



## Identifying factors linked with persistence of reintroduced populations: Lessons learned from 25 years of amphibian translocations

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### ABSTRACT

Conservation translocations are increasingly used to help recover imperiled species. However, success of establishing populations remains low, especially for amphibians. Identifying factors associated with translocation success can help increase efficiency and efficacy of recovery efforts. Since the 1990s, several captive and semi-captive facilities have produced Chiricahua Leopard Frogs (*Rana chiricahuensis*) to establish or augment wild populations in Arizona and New Mexico, USA. During this same time, personnel associated with several programs surveyed translocation and non-translocation sites for presence of amphibians. We used 25 years (1995–2019) of survey and translocation data for the federally threatened Chiricahua Leopard Frog to identify factors linked with population persistence. Our dataset included approximately 40,642 egg masses or animals translocated in 314 events to 115 distinct sites and > 5800 visual encounter surveys from 641 sites; 120 of these sites were also surveyed with environmental DNA methods in 2018. We used a hierarchical dynamic occupancy model that accounted for imperfect detection to identify patch- and landscape-level attributes associated with site occupancy, and then used predictions from that model to evaluate factors associated with population persistence at translocation sites.

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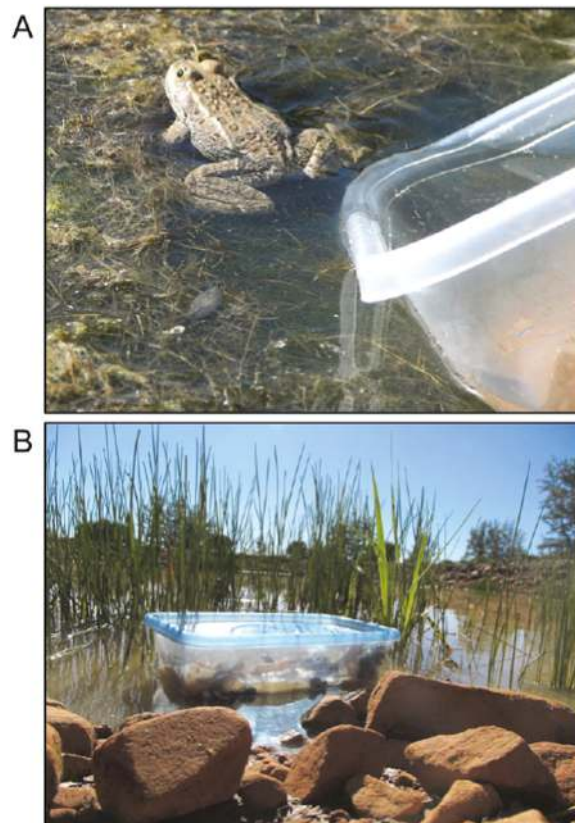
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Across all sites, extinction probability for Chiricahua Leopard Frogs was higher in lotic (stream) than lentic (pond) habitats and when Western Tiger Salamanders (*Ambystoma mavortium*) were present. Restoration of sites specifically for frog conservation reduced extinction probability. Colonization of unoccupied sites increased moderately with increasing numbers of translocation sites within 2 km, indicating a benefit of translocation efforts beyond sites where frogs were stocked. At translocation sites, persistence was greater in lentic than lotic habitats and was negatively correlated with the proportion of years tiger salamanders were present. Increasing numbers of translocation events, especially of late-stage larvae, increased persistence. There was little difference in population persistence based on whether stock was from captive, semi-captive, or wild sources, but translocations during the dry season (January–July) succeeded more than those after the typical arrival of summer rains (August–December). Based on the number of years translocation sites were predicted to be occupied, 2 or more translocations produced, on average, a > 4-yr increase in predicted occupancy compared to sites without translocations. While translocations have increased the number of populations across the landscape, continued management of water availability and threats such as invasive predators and disease remain critical to recovery of the Chiricahua Leopard Frog.

## 1. Introduction

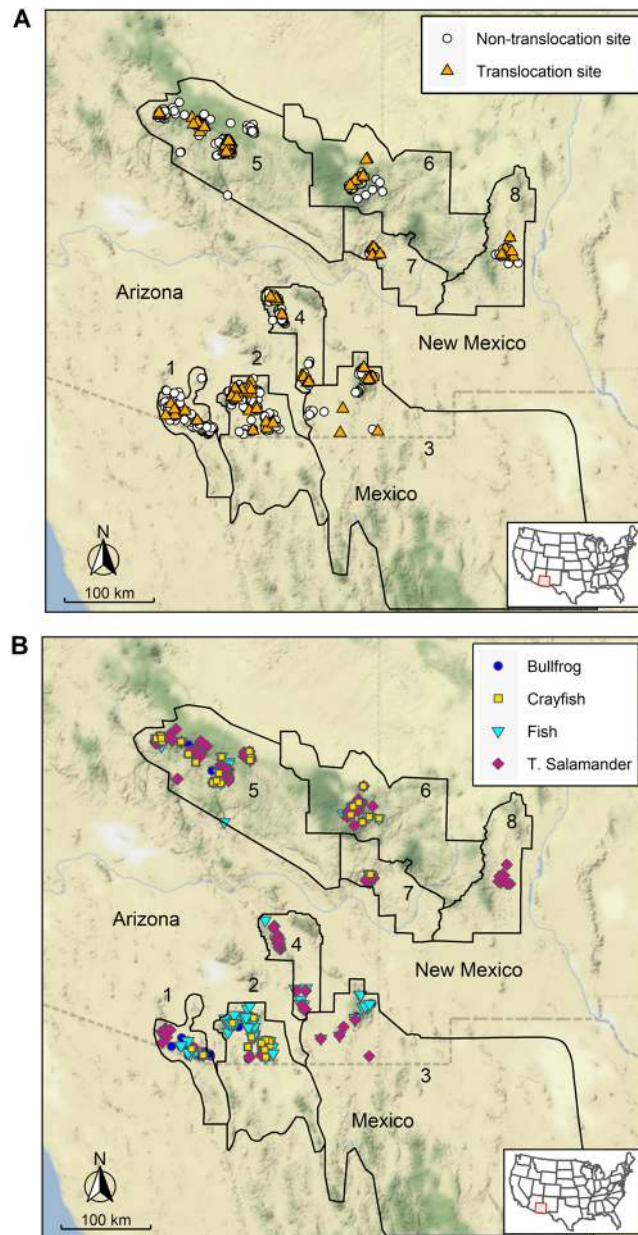
Translocation is a conservation strategy that is growing in use for a wide range of imperiled species (Germano and Bishop, 2009; IUCN/SSC, 2013; Seddon et al., 2007). Translocations for the purposes of conservation include re-introduction of species into habitats within a species' historical range as well as population supplementation or reinforcement (Armstrong and Seddon, 2008; IUCN/SSC, 2013). Although conservation translocations may not address the original causes of decline and are sometimes controversial (e.g., Germano and Bishop, 2009; Seigel and Dodd, 2002), they can be used to maintain populations on a landscape while management solutions are identified (Linhoff et al., 2021). While translocations have produced apparently self-sustaining populations in several cases (Chelgren et al., 2008; Denton et al., 1997; Howell et al., 2020), identifying factors associated with establishment of populations



**Fig. 1.** (A) Translocation of a Chiricahua Leopard Frog and (B) acclimation of juvenile frogs before release into a typical lentic habitat in Arizona, USA. (Arizona Game and Fish Department photos.).

is critical for improving translocation success and speeding recovery of imperiled species.

Although translocation programs are increasingly common, success rates remain low (Linhoff et al., 2021). Less than 50% of re-introductions for birds, mammals, and fish are deemed successful, and the success rate for amphibians and reptiles is even lower (Germano and Bishop, 2009; Griffiths and Pavajeau, 2008; Harig and Fausch, 2002). Amphibians in particular are often considered strong candidates for captive rearing, head-starting (wild-produced eggs or larvae reared in captivity and then released), and wild-to-wild translocations, especially because many amphibians mature quickly, have high rates of reproduction, and even endangered species can be locally abundant (Germano and Bishop, 2009; Seigel and Dodd, 2002). For example, captive rearing and population supplementation has been critical for the persistence of the Wyoming Toad (*Anaxyrus baxteri*) (Dreitz, 2006) and Dusky Gopher Frog (*Rana [Lithobates] sevosa*) (Roznik and Reichling, 2021), and supplementation of Oregon Spotted Frog (*R. pretiosa*) in the northwestern USA and southwestern Canada has likely reduced its extinction risk (Duarte et al., 2017; Kissel et al., 2014). Reintroductions were also key to recovery of the Natterjack Toad (*Epidalea calamita*) in Britain (Denton et al., 1997). While specific life-history



**Fig. 2.** (A) Distribution of sites surveyed for Chiricahua Leopard Frogs and where translocations occurred and (B) sites where native and non-native predators were ever detected during visual encounter surveys, 1995–2019. Polygons indicate boundaries of the 8 Chiricahua Leopard Frog Recovery Units, as defined in the species’ recovery plan (USFWS, 2007).

characteristics of some amphibians might make them good candidates for translocation programs, bi-phasic life histories and a tendency to disperse from aquatic sites add unique challenges compared to other aquatic vertebrates (Linhoff et al., 2021). However, these same characteristics (e.g., bi-phasic, local abundance) also provide the opportunity to fine-tune translocation programs, such as identifying specific life stages and stocking intensities that optimize the likelihood of establishing self-sustaining populations.

In the southwestern USA, most native water frogs (family Ranidae) have declined in distribution and abundance, including the federally threatened Chiricahua Leopard Frog (*Rana [Lithobates] chiricahuensis*) (Clarkson and Rorabaugh, 1989; Hayes and Jennings, 1986; Rorabaugh et al., 2020). The Chiricahua Leopard Frog (Fig. 1A, B) is native to the southwestern USA and northwestern Mexico, where, when it was listed under the US Endangered Species Act, it had disappeared from > 80% of historical localities in the USA (USFWS, 2007). Declines were linked with habitat loss, spread of non-native invasive predators such as warm water fishes and the American Bullfrogs (*R. [Lithobates] catesbeiana*), and disease (Clarkson and Rorabaugh, 1989; USFWS, 2007). Recovery efforts for the Chiricahua Leopard Frog have focused on reversing or abating many of these threats, including by removing bullfrogs, constructing or modifying habitats, and translocating animals to supplement or hopefully establish wild populations (Jarchow et al., 2016; McCall et al., 2018; Rorabaugh et al., 2008; Rosen et al., 2013). Despite engagement from many public and private partners and significant progress in establishing additional populations, long-term recovery of the Chiricahua Leopard Frog in the absence of intense management, including the translocation program, remains uncertain.

Since the 1990s, several captive and semi-captive facilities have produced Chiricahua Leopard Frogs with the goal of augmenting or establishing wild populations in Arizona and New Mexico, USA (McCaffery et al., 2012; McCall et al., 2018; Rosen et al., 2013; Sprankle, 2008). During this same period, a long-term monitoring program coordinated by the Arizona Game and Fish Department (and supplemented with data from other public and private partners) provided data focused on translocation as well as non-translocation sites. This combination of a long history of translocations and extensive monitoring provides a rare opportunity to identify factors associated with establishment or persistence of local sub-populations (a defined site with frogs; hereafter, populations).

