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Informing recovery in a human-transformed landscape: Drought-mediated coexistence alters population trends of an imperiled salamander and invasive predators

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ABSTRACT

Understanding the additive or interactive threats of habitat transformation and invasive species is critical for conservation, especially where climate change is expected to increase the severity or frequency of drought. In the arid southwestern USA, this combination of stressors has caused widespread declines of native aquatic and semi-aquatic species. Achieving resilience to drought and other effects of climate change may depend upon continued management, so understanding the combined effects of stressors is important. We used Bayesian hierarchical models fitted with 10-years of pond-based monitoring surveys for the federally-endangered Sonoran Tiger Salamander (*Ambystoma mavortium stebbinsi*) and invasive predators (fishes and American Bullfrogs, *Lithobates catesbeianus*) that threaten native species. We estimated trends in occupancy of salamanders and invasive predators while accounting for hydrological dynamics of ponds, then used a two-species interaction model to directly estimate how invasive predators affected salamander occupancy. We also tested a conceptual model that predicted that drought, by limiting the distribution of invasive predators, could ultimately benefit native species. Even though occupancy of invasive predators was stationary and their presence in a pond reduced the probability of salamander presence by 23%, occupancy of Sonoran Tiger Salamanders increased, annually, by 2.2%. Occupancy of salamanders and invasive predators both declined dramatically following the 5th consecutive year of drought. Salamander occupancy recovered quickly after return to non-drought conditions, while occupancy of invasive predators remained suppressed. Models that incorporated three time-lagged periods (1 to 4 years) of local moisture conditions confirmed that salamanders and invasive predators responded differently to drought, reflecting how life-history strategies shape responses to disturbances. The positive 10-year trend in salamander occupancy and their rapid recovery after drought provided partial support for the hypothesis of drought-mediated coexistence with invasive predators. These results also suggest management opportunities for conservation of the Sonoran Tiger Salamander and other imperiled organisms in human-transformed landscapes.

1. Introduction

Additive or interactive threats can increase extinction risk, especially for populations that have declined substantially or for species with small distributions (Didham et al., 2007; Fagan et al., 2002; Laurance and Williamson, 2001). In highly-altered landscapes, effects of habitat loss or transformation are often compounded by invasive species that directly (e.g., predation) or indirectly (e.g., competition or disease) reduce survival and other fitness components of native species (Didham et al., 2007; Johnson et al., 2008; Lozon and MacIsaac, 1997). Imperiled species in altered landscapes are also at

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greater risk from extrinsic forces, such as stochastic variation in climate (Maschinski et al., 2006; Opdam and Wascher, 2004).

Forecasted increases in drought for many areas, and increased variation in precipitation as a whole, portend a bleak future for many aquatic species (Cook et al., 2015; IPCC, 2013). Accelerated drying of water bodies during drought increases the risk of losing entire cohorts, and crowding of individuals into smaller volumes of water can increase predation and disease transmission (Greer et al., 2008; Holling, 1959). One strategy to reduce negative effects of climate change is to manage for climate resilience, such as through maintenance of habitat heterogeneity and population connectivity or by protecting particularly important habitats that are resistant to change (Pittock et al., 2008; Wilby et al., 2010). For example, land managers can construct or modify basins or manage flows so water bodies hold water long enough to benefit target species (Chandler et al., 2015; DeMarais and Minckley, 1993; Hamer et al., 2016).

In landscapes with few natural water bodies, managing for climate resilience presents a dilemma, because increased permanence of water can aid invasion by non-native species (González-Bernal et al., 2012; Hobbs and Huenneke, 1992). Disturbances such as severe drought can also have unpredictable effects on community structure. In some cases, drought can facilitate coexistence between native and invasive species (Hobbs and Huenneke, 1992), but in other cases, drought can facilitate invasion or magnify species interactions (Bêche et al., 2009; Rehage et al., 2014). Therefore, understanding how the combination of increased drought and climate variation, habitat management, and invasive species affect imperiled species is critical for conservation.

In the southwestern USA, the compounded threats of land transformation, limited water, and spread of non-native, invasive predators have caused high rates of decline for many native, aquatic species (Fagan et al., 2002; Olden and Poff, 2005), including amphibians such as the federally-endangered Sonoran Tiger Salamander (*Ambystoma mavortium stebbinsi*) (USFWS, 2002). This subspecies occurs only in one valley along the USA–Mexico border. As is common in arid landscapes worldwide (e.g., González-Bernal et al., 2012; Davies et al., 2013), most naturally-occurring aquatic habitats were destroyed or highly altered and replaced with impoundments for livestock (Maret et al., 2006; Meffe, 1984). In these situations, persistence of some native species might depend upon continued human interventions. To design and manage for water body features that will provide resilience to climate change in the face of numerous pressures, managers need detailed information on status and trends of native species, what threatens them, and how habitat features can ameliorate those threats.

