



Effect of translocation on home range and movements of giant gartersnakes

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ABSTRACT

Conservation translocations are often used to connect disjunct populations or reintroduce them to otherwise suitable areas from which they have become locally extinct. Translocations, however, can alter wildlife movements and increase their exposure to hazards such as predation, thus increasing their risk of mortality. The giant gartersnake, *Thamnophis gigas*, is a wetland-dependent threatened species that has lost > 90% of its historical habitat. Certain species recovery may depend on the success of translocations in restoring populations. We translocated snakes from two donor sites—one managed wetland and one rice agriculture site—to a third restored wetland in Sacramento County, California, USA, to evaluate the impact of translocations on home ranges and movements. Translocated snakes had smaller home ranges after translocation for the 95% and 100% MCP estimation, had smaller net displacements, but had similar measures of sinuosity (index that measures the curvature of a movement path), total distance moved, and start-to-end distance compared to their individual measurements before translocation. Landscape type, however, had the greatest effect on home range estimates and movement measures, with resident snakes from the rice agriculture site having greater home ranges and net displacements, and greater, less sinuous seasonal movement paths than snakes from both the donor and recipient wetland sites. Results varied depending on the specific metric, but overall, translocated snakes tended to have intermediate values for home range size, movement distances, and sinuosity compared to the two resident groups. Our results suggest that although translocation did affect movement and space use relative to resident snakes, its effect depended on the donor habitat from which translocated snakes were removed. Because irregular movements are often linked to low survival after translocation, it is encouraging that translocated snakes did not move more than snakes from a donor rice agriculture site, a landscape that represents much habitat for remaining populations.

1. Introduction

Habitat loss and fragmentation has left many species in habitat patches surrounded by a matrix of untraversable barriers (Franklin et al., 2002; Haddad et al., 2015; Ricketts, 2001). Isolated populations face heightened conservation challenges from genetic drift, Allee effects, and demographic stochasticity, which can ultimately lead to local extinctions (González et al., 2020; Mantyka-Pringle et al., 2012; Miles et al., 2019). Populations in fragmented habitats may thus require outside intervention such as conservation

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translocations—the intentional movement of animals—to persist (Berger-Tal et al., 2020; International Union for the Conservation of Nature, 2013; Morris et al., 2021). Conservation translocations can be used to reintroduce species to newly restored habitat or to existing habitat from which they have become locally extinct, and to augment isolated populations and improve genetic connectivity (Germano and Bishop, 2009, International Union for the Conservation of Nature, 2013).

Although translocation may aid in the recovery and continued persistence of species, translocation success is highly variable (Seddon et al., 2007), and the practice is often criticized. Translocations can fail due to unsuitable habitat, management issues, population collapse, genetic complications, and disease spread (Berger-Tal et al., 2020, Bubac et al., 2019). There is also a general trend of increased mortality in translocated wildlife compared to their resident counterparts (Cornelis et al., 2021; Nguyen et al., 2023; Plummer and Mills, 2000; Roe et al., 2010). Understanding and documenting the reasons translocations fail and why translocated wildlife have lower survival is important to improve translocation success (Fischer and Lindenmayer, 2000; Sutherland et al., 2010). Given the wide range of species facing habitat loss (Foley et al., 2005; Gonçalves-Souza et al., 2020; Lewis and Maslin, 2015), conservation scientists increasingly use translocations to enable species to persist in modern, fragmented landscapes (Novak et al., 2021; Swan et al., 2018; Weeks et al., 2011).

Even under normal circumstances, animal movements can carry energetic costs and increase exposure to predators, inclement weather, or other hazards in the environment (Bélíchon et al., 1996; Cornelis et al., 2021; Fahrig, 2007; Germano and Bishop, 2009). One of the main causes of decreased survival after translocation is a disruption of movements that leaves wildlife vulnerable (Berger-Tal et al., 2020, Cornelis et al., 2021, Germano and Bishop, 2009). Translocated animals tend to move more often or greater distances after translocation (Butler et al., 2005; Germano and Bishop, 2009), which may result from animals trying to acclimatize to new surroundings or because they are attempting to return to their previous locality (Bilby and Moseby, 2023; Jensen et al., 2021; Jreidini and Green, 2022). An increase in long, directed movements after translocation is often interpreted as animals attempting to return to their previous home range, whereas an increase in sinuous, meandering paths is thought to represent searching behavior as animals familiarize themselves with a new landscape (Hinderle et al., 2015, (Reinert and Rupert Jr, 1999). Home range sizes, which are inherently connected to animal movement, can also increase after translocation (Barve et al., 2013; Butler et al., 2005; Plummer and Mills, 2000). Aside from translocation, the structure of the landscape and the distribution of resources can also affect movement patterns (Börger et al., 2008; Fahrig, 2007; McIntyre and Wiens, 1999). Given all the factors that can influence an animal's movement—and the relationship between movement and survival—understanding the impact of translocation on animal movement may influence the overall success of an animal reintroduction.