Our primary objective was to identify factors associated with translocation success of Chiricahua Leopard Frogs. We define success as the establishment of a persistent population, with persistence varying from 1 to several years. Specifically, we first constructed a hierarchical dynamic occupancy model based on > 5800 surveys of 641 lentic (standing water) and lotic (flowing water) sites sampled during 1995–2019. We used this model to identify landscape- and patch-level attributes associated with site occupancy. We then used site-level predictions from the occupancy model informed by 25 years of surveys to evaluate factors associated with translocation success and to estimate the net increase in population persistence attributable to translocations. We examined the role of system type (lentic vs. lotic) and site isolation, presence of predatory Western Tiger Salamanders (*Ambystoma mavortium*), whether a site had been restored specifically to aid conservation of Chiricahua Leopard Frog, variation in life stages stocked (e.g., egg masses vs. juveniles), source of translocated animals (captive, semi-captive, and wild), number of translocation events, and number of translocation sites within 2 km in the establishment and persistence of populations based on 314 translocation events at 115 sites. Ultimately, a greater understanding of factors associated with successfully establishing populations will speed recovery of the Chiricahua Leopard Frog and can inform recovery programs of other amphibians with similar life histories.

**Table 1**

Characteristics of 641 sites surveyed for Chiricahua Leopard Frogs in Arizona and New Mexico, 1995–2019, from surveys conducted during 01 March through 15 July. Values represent the mean (range) or proportions based on visual encounter and eDNA surveys. Detection data are summarized based on whether a species was detected during a given survey (survey) and whether it was ever detected at a site (ever), regardless of number of surveys. Covariates with fixed values (e.g., lentic vs lotic) are also coded as “ever”. Most translocation sites were represented in the database before they became the focus of translocation efforts and are thus represented as both non-translocation (n = 609) and translocation sites (n = 115). Information from 2019 translocations was excluded here because it was not used in the analyses.

	Non-translocation	Translocation
Number of surveys	7.64 (1–75)	10.25 (1–57)
Proportion of sites lentic (ever)	0.75	0.74
Maximum site area (m <sup>2</sup> ; ever)	2977 (1–320,000)	5003 (2–260,753)
Topographic variation (5 km; ever)	118.29 (8.32–374.08)	126.76 (25.67–362.65)
No. restored sites (ever)	13	14
No. translocation sites within 2 km (ever)	0.76 (1.36; 0–6)	1.61 (1.56; 0–6)
Survey time (minutes)	32.42 (0 – 1427)	32.95 (2–242)
Air temperature (°C; survey)	24.48 (4.0– 46)	24.37 (1.3–46)
Wind force (Beaufort scale; survey)	4.08 (0–9)	2.35 (0–8)
Chiricahua Leopard Frogs detected (survey)	0.21	0.61
Crayfish detected (survey)	0.04	0.02
American Bullfrogs detected (survey)	0.03	0.01
Tiger Salamanders detected (survey)	0.12	0.15
Fish detected (survey)	0.04	0.05
Chiricahua Leopard Frogs detected (ever)	0.40	1.0
Crayfish detected (ever)	0.08	0.04
American bullfrogs detected (ever)	0.11	0.13
Tiger salamanders detected (ever)	0.20	0.43
Fish detected (ever)	0.16	0.24

## 2. Materials and methods

### 2.1. Study system and visual encounter surveys

The Chiricahua Leopard Frog occurs between ~1000 and 2700 m elevation in central and southeastern Arizona, west-central and southwestern New Mexico (USA), and south into central Mexico (Platz and Mecham, 1979; Rorabaugh and Lemos-Espinal, 2016). The species requires semi-permanent or permanent water for breeding and long-term persistence, and historically occurred in a variety of aquatic habitats, including rivers, streams, and spring-fed wetlands (ciénegas) (Platz and Mecham, 1979; Rorabaugh and Lemos-Espinal, 2016). Although the frogs are still found in a wide variety of aquatic habitats, because of widespread loss or modification of native spring and wetlands and the presence of non-native predators in these habitats, most populations are now limited to small streams and earthen ponds created for livestock (McCall et al., 2018; USFWS, 2007). Management of the species is based on 8 recovery units that encompass the species' native range in Arizona, New Mexico, and Mexico (Fig. 2A) (USFWS, 2007). Notably, there is taxonomic uncertainty for the Chiricahua Leopard Frog. Recent nuclear and mitochondrial DNA evidence suggests *Rana chiricuensis* in the USA are consistent with the (formerly) extinct *Rana fisheri* (Hekkala et al., 2011; Holycross et al., 2022).

Surveys for frogs were conducted by a combination of visually scanning the shoreline and surface of waterbodies and using dipnets to sweep through vegetation or other areas likely to host target species (McCall et al., 2018). Since 2002, persons permitted to sample for Chiricahua Leopard Frogs have been required to complete a certification workshop in which participants are trained to perform protocol surveys and complete standardized visual encounter survey forms (McCall et al., 2018). For practical reasons, monitoring programs for the Chiricahua Leopard Frog are typically based on detection of any life stage, but most detections are of juveniles or adults (McCaffery et al., 2012; McCall et al., 2018).

During each survey, surveyors recorded detections of important potential predators, including American Bullfrogs, tiger salamanders, fish, and crayfish (Table 1, Fig. 2B). In the Southwest, there are 2 native sub-species of the Western Tiger Salamanders (*Ambystoma mavortium nebulosum*, *A. mavortium stebbinsi*) and a non-native sub-species (*Ambystoma m. mavortium*) that was introduced by anglers and the bait trade (Jones et al., 1988, 1995). Aquatic forms of tiger salamanders can be large ( $\leq 385$  mm total length) and can spend several months in the water (Rorabaugh and Lemos-Espinal, 2016). In sites with persistent water, tiger salamanders can mature in the larval form (paedomorphs or branchiate adults) and spend several years in the water, where they are often the top predators and prey upon other amphibian larvae (Collins and Holomuzki, 1984; Holomuzki et al., 1994). Because of a lack of defined boundaries among sub-species that are difficult to distinguish morphologically and known distribution overlap in some areas (Holycross et al., 2022), we treated all tiger salamanders as the same.

We collected information for several habitat covariates during standardized surveys. For our analyses, we limited the set of covariates to those that, based on previous analyses and consultations with experts (Chandler et al., 2015; Howell et al., 2020, 2018), were likely to help explain Chiricahua Leopard Frog population dynamics and represented data fields that were collected consistently. During surveys, each site (a habitat patch surveyed for frogs) was coded as lentic or lotic. Lentic sites included small lakes and reservoirs, stock ponds, and ponds created for wildlife. Lotic sites included streams, springs, and wetland habitats within or connected to stream channels (Table 1).

Waterbody or patch size is often an important predictor of occupancy and population size (Bradford et al., 2003; Hanski, 1999; Hossack et al., 2013a). However, waterbody size often varies dramatically over time in this arid landscape and measures can depend greatly upon survey timing. To help account for variation in waterbody size, we used the maximum size that had ever been recorded for a site, based on the data sources described below. Air temperature, wind speed, and time spent surveying were also recorded during surveys; all can affect the activity and visibility of frogs or the probability that frogs are detected, when present. To provide an index of site isolation (fewer waterbodies in steep landscapes) and resistance to movement across the surrounding landscape (Hossack et al., 2013b; Howell et al., 2018), we used digital elevation maps in a GIS to measure the standard deviation of elevation (i.e., landscape complexity or ruggedness) within a 5 km buffer around each site (Table 1).

Restored sites were created or re-engineered specifically for Chiricahua Leopard Frog conservation. Stock ponds require maintenance such as removing sediment, clearing dense vegetation, and repairing water retention structures; all of these actions might benefit Chiricahua Leopard Frog and other aquatic species. But because it was impossible to know the history of all human-created or modified waterbodies in our analysis, we used a strict definition of site restoration to only include sites created or modified for Chiricahua Leopard Frog conservation.

Most sites in Arizona were surveyed only once during a season in a given year (e.g., 01 March–15 July) during which we thought it was reasonable to assume a site was closed to changes in occupancy, an important aspect of analyses (described in more detail below). Sites were usually surveyed during daytime (McCall et al., 2018). A notable exception occurred at Buenos Aires National Wildlife Refuge, where since 2007, most sites were surveyed 2 times during a short time period (e.g., <1 week) and at night (Howell et al., 2020; Jarchow et al., 2016). Some other areas, such as sites on the Ladder Ranch, a private conservation property in New Mexico, were also surveyed several times per season (McCaffery et al., 2012).

### 2.2. Data acquisition

All 1995–2019 Chiricahua Leopard Frog data were acquired from the Arizona Game and Fish Department's centralized database or from the Ladder Ranch (McCaffery et al., 2012; McCall et al., 2018). Importantly, the database does not include all known surveys from all areas. We excluded incidental observations, surveys that were not part of long-term monitoring or focused research programs, and sites that were enclosed so frogs could not move in or out. With the exception of sites targeted for environmental DNA (eDNA) sampling

in 2018 (see below), we also excluded sites that had been surveyed only once; otherwise, there would have been a large number of single-survey sites in the early years of the monitoring program, when the focus was partly on determining where Chiricahua Leopard Frogs still occurred (Sredl, 1997). To help ensure the analysis reflected more than short-term survival of recently released animals, for translocation sites, we only included surveys that were conducted at least 1 winter after a translocation event. For example, frogs were released at Cave Creek, New Mexico, in July 2018. As a result, we did not use the August 2018 survey of the site.

Occupancy models assume sampled sites are closed to changes in status between survey events (Kéry and Schaub, 2012; MacKenzie et al., 2002). There is often great variation in the population and patch-level dynamics of Chiricahua Leopard Frogs and other anurans in the Southwest, much of it driven by changes in surface water availability (Hinderer et al., 2017; Hossack et al., 2017; Zylstra et al., 2015). Local populations may go extinct within a season. Frogs may also disperse and potentially change the occupancy status of sites, especially after summer rains arrive (Hinderer et al., 2017). To help control for potential bias in estimates caused by lack of closure, we limited analyses to surveys conducted during 01 March–15 July each year. We used this time period because it is before the summer rains typically arrive, which promotes dispersal among sites and decreases the validity of the assumption of site closure (Adams and Comrie, 1997; Sall et al., 2020). Consistent presence of adults at sites during this dry spring/early summer season has traditionally been used as an indicator of a local population (Chandler et al., 2015; Howell et al., 2018; McCall et al., 2018). There was also a sharp decrease in number of surveys conducted during late July, before survey efforts increased again in August.

### 2.3. Translocation records

We incorporated site-specific translocation records from a centralized database maintained by the Arizona Game and Fish Department, records from the Ladder Ranch, and records from a small number of biologists closely aligned with the Chiricahua Leopard Frog monitoring and recovery program (McCaffery et al., 2012; McCall et al., 2018; Rosen et al., 2013). Most translocations in Arizona have been conducted or coordinated by state or federal biologists. We only include information for sites that had a survey history in the Arizona Game and Fish Department or Ladder Ranch databases. Translocation records included date of release and number of egg masses, larvae, juveniles (including recent metamorphs), and adults stocked to a site (Tables 2 and 3, Supplemental Table S1). We did not have enough information to include size or development of animals in analyses; however, most stocked larvae were late-stage animals (Rorabaugh et al., 2008). The number of larvae stocked was sometimes estimated (e.g., 100) rather than counted precisely. Similarly, egg masses were sometimes split into portions so they could be stocked into > 1 site or to leave a portion of the mass at the natal site, as indicated by fractional shares of masses (Tables 2 and 3, Supplemental Table S1). Notably, translocation efforts and the number of animals released have increased substantially since approximately 2010 (Fig. 3).