To determine the status of the Sonoran Tiger Salamander and changes in its stressors, we used hierarchical models to estimate annual occupancy of salamanders and invasive, non-native (hereafter, invasive) fishes and American Bullfrogs (*Lithobates catesbeianus*) using 10-years (2004–2013) of surveys of water impoundments (hereafter, ponds). We had four objectives. First, we estimated changes over time (trend) in proportion of ponds occupied by the Sonoran Tiger Salamander with models that incorporated hydrological dynamics of ponds. Second, we assessed changes in threats to salamanders by estimating trends in annual occupancy of invasive predators. Third, we used a two-species interaction occupancy model (MacKenzie et al., 2004; Richmond et al., 2010) that incorporated variation in habitat features to explicitly estimate how presence of invasive predators affected the probability of presence of salamanders. Last, we used different time lags (1 to 4 years) of the Standardized Precipitation Evaporation Index (Vicente-Serrano et al., 2010) to evaluate a conceptual model developed for this system that predicted drought could mediate coexistence of native and invasive species (Maret et al., 2006). Our objectives and analyses provide important information for the management and recovery of an endangered salamander and inform how interactions among land-use change, invasive species, and climate change can affect resilience of rare species.

2. Materials and methods

2.1. Study system

The Sonoran Tiger Salamander is limited to the upper drainages of the Santa Cruz and San Pedro rivers in the San Rafael Valley and surrounding foothills in Arizona, USA, and northern Sonora, Mexico (Jones et al., 1988; USFWS, 2002). This valley is a mix of private and public lands characterized by grasslands, evergreen woodlands, and narrow riparian forests. The salamander was federally listed as endangered without critical habitat in 1997, with primary threats including small geographic range, predation from invasive fishes and American bullfrogs, frequent die-offs from disease, and introgression with Barred Tiger Salamanders (*A. mavortium mavortium*) that were introduced as part of the bait trade (Jones et al., 1988; USFWS, 2002). Small population sizes and limited gene flow have caused inbreeding that may further reduce population viability (Jones et al., 1988; Storfer et al., 2004). Hybrid animals cannot be identified reliably in the field and the current extent of introgression is unknown, but for management purposes, all tiger salamanders in the San Rafael Valley are treated as Sonoran Tiger Salamanders (Hossack et al., 2016).

Sonoran Tiger Salamanders are large (>330 mm total length) and can metamorphose and colonize land, where they presumably spend most of their time underground (Petranka, 1998). Alternatively, in ponds that retain water for >1 year, salamanders can mature as gilled, aquatic paedomorphs (branchiate adults). Breeding occurs primarily from February through early April and larvae require 14–16 weeks to metamorphose (Collins et al., 1988). In the absence of fish, larval and paedomorphic tiger salamanders are often the dominant predators (Holomuzki et al., 1994). Historically, Sonoran Tiger Salamanders would have occurred primarily in ciénegas (spring-fed wetlands) and possibly riverine marshes and backwaters. Since most of these habitats were destroyed or heavily altered during the late 19th and early 20th centuries (Hendrickson and Minckley, 1984), most available water bodies are now impoundments that have been constructed or modified to provide water for livestock.

2.2. Data collection

Monitoring was conducted from 2004 to 2013 by sampling ponds for presence of salamanders and other aquatic species. Each year, 42–70 ponds were selected randomly from the population of ~300 accessible sites that had potential to hold water during the breeding season (Table 1, Fig. 1). In total, 156 ponds were sampled during December–July (mean = 19 March, range = 01 Dec – 01 July) for 1 to 8 years (mean = 3.5, SD = 1.9). Across all years, the distance to the nearest

Table 1
Surveys of ponds per year, detections of Sonoran Tiger Salamanders and invasive predators, and number of dry ponds in the San Rafael Valley, Arizona (USA), from 2004 to 2013.

Year	Surveyed once	Surveyed twice	Salamanders detected	Invasive predators detected	Dry
2004	15	27	13	8	17
2005	18	24	14	12	17
2006	46	10	8	10	22
2007	36	6	15	10	8
2008	39	5	17	13	18
2009	62	8	15	9	24
2010	49	4	24	8	8
2011	58	10	24	10	9
2012	62	8	23	15	21
2013	50	13	24	12	17