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RESEARCH ARTICLE

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Survival and establishment of captive-reared and translocated giant gartersnakes after release

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Abstract

Many imperiled species face increasing extinction risk that requires interventional management like translocation or captive rearing. The use of translocations to successfully restore or create populations requires that animals survive at recipient sites, information that is often lacking for imperiled species and that can be risky to acquire if not obtained before a species has dwindled in number. The giant gartersnake (*Thamnophis gigas*), a semiaquatic snake endemic to the Central Valley in California, USA, has declined after losing >90% of its historical habitat and may benefit from successful translocations to protected habitat. We released adult and captive-reared juvenile snakes from 2 donor sites into a recently restored wetland in 2019 and 2020 and compared their survival, movement, and activity using radio-telemetry through 2021. We monitored juvenile survival for 2 years in captivity after birth and then estimated post-release survival at the recipient site using radio-telemetry. Just 8% of translocated adult snakes survived >801 days (95% CI = 1–64%) compared with 39% of resident snakes at the donor sites surviving >1,154 days (95% CI = 23–68%). This equated to annualized survival rates of translocated adults ($\bar{x}$ = 0.32, 95% CI = 0.12–0.82) that were roughly half that of resident snakes ($\bar{x}$ = 0.74, 95% CI = 0.63–0.89). Translocation was negatively correlated with survival, but movement and activity received little support in models. Seventy-six percent of juvenile snakes survived captivity and, once released, juvenile survival was 60% (95% CI = 38–94%) for the 4-month monitoring period before winter. It is unclear why survival of translocated adult snakes was lower than that of resident snakes, but there was little evidence for differences in behavior (e.g., increased surface activity, average distance moved, emigration from the translocation site) that are commonly cited causes of mortality in other translocation studies. Our results suggest that, in the absence of a clear understanding as to what contributes to adult survival after release to a new site, future work using captive-rearing and juvenile translocation may be more promising for establishing and recovering populations than just translocating adults given the high survival of juveniles.

KEYWORDS

captive-rearing, Cox proportional hazard regression, giant gartersnake, head-starting, Kaplan-Meier curve, survival, telemetry, *Thamnophis gigas*, translocation

Habitat loss or degradation is the leading conservation threat for imperiled species (Wilson 1989, Wilcove et al. 1998, Pereira et al. 2010, Brondizio et al. 2019). While resource managers and conservation biologists are actively working to protect existing habitats and create or restore others, many populations and species may not persist to see these benefits without additional management intervention. One such management intervention is translocation—the intentional movement of animals from one location to another (Griffith et al. 1989, International Union for the Conservation of Nature 2013). Although translocation could benefit imperiled species, there is much debate on the effectiveness of translocation. Many translocated animals have higher mortality rates than non-translocated animals and many translocation projects fail to establish populations or to identify the reasons behind a failed translocation (Dodd and Seigel 1991, Seddon et al. 2007). Despite these challenges, imperiled species may ultimately require translocations to recover their populations, making it important to better understand the factors influencing effective translocations.

One taxon where translocation or captive-rearing could be particularly useful is reptiles. Not only have reptiles been significantly affected by habitat loss and degradation (Todd et al. 2010), but as ectotherms, they are often more sensitive to environmental conditions than are other taxa (Gibbons et al. 2000). Reptiles that rely on isolated habitats like wetlands for foraging or to move through the landscape may also suffer from low dispersal as habitat becomes more fragmented or as water availability declines because of drought, placing them at higher risk of imperilment (Gibbons et al. 2000, Roe et al. 2004, Attum et al. 2007, Todd et al. 2017). Reptiles stuck in fragmented habitat patches could also suffer from low genetic diversity and other complications of small population sizes if isolated from larger rescue populations (Madsen et al. 1996, Young et al. 1996, Keyghobadi 2007). Translocation may help in these cases to repopulate existing patches of habitat and maintain genetic diversity. Many reptiles also experience high mortality in juveniles and subadults in the wild, and translocation using head-started or captive-reared individuals is gaining popularity (Germano and Bishop 2009, Brichieri-Colombi et al. 2019).

The giant gartersnake (*Thamnophis gigas*) is a highly imperiled semi-aquatic snake that has declined after losing 93% of its historical wetland habitat (Frayer et al. 1989, Halstead et al. 2014). Giant gartersnakes now persist in disjunct populations separated by major highways and a matrix of agricultural lands. Giant gartersnakes are the longest species of gartersnake (max. length = 1.6 m) and vary from olive-green to almost black dorsal coloration with 3 dorsal stripes running from the back of the head to tail (Halstead et al. 2015). They are a non-venomous snake that preys mostly on aquatic prey such as frogs and fish (Halstead et al. 2015). Giant gartersnakes are listed as a threatened species under both federal and state law and part of their recovery criteria requires reintroductions into the San Joaquin Valley of the southern Central Valley, California, USA, where they have been almost completely extirpated (California Department of Fish and Game Commission 1971, U.S. Fish and Wildlife Service [USFWS] 1993). Translocation of adult snakes or captive-reared juveniles would be used to accomplish these reintroductions. The success of snake translocations is particularly variable because snakes are often seen as nuisance animals to the general public, so many translocations are executed to reduce human–wildlife conflict rather than for conservation purposes (Cornelis et al. 2021). Some snakes also have homing abilities, making translocations ineffective if individuals return to their original location (Pittman et al. 2014). Other snake translocations have been more successful, including the reintroduction of the endangered Antiguan racer (*Alsophis antiguae*), whose metapopulations grew from 51 to >1,100 individuals after translocations and invasive predator management (Daltry et al. 2017). Translocations have not been attempted in giant gartersnakes and the effectiveness of translocations for this species remains unknown.

Before attempting a large-scale reintroduction effort that incorporates 2 genetically separate populations, we implemented a small-scale study using wild-caught snakes and captive-reared snakes to test the feasibility of translocation in giant gartersnakes. The main objective of our study was to determine whether translocated giant gartersnakes survive and behave similarly to resident snakes or different after translocation. We also determined how well juvenile snakes respond to being raised in captivity and how their post-release survival compares to estimated survival of wild juveniles. We predicted that translocated snakes would have increased activity and movement behavior compared to wild-caught adults, and thus their overall survival would decrease because they are more exposed to predation and other environmental hazards.

