout (*Oncorhynchus mykiss*), red shiner (*Cyprinella lutrensis*), and various species of bass. American bullfrog and alien crayfishes are also known predators of dace (Moyle et al. 2015).

Santa Ana sucker *Catostomus santaanae* (ESA threatened, USFWS [2000]; Moyle et al. (2015) critical risk): Santa Ana sucker occupies stream reaches with alluvial/cobble substrate, riffles, high flow rates, and is well-adapted to the effects of seasonal and multi-year climate oscillations that result in boom-and-bust demography (Moyle 2002). While beaver is currently and historically unknown from the San Gabriel Mountains where populations of Santa Ana Sucker occur in two major watersheds (Los Angeles and San Gabriel Rivers), beaver has been introduced to the upper Santa Ana River Watershed in the San Bernardino Mountains (Hensley 1946) and was recently observed in the Cajon Creek tributary (R.N. Fisher, pers. obs.). The origins of beaver in Cajon Creek are unknown, with the nearest known occupied habitat being more than 20 km to the northeast in lower Deep Creek. Plans are currently underway to introduce Santa Ana Sucker to historic parts of the range in upper Santa Ana River Watershed and other areas with suitable habitat that may have been important for maintaining metapopulation structure and dynamics (https://www.sbvmwd.com). Extant populations remain in the lower Santa Ana River in a heavily urbanized area referred to as the 'Inland Empire' near Riverside. Presence of beaver has potential to alter preferred sucker habitat through sedimentation, reduced stream energy and by increasing the richness and abundance of invasive predators.

Tidewater goby *Eucyclogobius newberryi* (ESA endangered, USFWS [1994]; Moyle et al. (2015) high risk): The tidewater goby (*E. newberryi*) is listed as endangered under the U.S. Endangered Species Act. However, Swift et al. (2016) distinguish a southern species (*E. kristinae*), which occurs south of the Los Angeles Basin, from a northern species (*E. newberryi*). The two gobies are ecologically similar to one another and references pertinent to both species are used to describe the biology here.

The species inhabits seasonal coastal lagoons with brackish, cool, and well-oxygenated water (Irwin and Soltz 1984; Swift et al. 1989). Because populations occur in the lowest parts of a watershed, any upstream disturbance has the potential to affect this species. Individuals prefer shallow sandy bottoms surrounded by emergent vegetation, and sandy substrate is required for breeding burrows (Swenson and McCray 1996; Swenson 1999). Beaver ponds trap nutrients in muddy, benthic sediments, preventing them from reaching lagoons and potentially affecting the composition of sediments and nutrient levels in lagoons (Naiman et al. 1994; Anderson and Rosemond 2010). Evidence suggests that beaver dams and deeper ponded water are obstacles to the upstream passage of tidewater goby unless strong storm flows remove the dams at least seasonally (Swift et al. 1997). Tidewater goby has been extirpated at several historic localities soon after non-native centrarchids were introduced or washed into lagoons from upstream areas, with largemouth bass *Micropterus salmoides*, green sunfish *Lepomis cyanellus*, black bullhead *Ameiurus melas* being known predators (Swift et al. 1989, 1994, 2018). Other introduced non-native gobies (i.e., yellowfin goby *Acanthogobius flavimanus*, and Shimofuri goby *Tridentiger bifasciatus*) are also known predators and competitors of tidewater goby (Matern 2001), as are American bullfrog (*Lithobates catesbeianus*) and red swamp crayfish (*Procambarus clarkii*) (Swift et al. 2018).

Pacific lamprey *Entosphenus tridentatus* (ESA not listed; CA SSC; Moyle et al. (2015) moderate risk): Ammocoetes (i.e., larvae) are usually burrowed into well-oxygenated, fine to coarse sandy substrate in slow to moderate flows of streams. They have also been collected in beaver dams, reservoirs, freshwater mussel beds and the hyporheic zone, but it is unknown whether these are preferred habitats (Goodman and Reid 2012). Migration from freshwater natal habitat to marine feeding grounds is dependent on punctuated, high flow events during the winter and spring (Goodman et al. 2015). Because longer migration duration can reduce fitness and increase mortality in anadromous fishes (Schaller et al. 2014), Pacific lamprey rely on strong currents during these storm events to reduce the travel time required to reach estuaries (Goodman et al. 2015). Stabilization of the habitat and disruption of natural flow regimes, therefore, has potential to decrease survivorship of emigrating individuals, while at the same time create conditions that are favorable to invasive predators.

While it is widely agreed that larval and juvenile lamprey are preyed upon by introduced bass, green sunfish, and bullhead (USFWS 2019), the U.S. Fish and Wildlife Service does not consider them to be a major threat on the grounds that invasive predators 'have generally occupied the system (i.e., CA South Coast Region) since the late 1800s'. In Denmark, dams constructed by reintroduced Eurasian beaver (*Castor fiber*) in Denmark are capable of impeding threespine stickleback (*Gasterosteus aculeatus*) and brook lamprey (*Lampetra planeri*) in narrow stream systems (Elmeros et al. 2003).