Translocation records also included the source of animals, which we grouped as wild, semi-captive, or captive (Table 2, Supplemental Table S1). Wild-to-wild translocations were animals moved from one site in the landscape to another. Semi-captive sources include outdoor facilities such as hatcheries or ranaria, which were special facilities or ponds (often fenced) used to rear frogs for release into the wild. Captive-to-wild translocations were animals moved from mostly indoor facilities where care was managed more closely than in semi-captive facilities. In captive facilities, testing for pathogens of concern was common practice. In semi-captive facilities, managers used a risk management protocol (Pessier and Mendelson, 2010) that included sampling water at least once per year to monitor for pathogens of concern. Animals from the Phoenix Zoo represented 92% of captive-sourced translocation events and 96% of animals released (Supplemental Table S1). Most, but not all, animals in semi-captive and captive facilities were produced from eggs brought in from the wild, a form of head starting (Sprankle, 2008). In total, our dataset used for analysis contained approximately 40,642 egg masses or animals translocated in 314 events to 115 sites from 1995 through 2018.

### 2.4. 2018 surveys and eDNA sampling

With a few exceptions (e.g., Buenos Aires National Wildlife Refuge and Las Cienegas National Conservation Area, Arizona), monitoring of sites in the region has historically been biased towards sites with known or recent presence of Chiricahua Leopard Frogs

**Table 2**

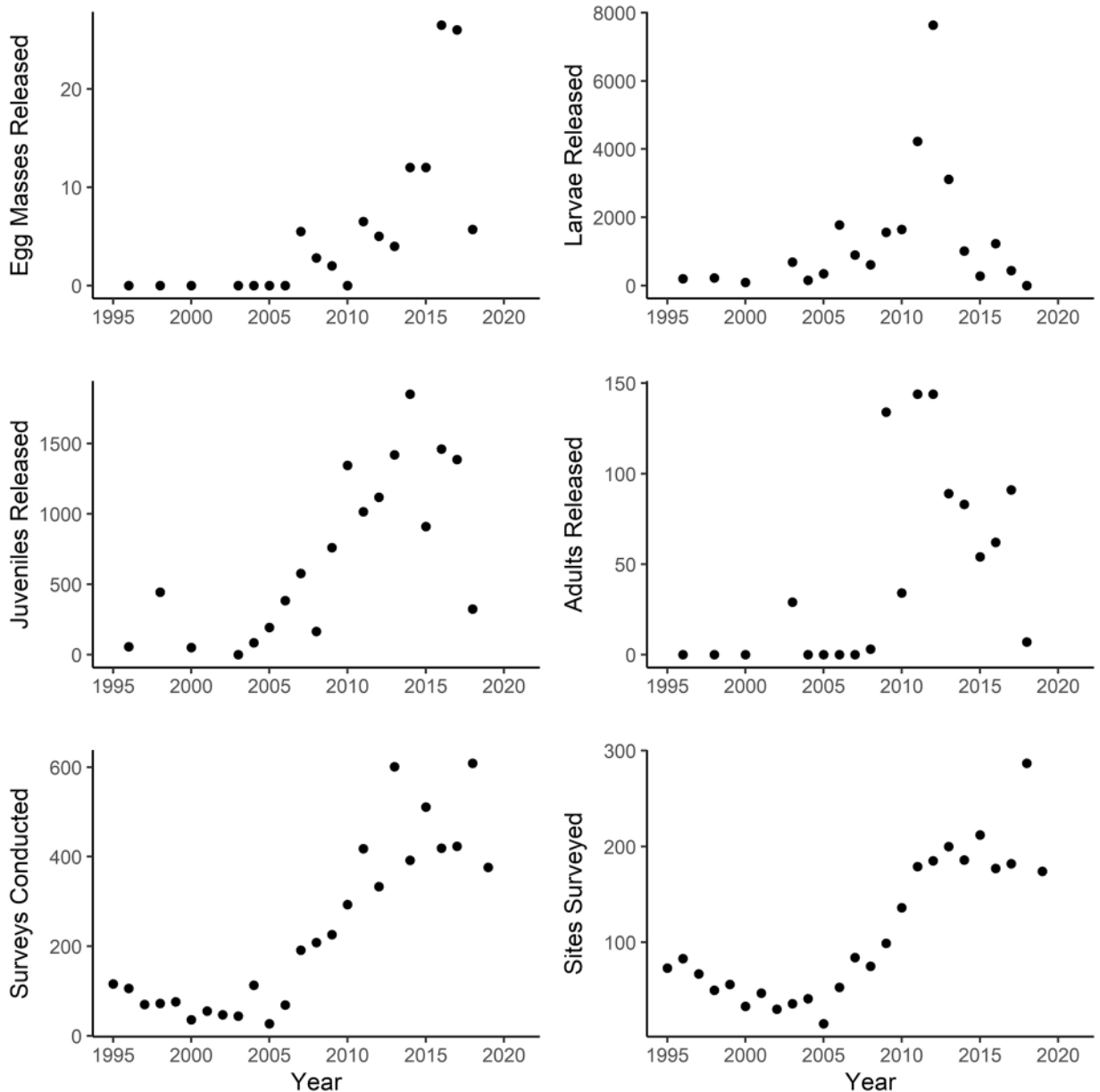
Summary of Chiricahua Leopard Frog translocation efforts documented at 115 translocation sites. Values are summarized by mean (SD; range) or proportions of events. See Supplemental Table S1 for more information on sources (e.g., captive facilities) of animals. Information from 2019 translocations was excluded, because it was not used in the analyses.

	Mean (range)
Number of translocation events	2.67 (2.14; 1–16)
Wild-to-wild translocations	0.31
Semi-captive-to-wild translocations	0.35
Captive-to-wild translocations	0.34
Translocations during January–July	0.53
Number of egg masses released	0.92 (1.84; 0–10)
Number of larvae released	221.44 (344.32; 0–2367)
Number of juveniles released	114.66 (173.25; 0–708)
Number of adults released	7.41 (16.71; 0–91)

**Table 3**

Summary of 1996–2018 Chiricahua Leopard Frog translocation efforts used in the analysis, summed by Chiricahua Leopard Frog Recovery Unit.

Recovery Unit	No. Events	Years	No. Egg Masses	No. Larvae	No. Juvenile	No. Adults
1	6	2003–2017	0	1150	500	149
2	47	2005–2018	11	6671	1039	154
3	46	2009–2017	30.5	3545	151	119
4	29	2006–2016	29.3	1483	1029	170
5	126	1998–2018	28.5	9802	7625	79
6	37	1996–2018	6	2038	2375	82
7	11	2014–2018	2.7	87	794	86
8	13	2000–2014	0	1354	17	35
Totals:	315	1995–2018	108	26,130	13,530	874



**Fig. 3.** Summary of Chiricahua Leopard Frog survey and translocation efforts in Arizona and New Mexico (1996–2018) according to life stage released. These plots show all surveys conducted during 01 March – 15 July but include all translocations regardless of time period, because all translocation events were used in models.

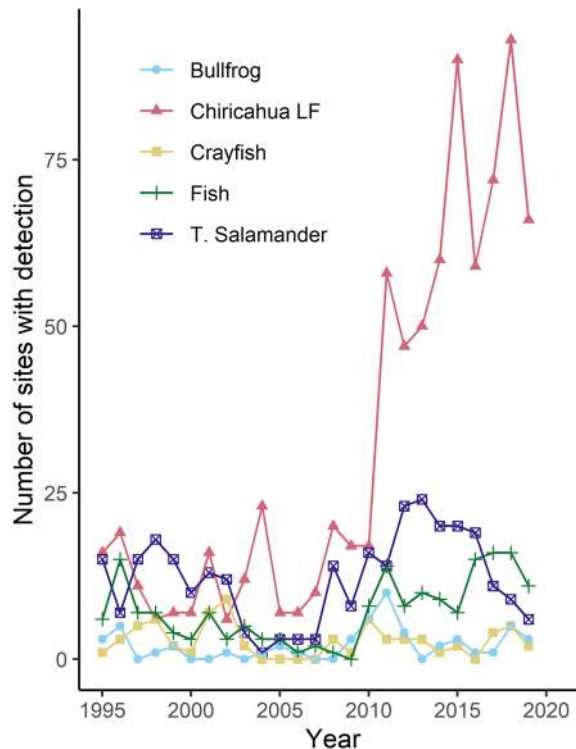
(McCall et al., 2018). To help account for this bias and to provide a measure of how often frogs colonized waterbodies where they were not reintroduced, in 2018 we emphasized sampling a broader range of waterbodies. For 42 Arizona translocation sites sampled in 2018, we sought to survey 2 nearby sites (within 10 km) of similar habitat type that had no history of translocations. These sites served as controls and were a mix of historical Chiricahua Leopard Frog sites that had not been surveyed in recent years and sites with no prior survey history. To account for bias that could be introduced due to sites being selected because they had a history of Chiricahua Leopard Frog presence, we distinguished these control sites as selected with a probability-based design compared to other sites that were not selected with a probability-based design. In some cases, we were unable to sample 2 control sites (e.g., sites were dry, there were access issues). For the Ladder Ranch, we sampled almost all accessible waterbodies since they were our only data from the eastern margin of the Chiricahua Leopard Frog's distribution; this resulted in 7 translocation sites and 20 non-translocation sites sampled. In total, we sampled 120 sites with eDNA methods.

Also during 2018, we paired eDNA methods with traditional visual encounter surveys at 120 translocation and control sites that we just described. These paired surveys allowed us to independently estimate error rates from traditional survey methods and helped to determine if populations were less likely to persist with predators of conservation concern. We used stratified random selection to ensure sites targeted for eDNA sampling represented the history of translocations in the region (e.g., 1999 vs. 2015), range of environmental conditions (e.g., stream vs. pond, geography), life stages stocked (e.g., egg masses vs. adults), and number of translocation events. Further, we ensured sites targeted for eDNA methods were not stocked with frogs earlier in 2018, before we collected water samples. Laboratory methods for the eDNA samples are described in Supplemental 1.

## 2.5. Statistical analyses

### 2.5.1. Analysis 1: landscape occupancy

We used a 2-stage modeling approach to identify attributes associated with (1) occupancy of the Chiricahua Leopard Frog across the landscape and (2) then used site-level occupancy predictions to identify factors associated with translocation success. First, we used all 01 March–15 July surveys from 1995 through 2019 in a dynamic occupancy model to estimate the effect of habitat and translocation-related covariates on initial occupancy, site colonization, and site extinction probability for frogs (Howell et al., 2018; MacKenzie et al., 2002). Translocation events were not considered surveys. Our detection process model consisted of a separate model for visual encounter surveys and eDNA surveys, linked by the true occupancy state of each site, each year. Below we describe each component of the ecological and detection process models.



**Fig. 4.** Number of sites where at least one individual of targeted taxa was detected during visual encounter surveys during 01 March–15 July (1995–2019) in Arizona and New Mexico. The number of sites surveyed each changed over time, so changes in number of detections should not be interpreted as a trend.