STUDY AREA

We conducted this study June 2018–August 2021 at 3 sites within the Natomas Basin in Sacramento County, California, including 2 donor sites with existing giant gartersnake populations and 1 site where they had occurred historically but were absent when this study began (Figure 1). The Natomas Basin is in the northern portion of the California Central Valley and has a Mediterranean climate characterized by hot, dry summers and mild, wet winters (Sivakumar et al. 2006). Historically, the Central Valley contained much wetland habitat that has been reduced by >90% and converted to agricultural fields and human developments over the last 150 years (Frayer et al. 1989, Halstead et al. 2014). The entire area encompassing our study sites was approximately 50.2 km^2, though the area of each individual site ranged between 2–4 km^2. The elevation of our study area ranged from 0–20 m above sea level.

The first donor site (Betts-Kismat-Silva [BKS]) was a wetland site composed of mature, managed tule (*Schoenoplectus* spp.) marshes. The second donor site (Sills) was a rice agriculture site with irrigation canals and rice fields that has served as habitat in the absence of much historical native habitat (Halstead et al. 2010, USFWS 2017). Both donor sites were well-connected to adjacent habitat and have maintained stable populations (Inner City Fund International [ICF], unpublished report). The third site (Sacramento Area Flood Control Agency [SAFCA]), to which we translocated giant gartersnakes, was a managed marsh complex developed in 2014 to provide additional habitat for giant gartersnakes (Architecture, Engineering, Construction, Operations, and Management [AECOM], unpublished report). There was no evidence of an existing population of giant gartersnakes in the SAFCA recipient site at the start of our study in 2018 (ICF, unpublished report). All 3 sites were close enough geographically that the sub-populations at each were not genetically differentiated (Wood et al. 2015, USFWS 2017). The vertebrate communities were also similar among the 3 sites, with common predators that included various hawk and harrier species, great blue heron (*Ardea herodias*), and mammalian predators like North American river otters (*Lontra canadensis*), American mink (*Mustela vison*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*; USFWS 2017). Introduced American bullfrogs (*Lithobates catesbeianus*) and largemouth bass (*Micropterus salmoides*) are also predators of juvenile and neonate snakes. Prey species included juvenile and larval American bullfrogs, several species of invasive fish (bass, sunfish, and bluegills

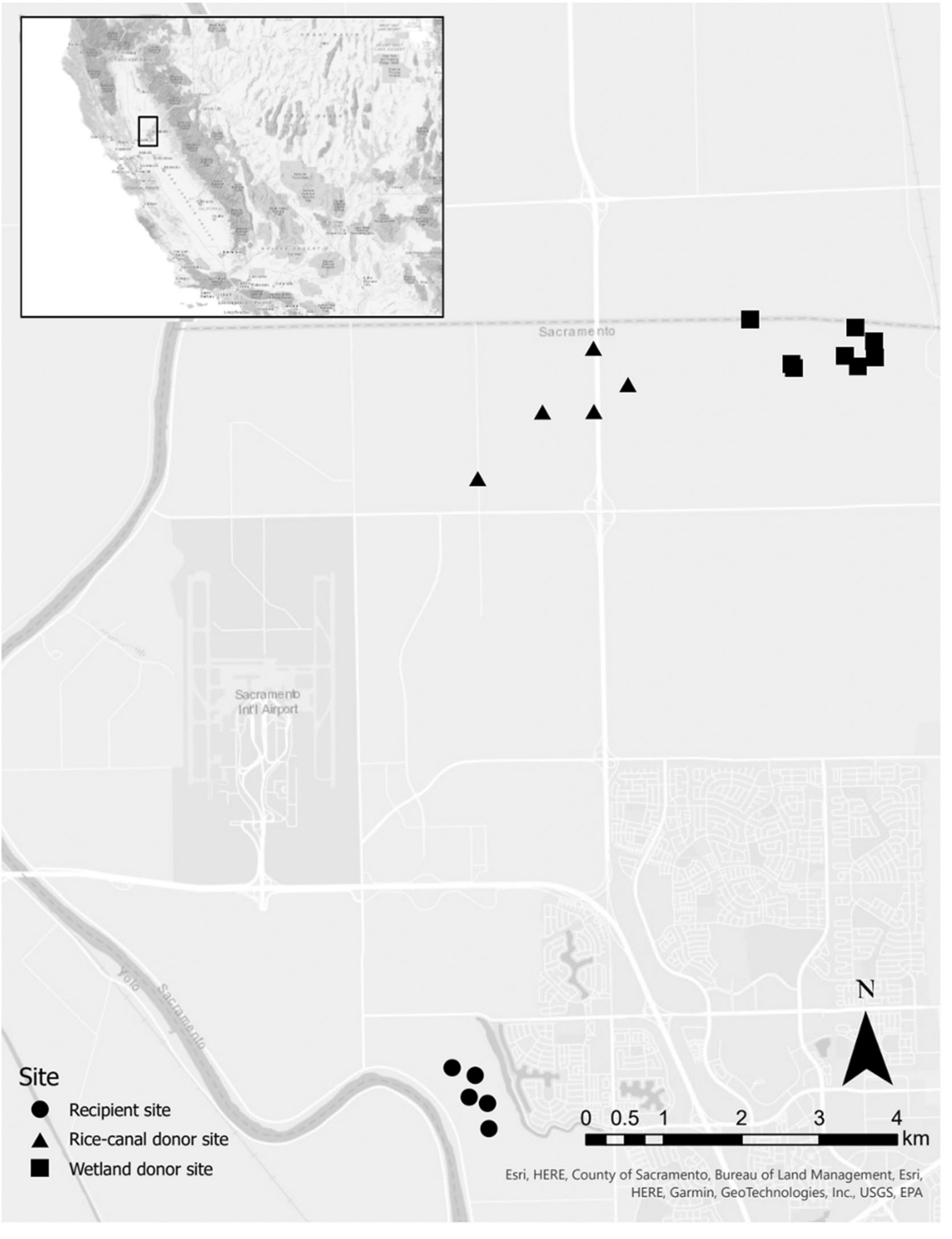

FIGURE 1 Donor and recipient sites for translocation of giant gartersnakes in the Natomas Basin, Sacramento County, California, USA, 2019–2021.