The giant gartersnake (*Thamnophis gigas*) is a good candidate for translocation as the species currently persists in disjunct populations separated by major roads or other land uses that pose barriers to movement (Halstead et al., 2010). The giant gartersnake is a wetland-dependent species endemic to the California Central Valley, USA. It is the species of gartersnake with the largest body size, with a maximum recorded length of 1.6 m and mass up to 930 g (Ernst and Ernst, 2003; Halstead et al., 2021). Male snakes grow faster and reach maximum size quicker than females (Rose et al., 2019), but female giant gartersnakes are larger than males overall (Halstead et al., 2021; Wylie et al., 2010). Females reached asymptotic lengths of 894 mm (866–909) compared to males that reached lengths of 673 mm (656–688) (Rose et al., 2018b). Additionally, the average log normal mean mass was 250 g [95-percent CI= 24–1030 g] for female snakes; and 101 g [95-percent CI= 26–274 g] for males, respectively (Halstead et al., 2015b; Wylie et al., 2010). Giant gartersnakes are nonvenomous and prey mostly on fish and frogs (Halstead et al., 2015b; Halstead et al., 2021). Giant gartersnakes have complex interactions with American bullfrogs (*Lithobates catesbeianus*) that are a main prey source for adult and sub-adult snakes, but also act as predators of smaller neonate snakes (Halstead et al., 2015b; Halstead et al., 2021). Along with adult bullfrogs giant gartersnakes are prey to a wide range of native and non-native species, including wading birds, raptors, mammals such as North American river otters (*Lontra canadensis*) and American mink (*Neovison vison*), and large centrarchid fishes (Halstead et al., 2021).

In addition to predation and competition pressure from introduced species, giant gartersnakes also face threats of disease from multiple parasites and from the introduction of snake fungal disease. The greatest threat to giant gartersnakes, however, is habitat loss and degradation, including land conversion for human development, agriculture—especially non-rice crops, and other hazards of living in human modified landscapes such as roads and use of pest control (Halstead et al., 2015b). For these reasons, the giant gartersnake was federally- and state-listed as a threatened species (California Department of Fish and Game Commission, 1971; U.S. Fish and Wildlife Service, 1993), and listed as a vulnerable species (VU) by the IUCN (International Union for the Conservation of Nature, 2013) after losing > 90% of its historical wetland habitat (Frayer et al., 1989; Halstead et al., 2014; Hammerson, 2007). Populations today remain in scattered wetlands around the Central Valley and in some rice agriculture sites, though the effects of living in this surrogate environment are not fully understood (Halstead et al., 2019). The reintroduction of giant gartersnakes into historical habitat in their range is a conservation objective for the long-term recovery of the species (California Department of Fish and Game Commission, 1971, U.S. Fish and Wildlife Service, 1993, 2017), highlighting the need to assess the effectiveness of translocation as a conservation strategy. Results from a recent study found that adult giant gartersnakes translocated to restored habitat had lower survival than resident snakes that had not been moved from donor sites (Nguyen et al., 2023). While there was no evidence of a correlation between survival and the distance moved between resightings or the proportion of time snakes were surface-active (Nguyen et al., 2023), it remains unclear whether home ranges or other measures of animal movement differed in response to translocation. Current literature on snake translocations includes several species translocated for mitigation purposes to reduce human-wildlife conflicts given many snake species are viewed as nuisance animals by the general public (Cornelis et al., 2021; Sullivan et al., 2015). Mitigation translocations have been largely unsuccessful (Germano et al., 2015; Sullivan et al., 2015), and snakes moved for mitigation purposes exhibit a range of unfavorable responses, including altered movement patterns (Butler et al., 2005; Devan-Song et al., 2016; Wolfe et al., 2018), homing behaviors (Cornelis et al., 2021; Pittman et al., 2014), and often return to the removal site shortly after translocation (Brown et al., 2009; Butler et al., 2005; Pittman et al., 2014). These responses can also occur in conservation

translocations, although conservation translocations tend to be more successful overall because there is often more consideration and planning given to species' needs in these projects (Sullivan et al., 2015). Given the wide range of movement responses of snakes to translocation and the variation in responses among species, examining snake movement following translocation could have important implications for the success of conservation projects.