### 2.5.2. Covariate selection

Before fitting models to data, we tested for collinearity among our covariates with Spearman’s correlation coefficients, logistic regression, or a Fisher’s exact test, depending whether we compared combinations of continuous, continuous and categorical, or categorical covariates. We excluded covariates from the same ecological process model or detection model that had a Spearman’s correlation coefficient > 0.6 or p-value from Fisher’s exact test or logistic regression ≤ 0.05. Maximum site area was correlated with system type ( $p < 0.01$ ). Whether or not a site had been restored was correlated with topographic variation around a site ( $p < 0.01$ ) and the number of translocation sites within 2 km of a site ( $p < 0.01$ ). Therefore, these covariates were not included in the same ecological process models or detection process models. Similarly, parameter estimates for bullfrogs, fishes, and crayfishes were imprecise and overlapped with 0, indicating they either had little effect on the distribution of Chiricahua Leopard Frogs or — likely because of their general rarity in the sites used in this analysis (Table 1, Fig. 4) — there was insufficient information to model their effects on frog occupancy. Thus, we removed these predators from models to help with precision.

### 2.5.3. Ecological process models

We modeled expected occupancy state  $\psi_{i,1}$  in the first year at each site ( $i = 1, \dots, M$ ) as a logit-linear function of whether a site was selected to be surveyed (i.e., site selection) using a probability-based design (P) or not (NP).

$$\text{logit}(\psi_{i,1}) = \alpha_0 + \alpha_1 P_i, \tag{1}$$

$$z_{i,1} \sim \text{Bernoulli}(\psi_{i,1}), \tag{2}$$

where  $z_{i,1}$  is site occupancy in year one. The coefficient  $\alpha_0$  refers to sites that were not selected using a probability-based design. Site selection was represented as a dummy variable (NP = 0,  $n = 371$ ; P = 1,  $n = 269$ ).

In subsequent years ( $t = 2, \dots, T$ ), the occupancy state  $z_{i,t}$  for each site was modeled as:

$$z_{i,t} \sim \text{Bernoulli}(\psi_{i,t}), \tag{3}$$

$$\psi_{i,t} = \gamma_{i,t-1} (1 - z_{i,t-1}) + (1 - \epsilon_{i,t-1} (1 - \gamma_{i,t-1})) z_{i,t-1}, \tag{4}$$

where  $\gamma$  is colonization probability and  $\epsilon$  is extinction probability. We accounted for the rescue effect by modeling persistence (the complement of site extinction probability) as  $1 - \epsilon_{i,t-1} (1 - \gamma_{i,t-1})$  (Hanski, 1999; Howell et al., 2018). We modeled site-specific extinction  $\epsilon_{i,t-1}$  as a logit linear function of system type (lentic or lotic), estimated occupancy of tiger salamanders (tiger), and whether or not a site had been restored (restored, Table 1) as:

$$\text{logit}(\epsilon_{i,t-1}) = \beta_0 + \beta_1 \text{lotic}_i + \beta_2 \text{tiger}_{i,t-1} + \beta_3 \text{restored}_i, \tag{5}$$

where the subscripted  $\beta$ ’s refer to coefficients to be estimated for each covariate. The coefficient  $\beta_0$  represented lentic sites without restoration or tiger salamanders. System type (lentic = 0,  $n = 473$ ; lotic = 1,  $n = 160$ ) and restoration (not restored = 0,  $n = 613$ ; restored = 1,  $n = 27$ ) were represented as dummy variables.

We modeled inter-site colonization  $\gamma_{i,t-1}$  as a logit linear function of system type (lentic or lotic), tiger salamander occupancy (tiger), the number of translocation sites within 2 km (clustered), and topographic variation within the surrounding 5 km (topo; Table 1) as:

$$\text{logit}(\gamma_{i,t-1}) = \nu_0 + \nu_1 \text{lotic}_i + \nu_2 \text{tiger}_{i,t-1} + \nu_3 \text{clustered}_i + \nu_4 \text{topo}_i, \tag{6}$$

where the subscripted  $\nu$ ’s refer to coefficients to be estimated for each covariate (Table 1). The coefficient  $\nu_0$  represented lentic sites without restoration or tiger salamanders. The standard deviation (SD) of elevation (mean = 119, range = 8.3–374 m) and clustered covariate (mean = 0, range = 0–6 translocation sites) were standardized to mean 0, unit variance to aid in convergence.

The site occupancy each year for tiger salamanders was estimated simultaneously in the Chiricahua Leopard Frog occupancy model. The models shared information between the 2 species only for detection. We think that assumption is reasonable because detection of aquatic salamander and ranid frogs are often affected similarly by the same covariates (e.g., site size or depth) (Ray et al., 2016; Rowe et al., 2019). For tiger salamanders, site extinction was estimated as a logit-linear function of system type and colonization probability was estimated as a logit-linear function of system type and the SD of elevation within a 5 km buffer around each site. We did not include the effects of any covariates on initial occupancy of salamanders.

### 2.5.4. Detection process models

For years and sites with repeat surveys that occurred during 01 March–15 July, we modeled the observed detection non-detection data from visual encounter surveys conditional on true site occupancy and detection probability for site  $i$  on survey occasion  $k$  in year  $t$ :

$$y_{\text{ves}_{i,t,k}} \sim \text{Bernoulli}(z_{i,t} p_{\text{ves}_{i,t,k}}), \tag{7}$$

$$\text{logit}(p_{\text{ves}_{i,t,k}}) = \omega_0 + \omega_1 \text{lotic}_i + \omega_3 \text{time}_{i,t,k} + \omega_4 \text{temp}_{i,t,k} + \omega_5 \text{wind}_{i,t,k}, \tag{8}$$

where the subscripted  $\omega$ 's refer to coefficients to be estimated for each covariate of interest. We fit an additional model that included survey-level stochastic variation modeled using a Normal(0, 100) prior distribution to improve model fit. Inference from our ecological process model was similar when fitting each of these 2 detection process models; however, detection probability estimated from the more complex model was unrealistically high. Therefore, we present results from the simpler, albeit less well-fitting, detection process model. We modeled detection by visual encounter survey as a function of system type (lentic or lotic), search time (time), air temperature (temp), and wind speed (Beaufort scale [wind]; Table 1). The coefficient  $\omega_0$  refers to lentic sites. Search time (mean = 33 min, range = 0–1427 min), air temperature (mean = 24 °C, range = 1–46 °C), and wind speed (mean = 3.7, range = 0–9) were standardized to mean 0, unit variance.

In a similar manner, we modeled the observed detection non-detection data from eDNA surveys conditional on true site occupancy and detection probability for site  $i$  on survey occasion  $k$  in year  $t$ :

$$y_{\text{eDNA}_{i,t,k}} \sim \text{Bernoulli}\left(z_{i,t} p_{\text{eDNA}_{i,t,k}}\right), \quad (9)$$

$$\text{logit}\left(p_{\text{eDNA}_{i,t,k}}\right) = \eta_0 + \eta_1 A_i + \eta_2 \text{vol}_{i,t,k}, \quad (10)$$

where the subscripted  $\eta$ 's refer to coefficients to be estimated for each covariate of interest. Maximum site area ( $A$ ; mean = 3416, range = 1–320,000 m<sup>2</sup>) and volume filtered (vol; mean = 197, range = 10–500 mL) were standardized to mean 0, unit variance. For eDNA surveys, each filter was treated as a replicate (Hossack et al., 2021).

Many sites were surveyed only 1 time within the 01 March–15 July period during which we assumed site closure. We still used this information in models, but estimates of detection probability were based on sites sampled  $\geq 2$  times. We used the same detection process model for tiger salamanders, sharing information between the Chiricahua Leopard Frog and salamanders. We constructed models to share information for the 2 species so we could estimate true occupancy state of salamanders and incorporate that uncertainty into estimates of frog occupancy.

### 2.5.5. Model fitting procedure

We fit all models in a Bayesian framework in JAGS called from R using the jagsUI package (Kellner, 2019; Plummer, 2012; R Core Development Team, 2020). For all coefficients in our logit-linear models, we used Normal(0, 0.37) prior distributions. We sampled from posterior distributions using 3 Markov chains, each of length 40,000, discarded the first 20,000 iterations as burn-in and used an adaptation phase of 5000 iterations. We did not thin chains (Link and Eaton, 2012). We assessed model convergence using the Gelman-Rubin diagnostic and by visually inspecting chains for mixing. For continuous covariates, we imputed missing covariate values from a Normal(0, 1) distribution. For system type, we imputed missing values using a logit linear model of system type as a function of maximum area. For inference, we reported posterior medians and 95% credible intervals. We regarded an effect as significant when the posterior probability (e.g., posterior  $p$ -value) was  $> 0.95$  (Chandler et al., 2013). JAGS model code can be downloaded from our figshare repository (<https://figshare.com/s/697e3ed91ab721bb417c>).

### 2.5.6. Evaluating model fit

We evaluated model fit by computing a Chi-square fit statistic ( $C$ ) on the total number of detections in the study, by pooling data across all years, sites, and surveys for VES and eDNA surveys, respectively. At each Markov chain Monte Carlo (MCMC) iteration, we computed this statistic for the observed data and simultaneously for a new dataset simulated from the posterior distribution. We calculated the Bayesian  $p$ -value (i.e. posterior probability  $\Pr(C(\mathbf{y}^{\text{new}}) > C(\mathbf{y}))$ ), which should be close to 0.5 for a model that fits well; values  $\geq 0.95$  or  $\leq 0.05$  would indicate a poor fit (Gelman et al., 1996). We aggregated data because posterior predictive checks based on binary data are uninformative otherwise (Kéry and Schaub, 2012; McCullagh and Nelder, 1997).

### 2.5.7. Analysis 2: translocation success

To identify factors associated with successful establishment and persistence of populations at the 115 translocation sites, we used the median predicted site occupancy from the landscape occupancy model as the response variable. We fit these data to a regression model that estimated the proportion of all years a translocation site was occupied as a function of the translocation history and covariates associated with each site, starting the first year in which a translocation occurred at each site. We had planned to use dynamic occupancy models that would have allowed us to isolate the effect of individual translocation events, but those models did not fit the data well.

### 2.5.8. Correlates of translocation success

We modeled the relationship between the proportion of years each site was occupied and a site's translocation history:

$$z_i \sim \text{Binomial}(N_i, \psi_i), \quad (11)$$

where  $z_i$  are estimates of the number of years a site was occupied from our dynamic occupancy model,  $N_i$  are the number of years in which a site could possibly be occupied (including the year of first translocation), and  $\psi_i$  is the probability of occupancy. We fit 4 separate models to avoid issues of collinearity among our predictor variables. In the first model (Model 1) we modeled  $\psi_i$  as a function of system type (lentic,  $n = 92$ , or lotic,  $n = 35$ ), the SD of elevation within a 5 km buffer around each site (median = 103.82, range = 25.68–362.65 m), the proportion of years in which tiger salamanders were estimated to occur at each site (median = 0.04, range =

0.00–0.76), and the total number of translocations that occurred at each site (median = 2, range = 0–17). In our second model (Model 2) we modeled  $\psi_i$  as a function of the source of translocated individuals: wild (median = 0.00, range = 0.00–8.00), semi-captive (median = 0.00, range = 0.00–10.00), and captive (median = 0.00, range = 0.00–8.00). For the third model (Model 3) we modeled  $\psi_i$  as a function of the timing of translocations during January–July (median = 1.00, range = 0.00–10.00) and during August–December (median = 1.00, range = 0.00–6.00) (Supplemental Table S2). Our final model (Model 4) evaluated the relative importance of different life stages and numbers of animals released in translocation events for each site: eggs (median = 0.00, range = 0.00–10.00), larvae (median = 107.5, range = 0.00–2367.00), juveniles (median = 27.0, range = 0.00–708.00), and adults (median = 0.00, range = 0.00–94.00). All continuous covariates were standardized to mean 0, unit variance to aid convergence. System type was represented as a dummy variable.