[centrarchids], western mosquitofish [*Gambusia affinis*], and minnows (cyprinids]), and Sierran treefrogs (*Pseudacris sierra*) in lower abundances (Ersan et al. 2020, ICF, unpublished report).

The vegetation species fluctuated at the 3 sites seasonally, especially at the rice–canal donor site (Sills), where rice is typically grown in April–October and then harvested, leaving fallowed fields for the remainder of the year.

The rice growing cycle coincides with the giant gartersnake active (Apr–Sep) and overwintering (Oct–Mar) seasons. The wetland donor site (BKS) had a higher proportion of single-stem grasses (family Poaceae), the recipient site (SAFCA) had a higher proportion of tule, and the rice–canal donor site (Sills) had a higher proportion of water primrose (*Ludwigia hexapetala*) and rice (during the growing season) on average (personal observation). The wetland donor site and recipient site were more like one another than the rice–canal donor site, which we would expect given that they were both managed marsh sites. All 3 sites were part of the same watershed, presumably containing the same species of parasites and potential pathogens. The locations, however, remain separated enough that snakes have been unable to disperse to the recipient site, likely because of barriers like state and interstate highways with poorly connected canals.

METHODS

Adult translocations

We have monitored the 2 donor sites and 1 recipient site using capture-mark-recapture (CMR) trapping for >10 years (Rose et al. 2018*a*, *b*, 2019; Halstead et al. 2019). We captured snakes in 3 trapping seasons: 3 June–30 August 2018, 9 May–16 August 2019, and 14 June–27 July 2020. We captured snakes using modified funnel traps—set in the water along the banks or natural edges created by aquatic vegetation in irrigation canals and wetlands— and by hand opportunistically (Casazza et al. 2000, Halstead et al. 2013). We set traps in lines of 50–100 traps, spaced 10–20 m apart, and checked them daily for 21–28 days depending on the trapline. We marked all snakes individually with a microbrand (Winne et al. 2006) and a passive integrated transponder (PIT) tag for snakes >30 g. We recorded sex and measured snakes to the nearest millimeter (snout-to-vent length [SVL], tail length [TVL]). We measured mass to the nearest gram using spring scales (Pesola; JLM Instruments, Chicago, IL, USA). All snakes included in the study received a comprehensive health assessment including bloodwork, physical examinations, and radiographs. We did not catch any males >200 g (the minimum size to keep transmitters <4.5% of body mass), so all adult snakes studied with radio-transmitters were female. Veterinarians implanted radio-transmitters with a one-year battery life (9 g SI-2T; Holohil Systems, Carp, Ontario, Canada) following standard methods (Reinert and Cundall 1982). After all surgeries, we kept snakes in captivity for 7 days to recover where they received analgesics and antibiotics as recommended by the veterinarians and part of approved research permits.

We released 20 adult females at their capture locations in June 2018 at both donor sites (release-2018), including 12 at BKS and 8 at Sills. Snakes were given an additional week after release to reacclimate to the wild before radio-tracking began. We tracked each individual 1–5 times/week during the active season and once every 2–3 weeks during the overwintering season. We recorded each individual's location (±5 m) using handheld global positioning system (GPS) receivers and recorded whether or not the snake was in the same location (within 2 m) as the previous tracking. If the snakes were visible, we recorded activity (e.g., moving, not moving, foraging) and status (alive, dead). We assumed snakes were alive unless the snake's body or transmitter was found, confirming mortality.

After one year collecting baseline data at the donor sites, we began translocating snakes to the SAFCA recipient site. From May–August 2019, we recaptured 9 snakes from release-2018 and captured 18 new snakes (release-2019, 9 from BKS and 9 from Sills; Table 1). Eight snakes from release-2018 underwent transmitter replacement surgery. We released 1 snake at its capture location after transmitter removal without replacing the transmitter. Snakes from release-2019 also had radio-transmitters implanted.

Snakes from release-2019 were released at their capture locations after recovery. Two snakes from release-2018 were released back at their capture locations within the BKS wetland complex to serve as between-year controls. We translocated the other 6 snakes from release-2018 to the SAFCA recipient site (translocation-1; Table 1). We randomly assigned snakes to one of the 5 selected wetlands within the SAFCA site and released them near the center of the wetland in an area with dense tule, <5 m from the water. For translocated snakes, we located the

TABLE 1 Study site sample sizes for giant gartersnakes included in the telemetry study in the Natomas Basin, Sacramento County, California, USA, 2018–2020. The 3 sites included in the study are the Betts-Kismat-Silva (BKS) wetland donor site, the Sills rice–canal donor site, and the Sacramento Area Flood Control Agency (SAFCA) recipient site. Adult females (F) and the 14 captive-reared (CR) telemetry snakes were radio-tracked to provide post-translocation survival estimates. The captive-reared group contained both males (M) and females (F).

	Telemetry snake sample sizes		
Site	**2018**	**2019**	**2020**
BKS – wetland donor site	12 F	11 F	6 F
Sills – rice–canal donor site	8 F	9 F	6 F
SAFCA – recipient site		6 F	5 F, CR: 8 F, 6 M

transmitter signal from a distance 3–5 days after release (rather than a full week of re-acclimation like for residents) to ensure we did not lose any snakes if they displayed homing behaviors or irregular movement. Tracking then continued as described above through the active and overwintering season.

We continued the project in 2020 following the same pattern as previous seasons. We collected the 6 surviving snakes still being tracked from release-2018 and release-2019. Five from release-2019 were implanted with replacement transmitters. One from release-2018 was recaptured and had the transmitter removed before being released at its capture site. We collected 12 additional snakes (release-2020, 6 from BKS and 6 from Sills) in June–August 2020 and outfitted them with transmitters. Release-2020 snakes were released at their capture locations and the 5 release-2019 snakes were translocated to the SAFCA site (transloaction-2; Table 1).