The main objective of this study was to examine the movement and space use of giant gartersnakes in response to translocation. Specifically, we were interested in how home range sizes and movement metrics compared between resident snakes from two different habitats—one managed wetland site and one rice agriculture site—and translocated snakes at a recently restored managed wetland. There has been one previous study comparing home range size of giant gartersnakes in rice agriculture versus wetland habitat that found snakes living in rice agriculture had smaller, less variable home ranges compared to those in wetlands—contrary to what the author had predicted (Valcarcel, 2011). We wanted to see whether the results of our study are consistent with this previous study and to look closer at the influence of landscape type on snake movement. We were also interested in determining whether home range and movement metrics of individual snakes differed before and after they were translocated. We expected to see an increase in home range sizes and net displacements after translocation, as seen in translocation studies of other snake species (Butler et al., 2005; Kelley et al., 2022; Lee and Park, 2011; Plummer and Mills, 2000; Wolfe et al., 2018), exceeding values commonly observed in resident snakes. We also expected that translocated snakes would make more sinuous or meandering movements and thus move greater total distances in response to translocation as they acclimated to their new habitat.

2. Methods

2.1. Study site

We conducted this study in the Natomas Basin, Sacramento, CA, USA. Our study included two donor sites and one recipient site. The wetland donor site was composed of mature, managed tule marshes with habitat similar to that known to historically support giant gartersnakes. The canal donor site was a rice agriculture site with irrigation canals and rice fields that has served as habitat in the absence of historical native habitat (Halstead et al., 2019). The recipient site was a managed marsh created in 2014 to provide additional habitat for giant gartersnakes (AECOM, 2016). There was no evidence of an existing population of giant gartersnakes in the recipient site at the start of our study in 2018 (ICF, 2016, 2021; Nguyen, 2023). All three sites were part of the same watershed and close enough geographically (<11 km) that the snakes from all three sites were considered part of the same genetic population (U.S. Fish and Wildlife, 2017, Wood et al., 2015). However, the area surrounding the recipient site has been more heavily developed and there were several barriers to dispersal—including roads and large highways—that separate the recipient site from the two donor sites, making it unlikely for snakes to naturally disperse to the recipient site on their own. Wildlife managers have made efforts to increase connectivity of the recipient site to the rest of the Natomas Basin sites through the creation of the Giant Gartersnake Drainage Canal which connects the main drainage canal in the north basin to the second main drainage canal in the south (EDAW, 2009, ICF, 2023). These canals have not yet resulted in natural colonization of the recipient site, but could be important for dispersal if a population is established in the recipient site and approaches the carrying capacity of the site.

2.2. Data collection

We collected snakes for translocation using aquatic minnow traps as part of a larger population monitoring project (Rose et al., 2018a,b, 2019, ICF, 2021). We captured snakes 3 June 2018 – 30 August 2018, 9 May 2019 – 16 August 2019, and 14 June 2020 – 27 July 2020. When we captured a snake, we recorded its mass to the nearest gram using spring scales (Pesola; JLM Instruments, Chicago, IL). We collected only snakes > 200 g to have radio-transmitters implanted; these ended up being all females given this size requirement. Ideally, we would have included both male and female snakes in the study. However, because we were working with a threatened species, we wanted to maximize the amount of data we could collect while minimizing the amount of surgeries required for individuals. Using the transmitters we did allowed us to collect a year of baseline data before translocation, capture snakes to replace transmitter batteries, and then collect an additional year of data after translocation. Even though transmitter size limited our data to only females, because we were interested in differences before and after translocation, and because we had not translocated this species before and were unsure how long it would take snakes to acclimate to the recipient site, if at all, we considered having a year of data in each site would allow us adequate data for comparison while avoiding the multiple surgeries per year that smaller transmitters would have required.

We marked all snakes with unique IDs using a microbrand and PIT tag and recorded length to the nearest mm (snout-to-vent length—SVL and tail length—TVL) and sex. We transported snakes to the Sacramento Zoo where veterinarians performed physical examinations, radiographs, and bloodwork and implanted radio-transmitters (9 g SI-2 T; Holohil Systems Ltd, Carp, Ontario, Canada; <http://www.holohil.com/>) in snakes healthy enough for surgery following standard implantation methods (Reinert and Cundall, 1982). We held snakes in captivity for 7 days after surgery to recover and receive analgesics and antibiotics (USFWS Recovery Permit TE-157216-4; MOU CDFW SC-10779; UC Davis IACUC #20405; USGS WERC IACUC #WERC-2014-01).