We fit all models in a Bayesian framework in JAGS called from R using the jagsUI package (Kellner, 2019; Plummer, 2012; R Core Development Team, 2020). For all coefficients in our logit-linear models, we used Normal(0, 0.37) prior distributions. We sampled from posterior distributions using 3 Markov chains, each of length 5000 and used an adaptation phase of 5000 iterations. We did not thin chains (Link and Eaton, 2012). We assessed model convergence using the Gelman-Rubin diagnostic and by visually inspecting chains for mixing. For continuous covariates, we imputed missing covariate values from a Normal(0, 1) distribution. For system type, we imputed missing values using a logit linear model of system type as a function of maximum area. For inference, we reported posterior medians and 95% credible intervals. We regarded an effect as significant when the posterior probability of a difference (e.g., posterior p-value) was > 0.95 (Chandler et al., 2013). JAGS model code can be downloaded from our figshare repository (<https://figshare.com/s/697e3ed91ab721bb417c>).

### 2.5.9. Effect of translocations on population persistence

To explore the net benefit of translocations on continued presence of a population (persistence), as well as whether there has been an improvement in translocation success as the recovery program has matured, we split all sites that were ever stocked into 2, 12-yr time series and estimated the number of years a translocation site was predicted to be occupied. The first group was the total years each site was estimated to be occupied, from 1995 through 2006. The second group was the total years each site was estimated to be occupied, from 2007 through 2018. We did not have sufficient data to subset into smaller groups of years, and we limited estimates to 3 or fewer translocation events because that was the largest number that occurred at an analysis site during 1995–2006. Fitting these data using Poisson regression resulted in poor model fit due to substantial overdispersion. Consequently, we estimated the relationship between number of translocations and years occupied using Zero Inflated Poisson regression in R package pscl (Jackman, 2020). We modeled the effect of total number of translocations on the probability a translocation site was occupied (inflation portion of the model) and the number of years occupied as a function of the total number of translocations.

## 3. Results

The number of sites with detections of Chiricahua Leopard Frogs during 01 March–15 July visual encounter surveys increased from 1995 through 2019, whereas detections of all predators tended to remain low throughout the time series (Fig. 4). Chiricahua Leopard Frogs and tiger salamanders were detected at 43 and 29 sites via eDNA sampling, respectively.

**Table 4**

Parameter estimates on the logit scale (median, lower bound of 95% credible interval =  $q_{0.025}$ , upper bound of 95% credible interval =  $q_{0.975}$ ) for detection ( $\omega$ ), initial occupancy ( $\omega$ ), extinction ( $\beta$ ), and colonization ( $\nu$ ) probability. Estimates are from a dynamic occupancy model fitted to 25 years of Chiricahua Leopard Frog visual encounter survey (VES; 1995–2019) and eDNA surveys (2018). We used a global intercept for initial occupancy, so the effect of a site being selected with a probability-based design (P) rather than non-randomly reduced the probability of occupancy relative to the global mean. The detection estimates are for both the Chiricahua Leopard Frog and tiger salamanders, which had a shared detection model.

Symbol	Description	$q_{0.025}$	median	$q_{0.975}$
$\omega_0$	Detection probability at lentic sites for VES surveys	0.92	1.05	1.18
$\omega_1$	Detection probability at lotic sites for VES surveys	-0.56	-0.25	0.08
$\omega_2$	Effect of search time on detection probability for VES surveys	0.06	0.28	0.55
$\omega_3$	Effect of ambient temperature on detection probability for VES surveys	0.16	0.26	0.37
$\omega_4$	Effect of wind speed on detection probability for VES surveys	-0.30	-0.17	-0.04
$\eta_0$	Intercept of detection probability model for eDNA surveys	0.76	1.55	2.55
$\eta_1$	Effect of pond area on detection probability for eDNA surveys	-0.12	0.73	1.80
$\eta_2$	Effect of volume filtered on detection probability for eDNA surveys	-0.43	-0.16	0.05
$\alpha_0$	Initial occupancy probability for sites selected through a non-probability-based design	-1.58	-1.03	-0.54
$\alpha_1$	Initial occupancy probability for sites selected through a probability-based design	-2.25	-0.84	0.24
$\beta_0$	Extinction probability at lentic sites	-2.04	-1.73	-1.44
$\beta_1$	Extinction probability at lotic sites	-1.01	-0.42	0.16
$\beta_2$	Effect of tiger salamander occupancy on extinction probability	0.21	0.83	1.45
$\beta_3$	Effect of pond restoration on extinction probability	-1.81	-0.76	-0.01
$\nu_0$	Colonization probability at lentic sites	-2.96	-2.72	-2.49
$\nu_1$	Colonization probability at lotic sites	-0.62	-0.10	0.42
$\nu_2$	Effect of tiger salamander occupancy on colonization probability	-0.94	-0.27	0.35
$\nu_3$	Effect of number of translocation sites within 2 km on colonization	0.00	0.16	0.31
$\nu_4$	Effect of topographic variation (1 SD of mean elevation) within 5 km of a site on colonization probability	-0.19	-0.03	0.11

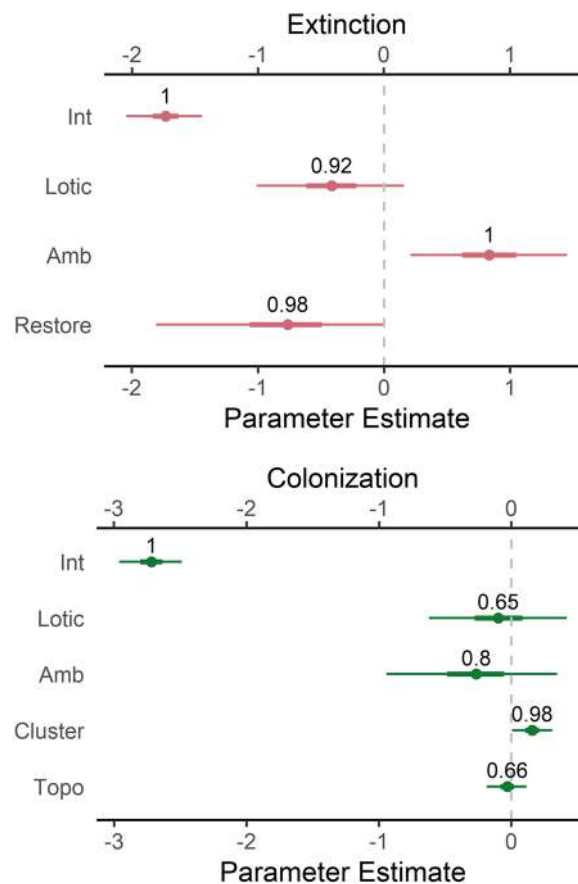
### 3.1. Landscape occupancy: model performance and fit

The Gelman-Rubin diagnostic for all parameters was  $< 1.05$ . Trace plots also provided evidence for adequate mixing and convergence (Supplemental Figs. S1–S2). The mean Bayesian  $p$ -value was 0.11 and 0.60 for VES and eDNA data, respectively, when including survey-level stochastic variation. The mean Bayesian  $p$ -value was 0 and 0.05 for VES and eDNA data, respectively, when omitting the survey-level stochastic variation. We drew inference from the latter model, which, despite having worse fit, produced nearly identical estimates for the ecological process models and much more realistic estimates of detection probability (Table S3), given our previous work in this system (Chandler et al., 2015; Howell et al., 2018).

### 3.2. Landscape occupancy: colonization, extinction, initial occupancy process models

Initial occupancy probability for Chiricahua Leopard Frogs was lower for sites selected using a probability-based design relative to sites selected non-randomly (Table 4). This relationship was expected but accounting for differences is important to reduce bias in estimates. Site-level extinction probability for Chiricahua Leopard Frogs was higher for sites occupied by tiger salamanders versus sites that did not have salamanders and was higher in lotic sites than lentic sites. Restored sites had lower extinction probability than unrestored sites (Table 4, Fig. 5). Colonization probability was lower in lentic sites relative to lotic sites but increased moderately with increasing numbers of translocation sites within 2 km (Table 4, Fig. 5). Colonization was not related to whether a site was occupied by tiger salamanders or to topographic variation in the surrounding 5 km (Table 4, Fig. 5).

Site-level occupancy of tiger salamanders was estimated concurrently with that of the Chiricahua Leopard Frog, allowing the 2 species to share a detection structure. For tiger salamanders, colonization and extinction probabilities were higher at lotic sites than at lentic sites, indicating more turnover in stream sites (Table 5).



**Fig. 5.** Median (colored circle), 50% credible intervals (thick bars) and 95% credible intervals (thin bars) for the effect of each covariate on site extinction probability (red) and inter-site colonization probability (green) for Chiricahua Leopard Frogs during 1995–2019 relative to habitat (Int, Lotic), presence of tiger salamanders (Amb), number of translocation sites within 2 km (Cluster), and topographic variation in the surrounding 5 km (Topo). Numbers above bars indicate the proportion of the posterior distribution in the same direction as the posterior mean. All estimates are on the logit scale.

### 3.3. Landscape occupancy: detection process models

The probability of detecting a frog or salamander during a visual encounter survey was higher in lentic versus lotic sites (Table 4, Fig. 6). Furthermore, detection probability increased with survey search time and air temperature but decreased with increasing wind speed (Table 4, Fig. 6). Detection probability via eDNA surveys increased with volume of water filtered and decreased as site size increased; however, 95% credible intervals for both of these covariates overlapped with 0, indicating the relationships were not strong (Table 4, Fig. 6).

### 3.4. Translocation success: model performance and fit

The Gelman-Rubin diagnostic for all parameters was  $< 1.05$ . Trace plots also provided evidence for adequate mixing and convergence (Supplemental Figs. S3–S6).

### 3.5. Translocation success: proportion of years occupied as a function of translocation history

Based on estimated site-level occupancy for each site–year combination from the occupancy model (Analysis 1), Chiricahua Leopard Frogs were more likely to persist at lentic versus lotic sites (Model 1 in Table 6, Fig. 7A). Persistence was negatively correlated with the proportion of years in which tiger salamanders were estimated to occur at a site (Model 1 in Table 6, Fig. 7B). Increasing numbers of translocation events were linked to increasing site-level persistence of Chiricahua Leopard Frogs (Model 1 in Table 6, Fig. 7C). Animals sourced from wild populations resulted in the greatest mean increase in probability of persistence, whereas animals from captive and semi-captive facilities had similar mean effects (Model 2 in Table 6, Fig. 7D). However, the effect of animal source was not estimated precisely and none of the sources were significantly different from each other. Timing of the translocation events was important. With the exception of very small numbers ( $\leq 2$ ) of total translocation events to a site, persistence was higher for the same number of Jan–Jul translocations versus Aug–Dec translocations (Model 3 in Table 6, Fig. 7E).