Captive-rearing

In addition to translocating adult giant gartersnakes, we reared neonates to larger sizes in captivity before release to increase the number of giant gartersnakes added to the new population while minimizing potential negative effects of removing adults from donor populations. In July–August 2018, we collected gravid females from the 2 donor sites. We kept gravid females in 38–76-L glass aquaria at the University of California Davis vivarium on aspen substrate with a hide and a water bowl large enough for them to completely immerse themselves (Ersan et al. 2020). We used broad spectrum light that included ultraviolet B wavelengths to keep snakes on a 12:12 light:dark cycle, consistent with summertime conditions (King and Stanford 2006). We used heat lamps or under-tank mats to establish a thermal gradient of 21–27°C on the cool side and 29–38°C on the warm side of the tank. We offered females a small adult bullfrog at least weekly as prey (Ersan et al. 2020).

In 2018, 4 adult females produced 42 viable offspring, which we kept to rear in captivity. We returned all females to their sites of capture shortly after birth. We housed neonates in groups of 3–6 littermates for the first several months and then moved snakes to individual housing (Ersan et al. 2020). We kept neonates under the same conditions as females, with the addition of Eco Earth® (Zoo Med Laboratories, Inc., San Luis Obispo, CA, USA) mixed into the substrate and humid hides to maintain higher ambient humidity. We fed neonates thawed tilapia (*Oreochromis* spp.) fillets, pinky house mice (*Mus musculus*), and Atlantic silversides (*Menidia menidia*), and live prey that included nightcrawlers, American bullfrog tadpoles, Sierran treefrog adults and tadpoles, and various fish species collected from the field sites (King and Stanford 2006, Ersan et al. 2020).

We reared snakes in captivity for 2 years from August 2018, when snakes were born, to 26 August–2 October 2020, when they were released. Over the 2-year rearing period, 10 juveniles died and 1 was transferred to a zoological institution because of developmental abnormalities that prevented release. We measured and marked the remaining 31 snakes; we did not implant a PIT tag in snakes <30 g. We implanted the 14 largest snakes with very high frequency radio-transmitters (Holohil, 2.5 g or 3 g PD2 depending on snake mass, with an average battery life of 3 and 4 months, respectively) before release into the wild. The surgical and recovery methods were the same as described above.

We released all 31 captive-reared juveniles (14 with transmitters and 17 without) into one of 5 SAFCA wetlands (translocation-CR; Table 1). We assigned snakes to wetlands using stratified random sampling, splitting the 14 telemetry snakes among the 5 wetlands and trying to maintain an even sex ratio among wetlands while also splitting up opposite-sex littermates into different wetlands when possible. We released juveniles in groups of 3–5 snakes. We radio-tracked the 14 radio-tagged juveniles 1–5 times per week from 26 August–11 December 2020, when the last of the transmitter batteries died. We recorded the same data as described above. When we found a mortality in the field, we photographed the snake and recorded observations about the condition and location of its body. We also necropsied the captive-reared juveniles that died in captivity.

Prey community composition

We wanted to examine differences in the prey community at the 3 sites, which may influence survival. We captured prey using the same trapping methods described above for snakes. To quantify the prey community, we recorded the number of American bullfrogs, Sierran treefrogs, bass, sunfish, and related species (centrarchids), carp, minnows and related species (cyprinids), and mosquitofish (*Gambusia* spp.) present in every fifth trap. We then calculated the catch per unit effort (CPUE) for each site by totaling the abundance of captured prey and dividing by the trap nights at each site. We grouped the frog species together and the fish species together and looked at the average CPUE of frogs and fish collectively.

Analyses

We monitored post-release survival of adult snakes from 29 June 2018–31 August 2021 and estimated survival using the Kaplan-Meier estimator in the R package survival (R Core Team 2021, Therneau 2021). The Kaplan-Meier curves calculate survival probabilities based on the time to an event (in this case death) and the number of individuals at risk of the event during a specified time period. We used a staggered-entry model with time 0 set as the date of the first snake release and all other times adjusted to the specific release dates of subsequent animals. Time stops when snakes die or are censored from the model (right-censoring; Williams et al. 2002). Snakes are censored whenever their fate, or status, becomes unknown, which occurs when transmitters fail, snakes move off-site and we could not locate them to confirm whether they were alive or dead, or when snakes were removed from the study. Translocated snakes had 2 stopping times: the first when they were translocated from their resident sites (censored from resident treatment groups and re-entered as translocated animals at a different site) and the second when they died or were censored after translocation.

To examine the effects of different predictor variables on adult survival, we constructed Cox proportional hazard models in the survival package (Cox 1972). We investigated 2 different covariates to capture the treatment group of the snake: one that split the snakes by site into wetland resident, rice–canal resident, or translocated, and one that used a binary covariate in which the 2 resident groups were a single resident category compared with a translocated category. We included an activity covariate representing the proportion of resightings where snakes were visually observed or disturbed out of all times they were tracked. To capture other individual variation in behavior, we used the adehabitatHR and adehabitatLT packages to transform the GPS coordinates from each location into spatial data and then calculated the average distance moved between resightings (average distance) for each individual (Calenge 2006). For translocated individuals, we calculated average distance before and after translocation. We chose to look at activity and average distance because the amount of surface activity and movement across the landscape both affect survival by increasing exposure to predators, environmental elements, or other hazards (Germano and Bishop 2009, Cornelis et al. 2021). All adults large enough to receive transmitters were females, so we did not include sex in the models. Using the covariates described above, we tested 9 models, including an intercept-only model. We used an information-theoretic approach to evaluate model support, using the corrected Akaike's Information Criterion (AIC_c) for small sample size. We calculated the relative variable importance for each predictor by summing the AIC_c weights of the models that contained that predictor, and ensured each predictor was included in an equal number of models to not inflate relative importance (Arnold 2010).

We monitored captive-reared juveniles daily during the captivity period and then monitored the 14 telemetry juveniles from August 2020 until December 2020 when the final transmitter batteries died. We calculated summary statistics on the growth and survival of juveniles during the 2-year captive-rearing period. We calculated the proportion of juveniles alive every 3 months to track how survival changed over time. We also calculated the average monthly SVL and mass measurements for the captive juveniles.