Western pond turtle *Actinemys marmorata* (ESA under review: CA SSC; Thompson et al. 2016) The western pond turtle is currently being reviewed for listing under the U.S. Endangered Species Act (https://ecos.fws.gov/ecp/species/1833). Predominant threats including land conversion, habitat fragmentation, and competition and predation by non-native species (Thompson et al. 2016). Invasive American bullfrog now occurs across much of the range of western pond turtle and is a known predator on the species, with hatchlings and small juveniles being the most vulnerable (Holland 1994; Lovich and Meyer 2002; Hallock et al. 2017; Lovich et al. 2017; Nicholson et al 2020). Invasive crayfish and centrarchid fish are also known predators. Introduced red-eared slider (from the pet trade) is also well-established throughout the range of western pond turtle and may be a competitor (Bury 2008).

Although western pond turtle occurs in broad range of habitats (e.g., rivers, streams, lakes, ponds, reservoirs, marshes, and other wetlands), the species primarily occupies semi-permanent or ephemeral water bodies with abundant basking substrate (e.g., downed trees, logs, and large rocks) in the southern part of the range (Stebbins 2003; Bury and Germano 2008). While it could be argued that non-native beaver provides these conditions, beaver-invaded areas may be dominated by invasive predators that require permanent, slow moving, pooled habitat for survival. Evidence suggests that the high abundance of invasive predators in coastal habitat of southern California has already led to the replacement of western pond turtle, as remaining populations tend to survive in remote areas that have yet to become occupied by these same predators (Nicholson et al. 2020).

California red-legged frog *Rana draytonii* (ESA threatened, USFWS [1996]: CA SSC; Thompson et al. 2016) The California red-legged has declined in southern California since the 1960s, and ecologists broadly agree that non-native aquatic predators and competitors are key drivers of this decline (Jennings and Hayes 1994; Thompson et al. 2016). In the southern California/Northern Baja California coast ecoregion, breeding occurs in ponded areas within streams that are subject to intermittent, flashy flows (USFWS 1996). Doubledee et al. (2003) showed that the California red-legged frog co-exists with bullfrog in some areas because intermittent scouring events cause enough bullfrog mortality to sufficiently reduce competition and predation to levels where the California red-legged frog does not become extirpated. Population re-establishment efforts are currently being conducted through collaborative efforts by the USGS, Fauno del Noroeste (https://www.faunadelnoroeste.org), the San Diego Natural History Museum, and the Nature Conservancy in the southern California/Northern Baja California coast ecoregion, with more anticipated given current success. Mitigation or elimination of threats such as invasive predators are typically considered by managers when evaluating the efficacy of re-establishment efforts.

The history of Beaver Hollow on U.S. Geological Survey topographic maps

Drew Decker (National Map liaison, U.S. Geological Survey) assisted us in using the Geographic Names Information System (GNIS) to trace the possible origin of the name 'Beaver Hollow' on USGS topographical maps for San Diego County. GNIS was cooperatively developed by the U.S. Geological Survey and the U.S. Board on Geographic Names to provide information about the official names for places, features, and areas in the states, District of Columbia, and territories of the United States (https://www.usgs.gov/core-science-systems/ngp/board-on-geographic-names). GNIS contains records on more than two million geographic names in the United States and includes all feature types except for roads and highways.

According to GNIS, Beaver Hollow extends across portions of both the Alpine and Dulzura 1:24,000 scale topo maps. The Alpine map is also within the larger El Cajon 1:63,000 scale map, and the Dulzura map is within the larger Jamul 1:63,000 scale map. Both Alpine and Dulzura are within the still larger Cuyamaca 1:125,000 scale map, the same area of which is covered by the 1:250,000-scale Southern California Sheet #2 map. The oldest Alpine 1:24,000-scale map from 1955 and the oldest Dulzura 1:24,000-scale map from 1972 both show Beaver Hollow. However, the oldest El Cajon 1:63,000-scale map from 1893 and subsequent versions from 1901 and 1903 do not show the feature. Later reprints of the original 1903 map from 1909, 1916, 1930, 1941 also do not have the name. However, the next version of the El Cajon 1:63,000-scale map from 1939 does include Beaver Hollow.

The oldest Jamul 1:63,000-scale map is from 1943 and the name is there. Similarly, the name appears in the oldest Cuyamaca 1:125,000-scale map printed in December 1903. Reprints of the Cuyamaca map from 1909, 1912, and later also include the name.

The oldest Southern California Sheet #2 1:250,000-scale map is from 1904, and the name is not there. However, the small scale of this map and its limited detail likely precludes many feature names from being included. The name is also not on the 1914 and 1948 reprints.

In summary, the oldest maps consisting of the El Cajon 1:63,000-scale map from 1893 and the subsequent version from 1901 do not show Beaver Hollow. The named feature first appears on the oldest Cuyamaca 1:125,000-scale map printed in December 1903, but the origins of the name itself could not be determined.

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