Probability of persistence varied based on life stages used for translocations, with the greatest net benefit attributable to larvae. Occupancy probability increased in accordance with number of larvae released (Model 4 in Table 6, Fig. 8B). Translocating adults also had a positive effect on persistence, but this required large numbers of adults and the estimated effect was imprecise compared to the effect of translocating larvae (Model 4 in Table 6, Fig. 8D). Stocking egg masses or juveniles had little effect on the proportion of years that a site was occupied after a translocation event (Model 4 in Table 6, Fig. 8A, C).

### 3.6. Effect of translocations on population persistence

Based on the predicted number of years a translocation site was occupied during 1995–2006 versus 2007–2018, increased translocation events were linked with an increasing probability that a site was occupied and how many years a population persisted (Table 7, Fig. 9). Comparison of the 2 time periods showed a moderate increase in the efficacy of translocations during 2007–2018, at least up to 2 translocation events. Notably, the estimate for the 1995–2006 time series was imprecise, but during both time periods, 2 or more translocations at a site produced a large increase ( $\geq 4$  yrs) in predicted number of years a site would be occupied (Fig. 9).

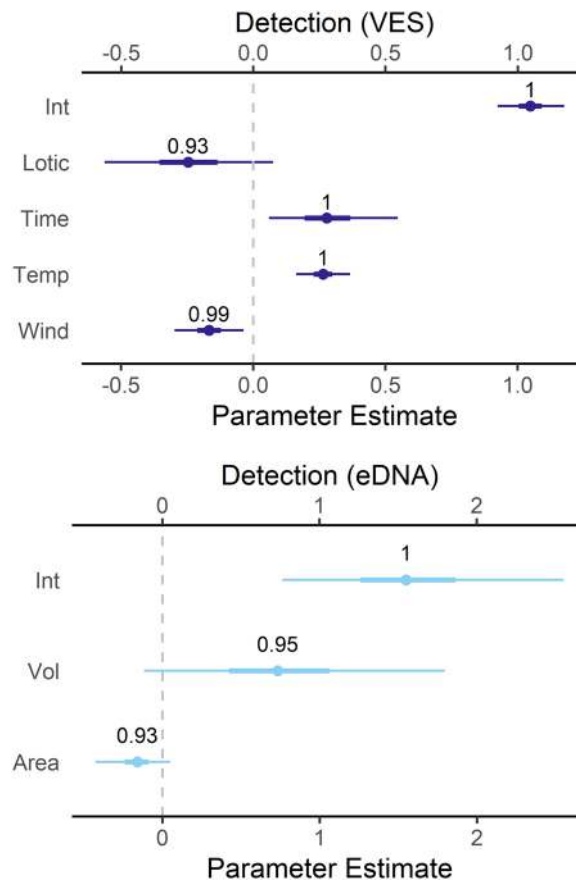
## 4. Discussion

Translocating animals to reduce population or species extinction risk is growing in use as a conservation tool. However, because initiating translocation programs is sometimes urgent, they are often implemented without knowledge of which strategies are most likely to succeed (Linhoff et al., 2021; Seddon et al., 2007). Our analysis of 25 years of translocation records and surveys from 641 sites in Arizona and New Mexico revealed several factors linked with site occupancy and population persistence by the federally threatened Chiricahua Leopard Frog. We were unable to incorporate some covariates that likely limit populations in some areas (e.g., water permanence), but across all sites, site-level colonization and extinction dynamics for the frog varied based on system type (lentic vs. lotic), presence of predatory tiger salamanders, site restoration, and the number of translocation sites in the surrounding landscape. At the 115 translocation sites (314 stocking events), persistence was linked with several of these same factors plus translocation effort, timing of stocking, and the rearing environment and life stages used in translocations. Translocations also produced a large increase in

**Table 5**

Parameter estimates (logit scale; median, lower bound of 95% credible interval =  $q_{0.025}$ , upper bound of 95% credible interval =  $q_{0.975}$ ) from a dynamic occupancy model fitted to Western Tiger Salamander data based on 1995–2019 visual encounter surveys (VES) and 2018 eDNA surveys.

Symbol	Description	$q_{0.025}$	median	$q_{0.975}$
$\alpha_0$	Initial occupancy	-1.28	-0.76	-0.30
$\beta_0$	Extinction probability for lentic sites	-4.08	-3.70	-3.36
$\beta_1$	Extinction probability for lotic sites	-1.20	-0.36	0.46
$\nu_0$	Colonization probability for lentic sites	-0.22	-0.01	0.19
$\nu_1$	Colonization probability for lotic sites	-2.13	-1.79	-1.46
$\nu_2$	Effect of topographic variation (1 SD of mean elevation) within 5 km of a site on colonization probability	0.68	1.59	2.91

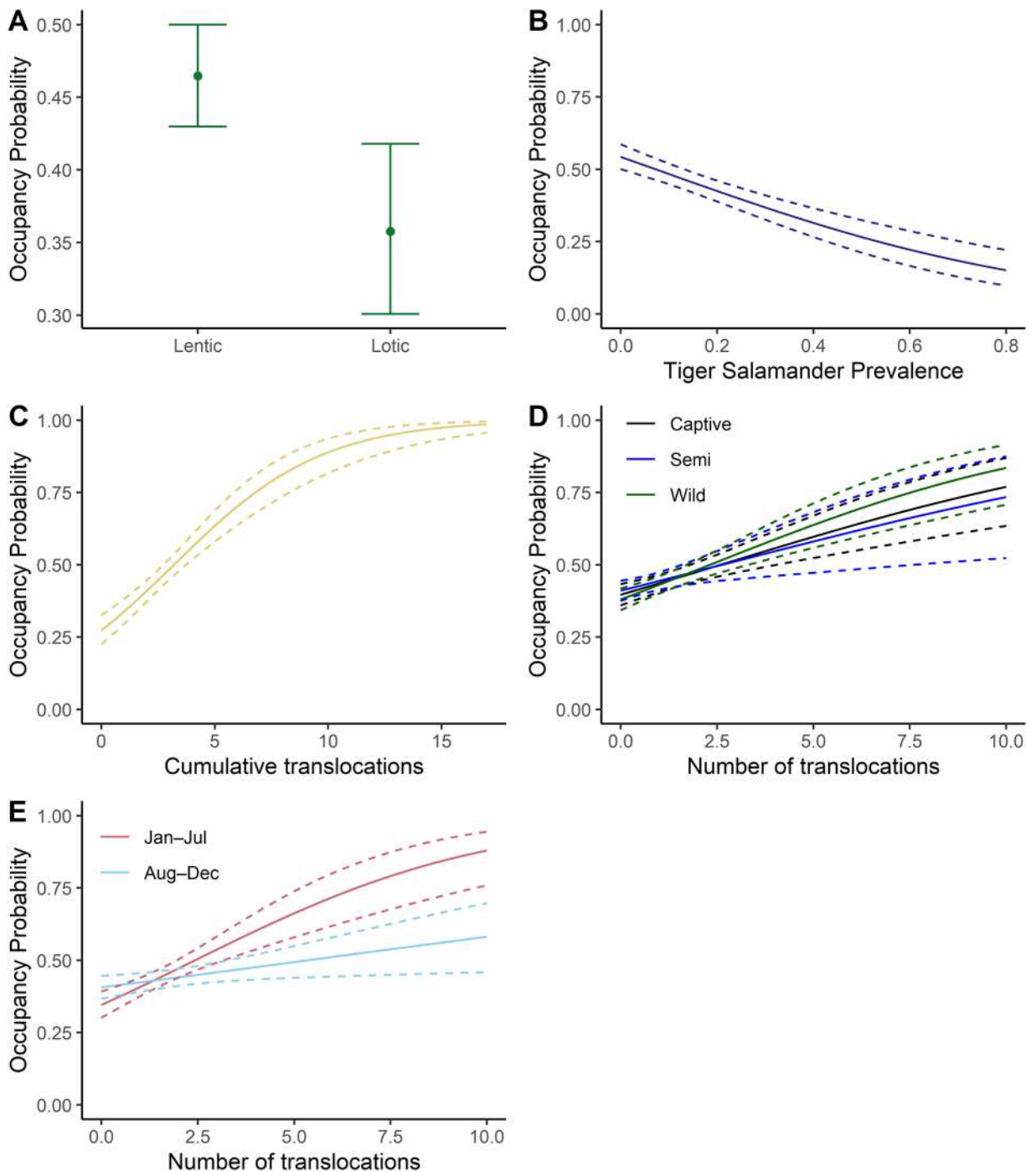


**Fig. 6.** Median (colored circle), 50% credible intervals (thick bars), and 95% credible intervals (thin bars) for the effect of each covariate on detection probability for visual encounter surveys (black) or eDNA surveys (purple; 2018 surveys only) for Chiricahua Leopard Frogs and tiger salamanders during 1995–2019. We used the same detection process model for frogs and salamanders, sharing information between the two species. Numbers indicate the proportion of the posterior distribution in the same direction as the posterior mean. All estimates are on the logit scale.

**Table 6**

Parameter estimates (logit scale; median, lower bound of 95% credible interval =  $q_{0.025}$ , upper bound of 95% credible interval =  $q_{0.975}$ ) and Bayesian  $p$ -values ( $p$ ) from models estimating the effect of site and landscape characteristics and translocation history on the proportion of years sites were estimated to be occupied by Chiricahua Leopard Frogs, including the year of the first translocation event at each site. We fit four separate models to avoid issues of collinearity among predictor variables. We regarded an effect as significant when the posterior probability of a difference (e.g., posterior  $p$ -value) was  $> 0.95$ .

Model	Estimate	Description	$q_{0.025}$	median	$q_{0.975}$	$p$
Model 1	$\beta_1$	Intercept (Lentic systems)	-0.28	-0.14	0.00	0.975
	$\beta_2$	Lotic systems	-0.74	-0.44	-0.15	0.999
	$\beta_3$	Effect of topographic variation	-0.19	-0.06	0.07	0.823
	$\beta_4$	Effect of tiger salamanders	-0.65	-0.50	-0.36	1.000
	$\beta_5$	Effect of total number of translocation events	0.52	0.69	0.87	1.000
Model 2	$\beta_1$	Intercept	-0.36	-0.24	-0.12	1.000
	$\beta_2$	Effect of wild source populations	0.22	0.36	0.50	1.000
	$\beta_3$	Effect of semi-captive source populations	0.06	0.23	0.39	0.997
	$\beta_4$	Effect of captive source populations	0.14	0.26	0.38	1.000
Model 3	$\beta_1$	Intercept	-0.36	-0.24	-0.12	1.000
	$\beta_2$	Effect of January–July translocation	0.24	0.38	0.53	1.000
	$\beta_3$	Effect of August–December translocation	0.03	0.16	0.29	0.990
Model 4	$\beta_1$	Intercept	-0.35	-0.23	-0.11	1.000
	$\beta_2$	Effect of egg life stage	-0.13	-0.02	0.10	0.603
	$\beta_3$	Effect of larval life stage	0.24	0.38	0.53	1.000
	$\beta_4$	Effect of juvenile life stage	-0.03	0.09	0.22	0.925
	$\beta_5$	Effect of adult life stage	0.01	0.16	0.30	0.982