We estimated post-release survival for the 14 telemetry juveniles; we did not include the other 17 non-telemetry captive-reared snakes because we could not determine the fate of these individuals after release. We analyzed survival using Kaplan-Meier curves and Cox proportional hazard models as with the adults. We used a staggered-entry model with time 0 set at the date of the first snake release and all other times adjusted from that date. We censored all snakes that survived until the overwintering period at the last date they were known to be alive based on movement. We fit several different Cox proportional hazard models to the juvenile data using all possible additive combinations of the predictors: sex, SVL at release, average distance moved (average distance), and activity. We used an information-theoretic approach to evaluate model support and calculated relative variable importance using the methods described above.

RESULTS

Adult snakes

Total captures ranged from 98–227 (average = 139) at the wetland donor site, 47–132 (average = 86) at the rice–canal donor site, and 0–8 (average = 1) at the recipient site from 2018–2021 (Table 2). Captures of unique individuals were also greatest at the wetland donor site, followed by the rice–canal donor site and then the recipient site (Table 2). The average CPUE at the wetland donor site was 0.015, 0.0082 at the rice–canal donor site, and 0.0005 at the recipient site (Table 2). No snakes were captured at the recipient site from 2017–2019, but 6 individuals were caught 2020–2021 after snakes were released there (Table 2).

We radio-tracked 50 resident snakes over the course of the study. Of these, 12 died, 20 had unknown fates, 11 were translocated (censored at their translocation date), and 7 were confirmed alive at the end of the study. We translocated and tracked 11 adult snakes in the SAFCA recipient site (6 in 2019, 5 in 2020); 7 died, 1 had an unknown fate, and 3 were confirmed alive at the end of the study. Four of the resident snake mortalities showed signs of predation, 1 died from unknown illness, 1 died when the banks of the canal were mowed, and the other 6 had unknown causes of death. For the translocated adults that died, 5 showed evidence of predation and 2 had unknown causes of death.

We resighted adult snakes 2,364 times. On average, snakes from the rice–canal donor site moved the farthest between resightings at 118.0 m (95% CI = 96.5–139.5 m), followed by snakes from the recipient site at 72.9 m (95% CI = 48.5–97.3 m), and finally snakes from the wetland donor site at 39.7 m (95% CI = 30.6–48.9 m). On average, resident snakes moved slightly farther between resightings than translocated snakes (residents: 75.7 m, 95% CI = 60.3–91.2 m; translocated: 72.9 m, 95% CI = 48.5–97.3 m). Translocated snakes moved 96.4 m (95% CI = 64.2–128.6 m) between resightings before translocation and 72.9 m (95% CI = 48.5–97.3 m) between resightings after translocation.

Surface activity was highest at the wetland donor site with snakes active 27.0% of the time (95% CI = 22.2–31.8%), followed by snakes in the rice–canal donor site, which were active 21.6% of the time (95% CI = 16.9–26.2%), and snakes from the recipient site, which were active 13.6% of the time (95% CI = 7.9–19.2%).

TABLE 2 Trapping effort, calculated as trap nights, captures, and catch per unit effort (CPUE) for giant gartersnakes at the 2 donor sites and the Sacramento Area Flood Control Agency (SAFCA) recipient site in the Natomas Basin, Sacramento County, California, USA, 2017–2021. Translocation to the recipient site occurred in 2019 and 2020.

	Trapping effort and captures				
Site	**2017**	**2018**	**2019**	**2020**	**2021**
Wetland donor site					
Trapping effort	13,291	8,575	8,440	3,991	4,900
Individuals	101	100	174	85	74
Total captures	143	125	227	103	98
CPUE	0.0076	0.0117	0.0206	0.0213	0.0151
Rice–canal donor site					
Trapping effort	7,544	10,325	9,538	2,799	7,200
Individuals	36	83	62	40	52
Total captures	71	132	97	47	82
CPUE	0.0048	0.0080	0.0065	0.0143	0.0072
SAFCA recipient site					
Trapping effort	8,485	4,349	4,191	1,400	9,200
Individuals	0	0	0	3	3
Total captures	0	0	0	8	5
CPUE	0	0	0	0.0021	0.0003

On average, resident snakes were active more (24.8%; 95% CI = 21.4–28.3%) than translocated snakes (13.6%; 95% CI = 7.9–19.2%). Translocated snakes were active 28.2% (95% CI = 20.1–36.4%) of the time before translocation and 13.6% (95% CI = 7.9–19.2%) after translocation.

The most parsimonious Cox proportional hazard model for adult snakes included the covariate translocated that split snakes into only translocated or resident without additional predictor variables (Table 3). The risk of mortality for translocated snakes was 6 times higher than resident snakes and the 95% confidence interval exceeded 1 (Hazard ratio: 6.1, 95% CI = 1.7–21.4, $P = 0.004$). Translocated also had the highest relative variable importance at 0.69 and was included in each of the 3 top models. There was little support for the other 3 variables; average distance, treatment group, and activity had relative variable importances of 0.29, 0.27, and 0.25, respectively.

We plotted a Kaplan-Meier survival curve for the entire group of adult snakes from both the resident and translocated groups. Survival for adult snakes was 0.27 (95% CI = 0.15–0.50) at the end of the study. We also created a second Kaplan-Meier survival curve stratifying the adult snakes into resident and translocated groups. Survival of resident snakes was 0.39 (95% CI = 0.23–0.68) after 1,154 days and 0.08 (95% CI = 0.01–0.64) for translocated snakes over 801 days (Figure 2). Annualized survival rates, ignoring variation among years or among seasons, were thus 0.74 (95% CI = 0.63–0.89) and 0.32 (95% CI = 0.12–0.82) for resident and translocated snakes, respectively.

Captive-reared juveniles

Over the captive-rearing period August 2018 to August 2020, there were 10 mortalities of the 42 snakes. The proportion of juvenile giant gartersnakes alive after 1 year in captivity was 0.93, and the proportion alive at the end

TABLE 3 Model selection results including Akaike's Information Criterion corrected for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and AIC weight (w_i) for the top 5 Cox proportional hazard models of adult giant gartersnake survival in the Natomas Basin, Sacramento County, California, USA, 2019–2021. The covariate translocated is a binary predictor to describe whether snakes were translocated, whereas the covariate treatment group splits the snakes into 3 treatment groups: wetland resident snakes, rice–canal resident snakes, and translocated snakes. Average distance refers to the average distance snakes moved between resightings and activity refers to the proportion of surface-active resightings.

Adult models	AIC_c	ΔAIC_c	w_i
Survival ~ translocated	97.90	0.00	0.31
Survival ~ translocated + average distance	98.74	0.83	0.21
Survival ~ translocated + activity	99.16	1.26	0.17
Survival ~ treatment group	99.52	1.61	0.14
Survival ~ treatment group + average distance	100.95	3.05	0.07

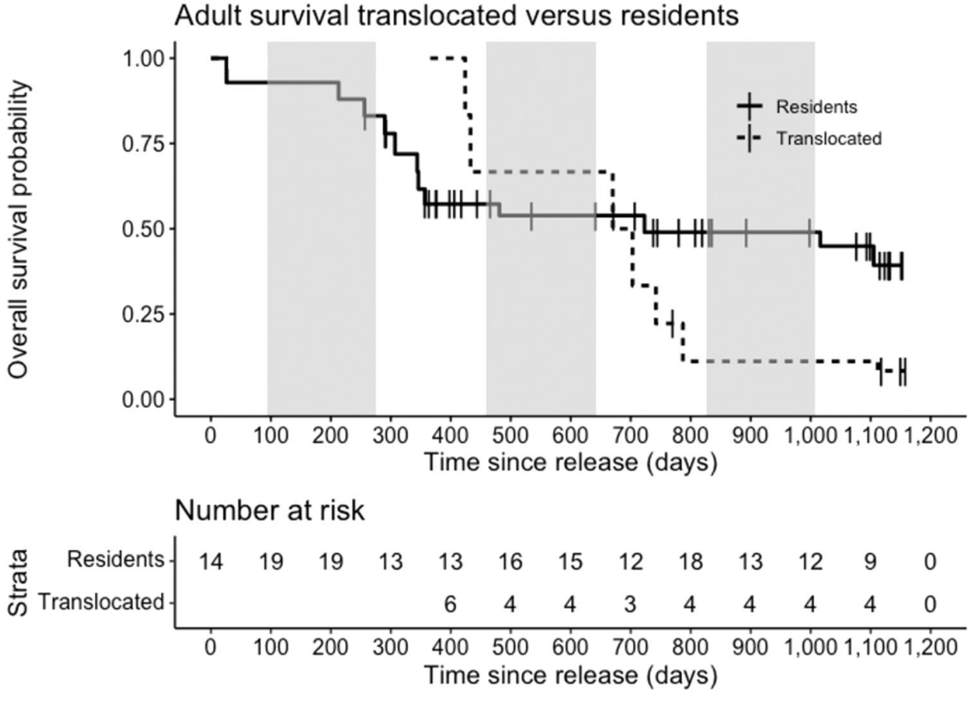

FIGURE 2 Kaplan-Meier survival curves for adult giant gartersnakes in the Natomas Basin, Sacramento County, California, USA, stratified by resident and translocated snakes. The timeframe ranges from 29 June 2018, when the first radio-tagged snake was released, until 31 August 2021, when the study concluded. The gray rectangles on the plot denote the overwintering periods (31 Oct–1 Apr) when snakes are brumating underground. Vertical tick marks along the survival curves mark where snakes have been censored from the model.

of the 2-year rearing period was 0.76. At birth, the average SVL of the colony was 196.5 mm ± 1.06 (SE) and the average mass was 5.1 ± 0.12 g. Surviving snakes grew to an average of 422.8 ± 9.6 mm SVL and an average mass of 56.4 ± 4.0 g at the end of the 2-year rearing period.

We identified 5 mortalities from the 14 radio-tagged juvenile snakes released at the translocation site. Three snakes were necropsied and all showed traumatic injuries implicating predation as the cause of death. One snake was missing at

TABLE 4 Akaike's Information Criterion corrected for small sample size (AIC_c), difference in AIC_c (ΔAIC_c), and AIC weight (w_i) for the Cox proportional hazard models of juvenile giant gartersnake survival in the Natomas Basin, Sacramento County, California, USA, 2021. Average distance refers to the average distance snakes moved between resightings, activity refers to the proportion of surface-active resightings, and 1 represents the null model. The snout-to-vent length (SVL) of each snake was measured prior to release.

Juvenile models	AIC_c	ΔAIC_c	w_i
Survival ~ 1	23.35	0.00	0.23
Survival ~ average distance	23.60	0.25	0.21
Survival ~ SVL	25.04	1.69	0.10
Survival ~ sex	25.44	2.09	0.08
Survival ~ activity + average distance	25.58	2.23	0.08

the beginning of the study and we were unable to determine its fate. Two snakes had unknown status at the end of the study; it is likely the transmitters died slightly earlier based on the timing and signal strength prior to disappearing. The other 6 snakes were assumed alive underground and had started over-wintering when their transmitters died.

We resighted the juvenile telemetry snakes 101 times between August and December 2020. On average, the juvenile snakes moved 60.5 m (95% CI = 45.6–75.5 m) between resightings. Juvenile snakes were also active 18.4% (95% CI = 10.0–27.2%) of the time during resighting.

The most parsimonious Cox proportional hazard model was the null model (Table 4). Average distance had the highest relative variable importance at 0.42, followed by SVL, activity, and sex at 0.24, 0.23, and 0.21, respectively. We plotted Kaplan-Meier curves for the juveniles. After 107 days, the estimated probability of survival was 0.599 (95% CI = 0.380–0.942; Figure 3). Given that our radio-tracking did not encompass at least one year with all seasons, we do not provide annualized estimates of survival. None of the predictors we evaluated had a significant effect on juvenile survival.

Characteristics of the study sites

The CPUE of prey species fluctuated at all 3 sites. The BKS donor site had the highest average CPUE of 2.09, followed by the Sills donor site and the SAFCA recipient site with an average CPUE of 1.73 and 1.05, respectively (Figure 4). There was a higher CPUE of fish species than frog species at all 3 sites. The BKS donor site had the greatest CPUE of fish, followed by Sills and then SAFCA (Figure 4A). The CPUE of frogs fluctuated between the 3 sites and appeared to be on a downward trend at all 3 sites in 2020 and 2021 (Figure 4B).