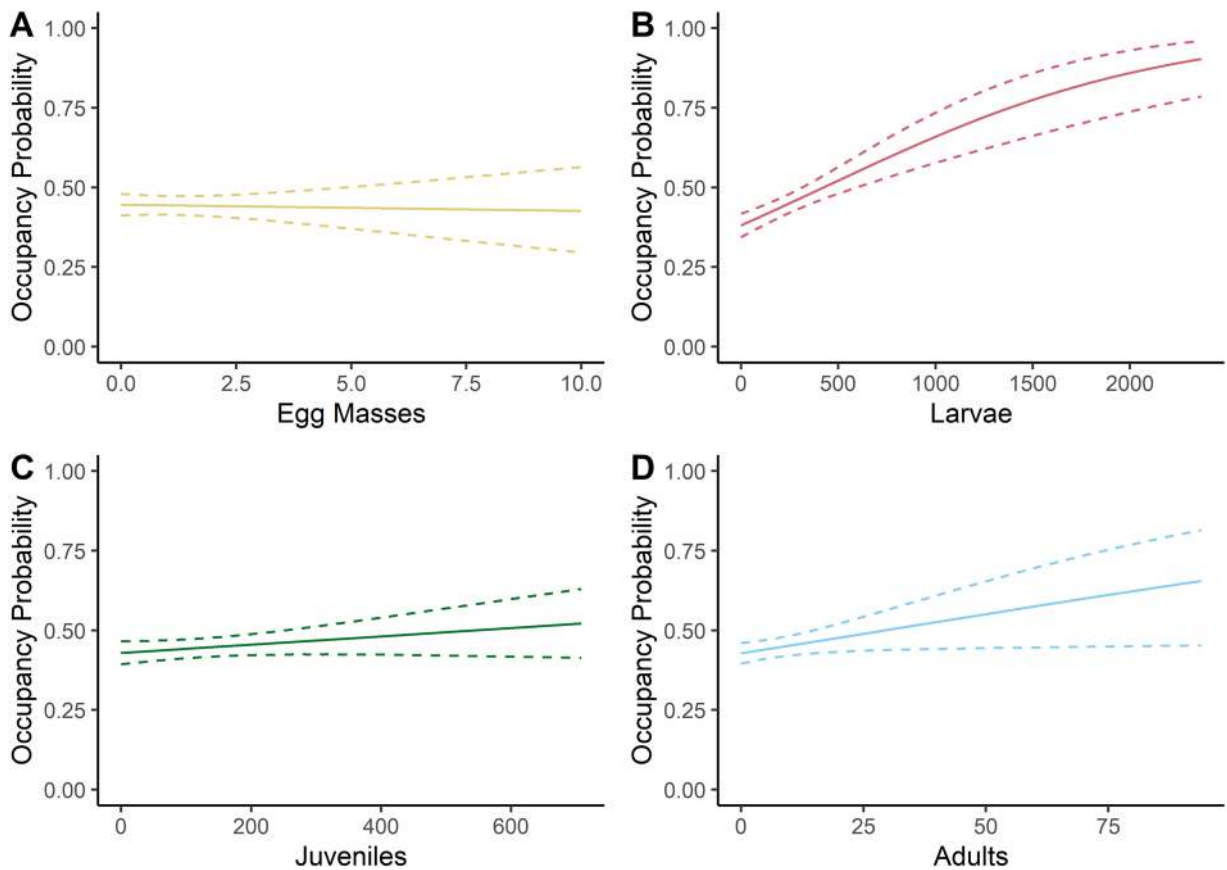


**Fig. 7.** (A) Effect of site type (lentic, lotic), (B) tiger salamander prevalence, (C) total number of translocations, (D) number of translocations from three different classifications of source population, and (E) timing of translocation events (Jan – Jul; Aug – Dec) on the proportion of years that translocation sites were estimated to be occupied by Chiricahua Leopard Frogs. Tiger salamander prevalence is the proportion of years they were predicted to be present in a site. Dashed lines represent 95% credible intervals.

the predicted number of years a site was occupied.

#### 4.1. Landscape occupancy

Identifying influential habitat characteristics and the role of co-occurring predators can be important elements of recovery for



**Fig. 8.** Effect of the cumulative number of each Chiricahua Leopard Frog life stage translocated to a site over time on the proportion of years that translocation sites were estimated to be occupied by Chiricahua Leopard Frogs. Dashed lines represent 95% credible intervals.

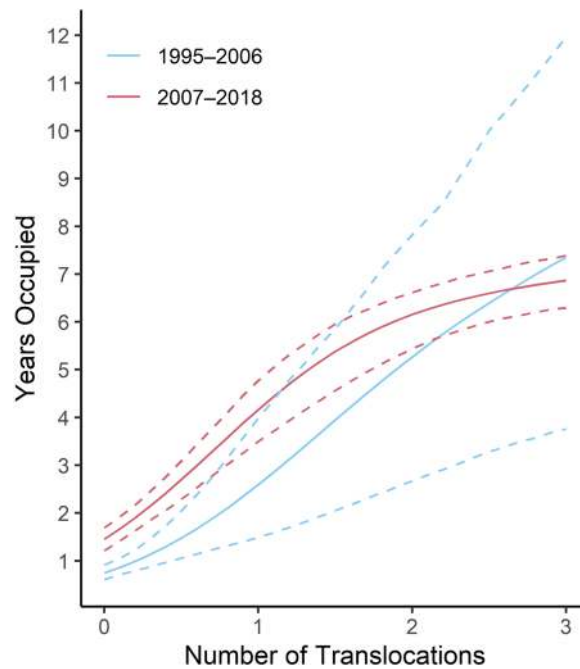
**Table 7**

Parameter estimates (Estimate), bias-corrected 95% confidence intervals (LCL, UCL) and p-values (*p*) from a zero-inflated Poisson regression model relating the total number of translocation events to the predicted number of years a site was occupied by Chiricahua Leopard Frogs during 1995–2007 (Time Series 1) and 2008–2018 (Time Series 2).

Time series 1 (1995–2007)	Estimate	LCL	UCL	<i>p</i>
<i>Count model coefficients (Poisson with log link)</i>				
Intercept	4.74	4.11	5.50	< 0.01
Total Translocations	1.18	0.93	1.67	0.08
<i>Zero-inflation model coefficient (binomial with logit link)</i>				
Intercept	0.84	0.81	0.87	< 0.01
Total Translocations	0.18	0.06	0.41	< 0.01
<b>Time series 2 (2008–2018)</b>				
<i>Count model coefficients (Poisson with log link)</i>				
Intercept	6.31	5.73	6.89	< 0.01
Total Translocations	1.03	0.98	1.07	0.02
<i>Zero-inflation model coefficient (binomial with logit link)</i>				
Intercept	0.77	0.73	0.80	< 0.01
Total Translocations	0.14	0.09	0.21	< 0.01

imperiled species. Across all sites sampled during 1995–2019, the strongest associations with Chiricahua Leopard Frog population dynamics were site type and presence of tiger salamanders. Frogs were more common in lentic than lotic sites. Site-level colonization and extinction probabilities for Chiricahua Leopard Frogs were higher at lotic (colonization = 0.48 [95% CrI = 0.35 – 0.60], extinction = 0.40 [0.27 – 0.54]) than at lentic sites (colonization = 0.06 [0.05 – 0.08], extinction = 0.15 [0.11 – 0.19]), reflecting greater stability in lentic sites (Table 4). Extinction probability for Chiricahua Leopard Frogs was higher in lentic sites when salamanders were present (0.29 [0.14 – 0.51]) compared to when they were absent (0.15 [0.12 – 0.19]). Survey evidence suggests non-native American Bullfrogs have a much greater negative effects than tiger salamanders on Chiricahua Leopard Frogs and other native ranid frogs in the Southwest (Fisher and Shaffer, 1996; Rorabaugh et al., 2018; Rosen and Schwalbe, 2002), but the translocation program has largely avoided





**Fig. 9.** Effect of the cumulative number of Chiricahua Leopard Frog stocking events (all life stages combined) on the predicted number of years that translocation sites were estimated to be occupied during 1995–2006 and 2007–2018. Dashed lines represent 95% credible intervals.

releasing frogs in sites occupied by bullfrogs and thus we could not estimate their effect on Chiricahua Leopard Frog occupancy.

Predators have been linked directly or indirectly with declines of many native amphibians in western North America and globally (Hayes and Jennings, 1986; Rorabaugh et al., 2018; Witte et al., 2008). Ranid frogs seem especially susceptible to predator-linked declines, partly because they share many habitat preferences, such as long hydroperiods, with many vertebrate predators (Hayes and Jennings, 1986; Rorabaugh et al., 2018). In some areas of Arizona and New Mexico, there has been concern that presence of tiger salamanders reduces translocation success or population viability of Chiricahua Leopard Frogs, possibly by consuming small frog larvae or by transmitting shared pathogens like ranaviruses and amphibian chytrid fungus (*Batrachochytrium dendrobatidis* [Bd]) (Brunner et al., 2004; Davidson et al., 2003; McCall et al., 2018). Although tiger salamanders and other large *Ambystoma* larvae commonly eat small amphibian larvae (Petranka, 1998; Walters, 1975; Wilbur, 1972), we are aware of little direct evidence indicating tiger salamanders are major predators of frog larvae in the Southwest (Collins and Holomuzki, 1984; Loeb et al., 1994; Sredl and Collins, 1992). Chiricahua Leopard Frogs and native tiger salamanders have co-evolved and still commonly co-exist, but they occurred historically in habitats that were more structurally complex than the simple livestock ponds that now serve as primary habitat for the frogs in many areas (McCaffery et al., 2012; McCall et al., 2018). Simple habitats can increase foraging efficiency of predators compared to habitats that provide cover for prey (Gotceitas and Colgan, 1989; Lewis and Eby, 2002; Sredl and Collins, 1992). Determining the conditions that facilitate co-existence of these 2 species, including the potential role of predation and shared diseases, could improve translocation success and recovery.

In cases where important habitat is lacking or is occupied by other species that preclude native species, restoration (including habitat creation) can be a critical component of translocation and recovery programs (Ewen et al., 2014; Seddon, 2010). In the southwestern USA and other arid landscapes, stock ponds are often maintained by removing sediment, clearing vegetation, repairing water retention structures, and by installing wells to ensure a reliable water supply (McCaffery et al., 2012; McCall et al., 2018; Sall et al., 2020). Because it was impossible to know the history of all human-created waterbodies in our analysis, we limited restored sites to those that were restored specifically for frog conservation (sensu Hossack et al., 2013a; McCall et al., 2018; Pilliod and Scherer, 2015). Our analysis showed that restored sites had much lower extinction probabilities (0.15 [0.11–0.19]) than unrestored sites (0.70 [0.55–0.81]). The often on-going nature of translocation efforts can make it difficult to distinguish persistence from near-term management actions, and in general, reintroduction science (Armstrong and Seddon, 2008; Linhoff et al., 2021) and restoration science are hampered by limited numbers of studies that have examined responses at broad spatial and temporal scales (McIntosh et al., 2018; McNeil et al., 2020; Menz et al., 2013). Our results are consistent with smaller-scale, restoration-linked increases in abundance or population growth rates for other imperiled ranid frogs in western North America (Duarte et al., 2017; Hossack et al., 2013a; Pilliod and Scherer, 2015) and adds to growing evidence of the important role of site restoration in abating or reversing declines.