DISCUSSION

Adult snakes

Translocated giant gartersnakes in our study had lower survival than unmoved animals at resident sites, a phenomenon that is common in other translocation studies (Plummer and Mills 2000, Roe et al. 2010, Cornelis et al. 2021). Lower survival following translocation is not entirely unexpected given that translocation introduces animals to an unfamiliar area, which may cause stress or behavioral changes (Berger-Tal et al. 2020). For species like giant gartersnakes that could benefit from translocation to restore extirpated populations, it is important to evaluate different outcomes to determine whether translocation is a viable management strategy.

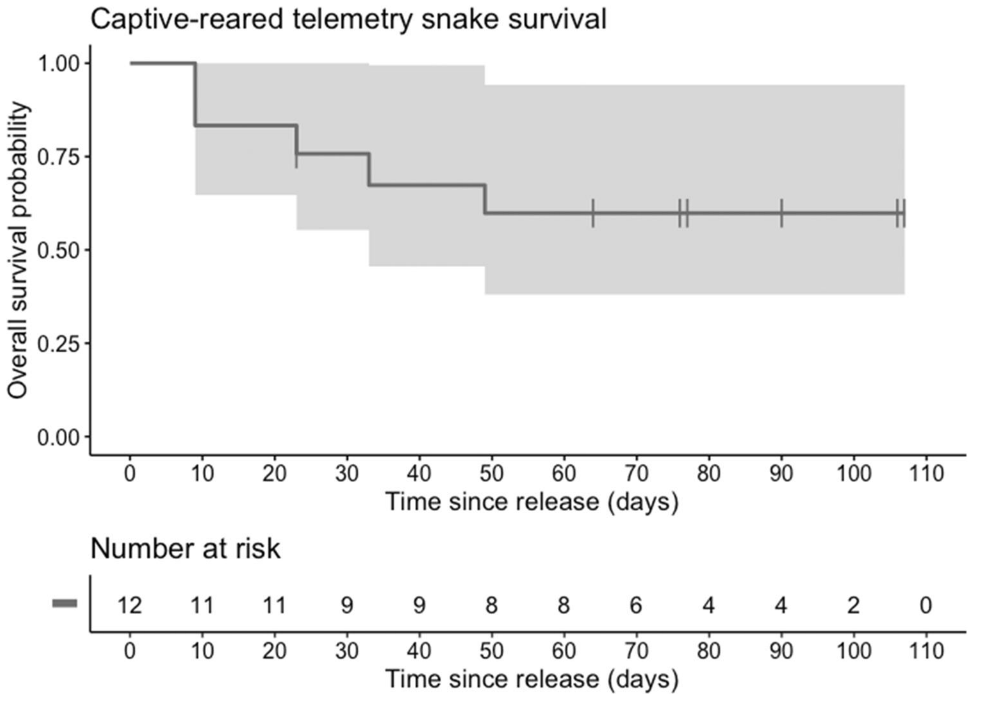

FIGURE 3 Kaplan-Meier survival curve for captive-reared juvenile giant gartersnakes in the Natomas Basin, Sacramento County, California, USA, monitored with radio-telemetry. The time series spans from 26 August 2020, the day the first individual was released, until 11 December 2020, when the last transmitter died. Of the 14 snakes released, there were 5 mortalities and 9 snakes that were censored because of transmitter failure, unknown fate, or end of battery life for the transmitters. Tick marks along the curve represent snakes that were censored; shading signifies the 95% confidence interval.

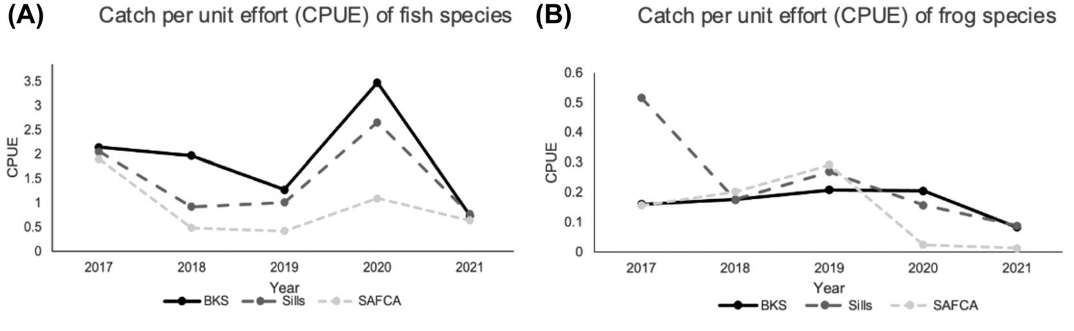

FIGURE 4 The annual catch per unit effort (CPUE) of all fish species (A) and frog species (B) sampled at 3 sites in the Natomas Basin, Sacramento County, California, USA, 2017–2021. The 3 sites that were sampled were the Betts-Kismat-Silva (BKS) wetland donor site, the Sills rice–canal donor site, and the Sacramento Area Flood Control Agency (SAFCA) recipient site.

We did not expect significant changes in the population size at the recipient site because our objective for the scale of the project was primarily to compare survival between resident and translocated snakes. We did not catch any giant gartersnakes in the SAFCA recipient site in the 3 years of monitoring prior to translocation. With any mark-recapture study efforts, especially for secretive species like snakes, there are questions about detectability (Durso et al. 2011, Willson et al. 2011). By releasing snakes within a known period that coincided with our trapping, we were able to remove the uncertainty of whether snakes were present at the site during translocation. The increase in captures during this period suggests that if snakes were present at the site before translocation, even in small numbers, we likely would have encountered them in traps. The increase in snake captures in 2020 identifies the likely absence of a population at the recipient site prior to translocation.