Increased isolation that occurs after species have declined in abundance and distribution can raise extinction risk further, because waning populations are less likely to be rescued by colonists from neighboring areas (Brown and Kodric-Brown, 1977; Hanski, 1994). Thus, connectivity among populations is generally considered critical for ensuring persistence, especially in disturbed or fragmented

landscapes (Ricketts, 2001; Thomas and Jones, 1993). Colonization rates for the Chiricahua Leopard Frog were unrelated to topographic variation within 5 km around sites (logit scale:  $-0.03$  [ $-0.19$  to  $0.11$ ]), but colonization was greater for sites that were surrounded by more translocation sites. For every added 1.4 translocation sites within 2 km of a given site ( $SD = 1.4$ , range =  $0 - 6$ ), the probability of colonization increased by  $0.54$  ( $0.50 - 0.58$ ). This evidence suggests concentrating efforts in a particular area would increase the likelihood that nearby habitat patches are colonized or that an existing population will be rescued by colonists.

While measures of population isolation or connectivity contributed to occupancy and persistence, covariates reflecting patch quality (e.g., site type, presence of tiger salamanders) tended to be more strongly associated with the distribution and dynamics of Chiricahua Leopard Frog populations. These results align with the hypothesis that population extinction is reduced by the presence of neighboring populations, although evidence for this hypothesis in amphibian meta-populations is often weaker than expected and context dependent, including limited support for Red-spotted Toads (*Anaxyrus punctatus*) in the southwestern USA (Bradford et al., 2003). More specifically, these results align with previous analyses of translocated Chiricahua Leopard Frogs in the Altar Valley of southern Arizona, where measures of patch quality were more strongly linked with meta-population dynamics than landscape characteristics such as topographic slope (Chandler et al., 2015; Howell et al., 2018; Jarchow et al., 2016). Inference from previous studies focused on the Altar Valley was limited by the small number of translocation sites, the relatively uniform landscape (for the region), and the exclusive focus on stock ponds. The current results from across a wide range of environmental settings in the southwestern USA support prioritizing patch quality over landscape characteristics when identifying potential translocation sites.

#### 4.2. Translocation success

Predictions from the landscape occupancy model for 115 translocation sites stocked since 1995 allowed us to derive estimates for factors associated with translocation success. Based on estimates for the proportion of years that translocation sites were occupied, site type and the presence of tiger salamanders were strongly linked with presence of Chiricahua Leopard Frogs. Accounting for site type, frogs were predicted to be present during approximately 50% of years in sites where tiger salamanders were rarely present, but in  $< 20\%$  of years in sites when tiger salamanders were common (Fig. 7B). Lentic translocation sites lacking salamanders (probability:  $0.46$  [ $0.43-0.50$ ]) were more likely to be occupied by frogs than were lotic translocation sites (probability:  $0.39$  [ $0.32-0.46$ ]), especially the relatively rare lotic site with salamanders (probability:  $0.25$  [ $0.16-0.38$ ]). Notably, lentic sites with salamanders (probability:  $0.38$  [ $0.34-0.41$ ]) had similar probabilities of translocation success as lotic sites without salamanders (probability:  $0.39$  [ $0.32-0.46$ ]).

Translocations that occurred from January through July (probability:  $0.38$  [ $0.24-0.53$ ]) were slightly more likely to produce persistent populations than translocations that occurred from August through December (probability:  $0.16$  [ $0.03-0.29$ ]) (Fig. 7E). We suspect timing was important because spring through early summer is typically the driest time of year in much of the study area (Adams and Comrie, 1997). Dry conditions might reduce the likelihood that released juveniles or adults disperse from translocation sites into the terrestrial environment, compared to later in the year when there is more water on the landscape that can facilitate dispersal (Hinderer et al., 2017; Martof, 1953; Zylstra et al., 2019). Translocations during spring through early summer also help ensure the selected habitats hold water reliably, because many sites are dry that time of year and do not re-fill until summer rains arrive (Hossack et al., 2017; Sall et al., 2020). It is also possible seasonal disease dynamics could affect survival of translocated animals. Prevalence and outbreaks of amphibian chytridiomycosis in the study area tend to be greater during the fall and winter than during the warm, dry months (Bradley et al., 2002; Savage et al., 2010).

Knowledge of specific life stages or sources of animals that contribute differentially to translocation success can be used to optimize recovery strategies (Duarte et al., 2017; Kissel et al., 2014; Seddon et al., 2007). For the Chiricahua Leopard Frog program, animals sourced from captive, semi-captive, and wild sources produced nearly identical effects on persistence. Our results provided greater support for targeting specific life stages to stock rather than the rearing environment of animals. Because of the large number of sources that have contributed animals for translocations (Supplemental Table S1), we could not investigate contributions based on specific donor populations or genetic lineages. We also could not estimate differences from specific combinations of life stages and sources (e.g., larvae from the wild vs. captive), partly because fewer wild animals were released than from other sources (Table S1). However, stocking egg masses (which were also predominantly wild-sourced) or juveniles had little effect on population persistence (Model 4 in Table 6, Fig. 8A, C). The lack of support for egg masses was surprising given evidence of success or the general perception of success based on stocking eggs in other systems and species (e.g., Denton et al., 1997; Semlitsch, 2002). Translocating adults (typically from the wild) had a weak positive effect on persistence, but this required large numbers of frogs (e.g.,  $>50$ ) and the estimated effect was imprecise (Model 4 in Table 6, Fig. 8A-D).

We found more support for stocking larvae than for other life stages. Estimated occupancy probability for the Chiricahua Leopard Frog increased to  $\sim 0.80$  when 1500 larvae were stocked, and to  $> 0.90$  when more than 2000 larvae were stocked to a site over time (Fig. 8B). Importantly, most larvae stocked as part of the translocation program have been small numbers of mid- to late-stage larvae rather than fragile, young larvae. Given the lack of a mean positive effect of stocking egg masses or juveniles and the impracticality of releasing large numbers of adults of a threatened species, repeated releases of large numbers of larvae would likely maximize the probability of establishing a population. Simulations to compare efficacy of captive breeding and head-starting programs for larvae versus metamorphs of the federally threatened Oregon Spotted Frog (*Rana pretiosa*) reached a similar conclusion: under most scenarios, captive-reared larvae provided the most cost efficient and ecologically effective options (Kissel et al., 2014). However, stocking larvae comes with its own complications, especially when transporting large numbers of animals during challenging conditions or to remote locations, so life stages and number of animals stocked should still be tailored to specific conditions.

Information on expected outcomes for a given intensity of efforts is important for managing translocation programs. Although the

number of translocation events for targeted sites ranged from 1 to 16, because we could not estimate within-year occupancy dynamics for translocation sites and because some sites did not have a high frequency of surveys, the data did not allow us to distinguish whether a particular stocking event represented translocation into a site lacking Chiricahua Leopard Frogs or whether it supplemented an existing population that had been established via translocation and persisted. We also could not account for the temporal distribution of stocking events (e.g., 2 in same year vs. 2 events 5 years apart). But based on the number of years that translocation sites were predicted to be occupied, translocation efforts markedly increased the probability of population persistence. The predicted number of years occupied during the 2007–2018 period increased from approximately 1.5 years to 4 years after 1 translocation event and levelled out around 7 years occupied with 3 translocation events. For the 1995–2006 period, there was less benefit of 1 translocation event, but 3 translocations had a similar net benefit as during 2007–2018. Notably, the estimate for the 1995–2006 time series was imprecise, but during both time periods, 2 or more translocations at a site produced, on average, a more than 4-yr increase in the predicted number of years a site would be occupied compared to no translocations.

#### 4.3. Synthesis

Differing goals and metrics among studies and systems, as well as a bias against publication of unsuccessful translocation efforts, make it hard to identify factors consistently associated with translocation success (Ewen et al., 2014; Germano and Bishop, 2009; Miller et al., 2014). A review of 38 translocation programs or efforts conducted for 25 amphibian species during 1991–2006 showed that approximately half were deemed successful, based on reported evidence of at least short-term recruitment into adult populations (Germano and Bishop, 2009). Similar to our results, the review concluded that translocation success was much higher for cases where > 1000 animals were stocked (65%) compared to when < 1000 animals were stocked (38%); success also was not strongly associated with animal source (wild vs. captive) (Germano and Bishop, 2009; Smith et al., 2020). Counter to the summary by Germano and Bishop (2009), we found strong evidence for differences among life stages, and the expansive spatial and temporal scope of the Chiricahua Leopard Frog translocation program, paired with long-term monitoring, allowed us to use empirical data to identify factors related to habitat, timing and number of releases, and presence of predators that increased the chances of establishing a persistent population.

Evaluating the success of translocation programs, especially after a large number of trials over many years, is important for optimizing success and efficiency of recovery efforts. Although definitions used for success of translocations vary widely, establishment of self-sustaining populations is a common recovery goal (Germano and Bishop, 2009; IUCN/SSC, 2013; Seddon et al., 2007). But documenting self-sustaining populations is difficult, especially across several populations and large geographic areas that experience substantial environmental variation. Evidence of near-term success can also be misleading (Linhoff et al., 2021). After mixed life stages of Sierra Yellow-legged Frogs (*Rana sierrae*) were translocated to 4 sites in Sequoia National Park, California (USA), short-term survival was high and metamorphs and adults were present at all sites at the end of the first summer. By the 4th year, no frogs remained at 3 sites and the number at the 4th site was deemed too small to sustain the population (Fellers et al., 2007). In the long-term, recovery of most species that are the focus of translocation programs and that exist in spatially structured populations will depend upon emigrants colonizing vacant patches and establishing new populations.

Our analysis is based on a large and long-term dataset and accounted for several sources of uncertainty, including detection error and different life stages and sources of animals stocked. Thus, we suspect our results represent reliable patterns that can be used to guide recovery of the Chiricahua Leopard Frog and other species with similar life histories. The combination of factors that would maximize translocation success include several stocking events of larvae (especially large numbers of larvae) into neighboring or clustered lentic sites that lack vertebrate predators. Our analyses were limited by high turnover of Chiricahua Leopard Frog and tiger salamander populations, but across all sites, we found little evidence that topographic complexity surrounding sites or the source of frogs used for stocking were important.

The large translocation program for the Chiricahua Leopard Frog has undoubtedly increased the number of extant populations across the landscape. For example, the meta-population in the Altar Valley, Arizona, resulted from translocations (Hossack et al., n.d.; Jarchow et al., 2016). Also, across all sites, colonization of unoccupied sites was higher when there were more translocation sites within 2 km, indicating a positive net effect of translocation efforts even at sites where frogs had not been stocked. However, cases like that described by Fellers et al. (2007) of short-term, apparent successes that did not persist and recent drought-related losses for the Chiricahua Leopard Frog meta-population in the Altar Valley, Arizona (A. Owens, pers. obs.), underscores the need for long-term monitoring that encompasses a wide range of environmental variation before we can be confident that populations are self-sustaining and likely to persist long-term. Positive responses to other recovery actions, such as bullfrog eradication and pond restoration (Chandler et al., 2015; Jarchow et al., 2016; McCall et al., 2018), also emphasize the importance of continued management of threats, including invasive predators and disease, while managing for availability of water will also be critical to recovery of the Chiricahua Leopard Frog.

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#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02078](https://doi.org/10.1016/j.gecco.2022.e02078).

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