Changes in movement, behavior, or both following translocation can lead to increased mortality in translocated animals because increased movement and surface activity makes animals more vulnerable to predation, vehicle strikes, or other hazards (Germano and Bishop 2009, Cornelis et al. 2021). Translocated animals can increase movement or activity and sometimes display homing behavior, especially in reptiles (Reinert and Rupert 1999, Sullivan et al. 2004, Cornelis et al. 2021). In our study, there was no support for the average distance moved between resightings or the proportion of surface-active resightings being correlated with survival of adult or juvenile snakes. Additionally, none of the translocated adult snakes emigrated from the recipient site after translocation, suggesting they did not exhibit homing behavior. Both results are promising signs that translocation may succeed in future giant gartersnake translocations if the cause of decreased survival in translocated snakes can be identified.

Another common source of mortality in translocated species is unsuitable recipient sites (Dodd and Seigel 1991). There may be little consideration given to the recipient site and its habitat quality if the focus is on reducing conflict rather than the animal's ecological preferences. In contrast, in conservation-driven translocations, like our study, sites are chosen specifically for the suitability for the species being translocated. It is still possible that there are characteristics of the recipient site that were not considered or known prior to translocation that reduced survival (Fellers et al. 2007). The recipient site we selected was a managed marsh designed for giant gartersnakes and other wetland-obligate species. The vegetation composition, prey and predator communities, and other site properties appeared similar to other managed wetlands in the Natomas Basin, including the wetland donor site (BKS), although the recipient site was built in 2016 and BKS was built in 2002 (AECOM, unpublished report). Perhaps, despite sharing similar prey species, the younger wetlands at SAFCA might not support large enough or stable prey populations; the prey CPUE at the recipient site was lower compared to either of the donor sites. Additionally, frogs are an important component of giant gartersnakes diet, and the decrease in frog species was greater at SAFCA than either of the 2 donor sites. More research is needed to determine whether the lower abundance of prey is a limiting factor to giant gartersnakes survival.

Another major difference among the sites is their proximity to the Sacramento River; the recipient site is <1 km from the river, whereas the wetland donor and rice–canal donor sites are 8.18 km and 4.61 km away, respectively. There may be subtle differences in the soil properties of the recipient site or other abiotic conditions due to the proximity of the river, and soil properties affect occupancy of giant gartersnakes at relatively small spatial scales (Hansen et al. 2017). The habitat directly bordering the river has a greater abundance of large trees than the 2 donor sites and previous research has found a negative association of giant gartersnakes with riparian areas, which could be linked to increased risk of predation from raptors (Van Denburgh and Slevin 1918, Fitch 1940, Wright and Wright 1957, Hansen 1980). Of the mortalities in the field, 33% of resident snakes showed signs of predation compared to 71% of the translocated adult snakes and 80% of the juvenile captive-reared snakes, but data on the predator abundances at each site would be needed to determine if predation is influencing the difference in survival among the sites.

Captive-reared juveniles

Juvenile snakes were released a year after the last group of translocated adults and were monitored for a much shorter period. Although we cannot directly compare survival between the adult and juvenile snakes, the initial survival of the captive-reared juveniles was promising. A similar captive-rearing study of plains gartersnakes (*Thamnophis radix*) reported survival during headstarting ranged 0.74–0.88 after the first year in captivity (King and

Stanford 2006); our snakes had higher survival rates in the first year and within this range in the second year. Most mortality in our study during the captive-rearing period was among smaller individuals that refused food regularly and required assisted feeding at some point.

The overall survival for the captive-reared telemetry snakes was 0.60 at the end of the 4-month monitoring period after release. We would have liked to continue tracking the juveniles through spring to confirm their emergence from overwintering, but we were limited by the battery life of the radio-transmitters for this size class. It is difficult to directly compare survival of the captive-reared juveniles to wild counterparts, but we can compare estimated survival by size given results from similar studies. The predicted mortality rates of neonates born directly into the wild are high because of the vast number of predators that prey on neonate snakes (Halstead et al. 2015). The estimated annual survival of giant gartersnakes with an SVL between 200 mm and 400 mm, the size of neonates, is 0.2 or less in wild populations (Rose et al. 2018*b*). Similarly, in a captive-rearing study of plains gartersnakes, researchers estimated the survival of wild born neonates to be 0.16 in the first year and 0.40 in the second without captive-rearing (King and Stanford 2006). In comparison, over the captive-rearing period when the average SVL of our snakes ranged from 200–400 mm, we observed survival that ranged from 0.76–1.0. Previous work on giant gartersnakes also supports the idea that captive-rearing could benefit population growth. Population modeling showed that, after survival of adult females, the next most influential factor affecting population growth was the size of snakes at one year of age (Rose et al. 2019). Therefore, rearing snakes in captivity would allow snakes to enter wild populations at a larger size when they are less vulnerable to predation, which could increase overall population growth.

For our juvenile survival models, the null model with no covariates had the most support. We had expected to see a significant effect of SVL on survival based on previous giant gartersnake studies (Rose et al. 2018*b*, 2019); however, we were only able to include 14 telemetry juveniles in our survival estimates because there is a minimum size requirement to be able to implant radio-transmitters. Therefore, all telemetry snakes were the largest snakes in the released group.

MANAGEMENT IMPLICATIONS

Translocated adult snakes had lower survival than resident adults despite not showing an increase in average distance moved or surface activity, which usually decrease survival in translocated animals. We could not parse out whether the site-level differences we observed caused reduced survival, but higher incidence of predation of translocated snakes suggests that differences in predation pressure might have reduced survival of translocated snakes in our study. In contrast, captive-reared snakes appeared to have relatively high survival even after release, and captive rearing could be an effective alternative to translocation of adults. For species like giant gartersnakes that will require translocation for re-establishment and recovery throughout their former range, using a small-scale adaptive approach to thoroughly test the outcomes of translocation before large-scale efforts are attempted may be beneficial.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

ETHICS STATEMENT

All methods and protocols performed during the project followed appropriate ethics and animal welfare protocols approved by the following permits: USFWS Recovery Permit TE-157216-4; Memorandum of Understanding California Department of Fish and Wildlife SC-10779; University of California, Davis Institutional Animal Care and use Committee [IACUC] #20405; United States Geological Survey Western Ecological Research Center IACUC #WERC-2014-01.

DATA AVAILABILITY STATEMENT

The data and metadata are available at https://doi.org/10.5066/P9KVX596 and the analysis code is available at https://doi.org/10.5066/P9I448M2.

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