We released the first group of 20 adult female snakes at their initial capture locations at the two donor sites in June 2018. We tracked each snake 1–5 times per week during the active season (Apr–Oct) and once every 2–3 weeks during the overwintering season (Nov–Mar). Tracking frequency has been shown to affect the error rates of some movement metrics, especially for metrics associated with the frequency of movements (Alexander and Maritz, 2015). To try to minimize this error, we followed the same tracking protocols each season, even if the frequency of tracking varied. On average, each individual was tracked 2–3 times per week during the active

season, and we switched which sites we visited so individuals were tracked evenly. We also rotated the order that snakes were tracked within a site to capture any variation in activity or movement based on time of day. For this study, we were more interested in capturing larger scale movement metrics and overall space use and these sampling techniques have been used in previous giant gartersnake studies and seem to be appropriate to capture these metrics based on the behavior of this species (Halstead et al., 2015a, 2019). We also chose analysis methods that were less sensitive to differences in time between observations when possible.

We recorded each snake's location ± 5 m using handheld GPS receivers. After one year collecting re-sightings at each of the two donor sites, we began translocating snakes to the recipient site. In May–August 2019, we collected the nine surviving snakes that had been radio-tracked at donor sites since 2018, as well as 18 new snakes from the two donor sites. Eight of the nine snakes from 2018 were taken to the Sacramento Zoo for follow-up health examinations and had radio-transmitters surgically replaced, one was retired from the study and released back at its capture location after transmitter removal and recovery. The snake was retired from the study due to a minor complication at the original incision site. Veterinarians did not anticipate any long term effects to the snake's overall health after recovery, but we felt it was best to not implant a new transmitter to prevent additional stress to the animal. This individual was the only snake that experienced complications related to the radio transmitters or surgery throughout the course of the study. Veterinarians also implanted the 18 new snakes collected in 2019 with new radio-transmitters.

We released the 18 newly collected snakes back at their capture locations in the donor sites along with two of the snakes from 2018, to serve as between-year controls. We translocated the other six surviving snakes from 2018 to the recipient site and released them in randomly selected locations near the center of the complex of wetlands in an area with dense tule (*Schoenoplectus* spp.), < 5 m from the water. We tracked snakes as described above at each of the sites through the active and overwintering seasons.

We continued the project in 2020. Five of the snakes newly captured in 2019 were recaptured and implanted with new transmitters and translocated to the recipient site. An additional 12 new snakes were collected from June – August 2020 and released back at their capture locations in the donor sites after being outfitted with radio-transmitters and recovering from surgery. In total, we monitored 23 snakes at the canal donor site and 27 at the wetland donor site from years 2018–2021; we monitored 11 snakes at the recipient site from years 2019–2021. All 11 snakes monitored at the recipient site were translocated from one of the two donor sites (8 from the canal donor site and 3 from the wetland donor site) after one year of radio-tracking at the donor site where they originated, giving us a total of 50 individuals tracked over the entire course of the study.

2.3. Analyses

We examined overall space use by calculating home ranges using the 'adeHabitat' package in R (R Core Team Version 4.2.2 2022, Calenge, 2006). We used three different estimation methods to calculate home range size: 100% and 95% minimum convex polygons (hereafter, MCP) and 95% adaptive local convex hulls (hereafter, a-LoCoH). We used both methods because MCP is a widely used metric that allows comparisons to other studies and because a-LoCoH is well-suited for linear habitat or landscapes that contain barriers (Getz et al., 2007). The primary habitat at our rice agriculture site was linear in nature given the irrigation canals and the square, seasonal rice-fields; there were also several areas across the three sites that were bordered by roads.

We plotted the change in home range size in response to the number of locations; the majority of snake home range sizes plateaued after 20 re-sightings or fewer. Thus, we included only snakes with at least 20 re-sighting locations in our home range analysis. We also included only locations from the active season (1 April – 31 October) in our home range estimation and we calculated a new home range each year for snakes that were included in multiple years of the study. To determine which alpha value to use for the a-LoCoH analysis, we calculated the maximum distance between points included in a home range and used that as the minimum alpha value for each snake (Getz et al., 2007). We calculated the average home range size for all snakes and compared home range sizes among the three sites, between translocated and resident snakes, and between translocated individuals before and after translocation occurred, as described below.

In addition to home range estimation, we also calculated several movement metrics, including total distance traversed, start-to-end distance (the straight-line distance between the start and end point of the seasonal trajectory), and sinuosity of seasonal movement paths. We used the 'trajr' package (McLean and Skowron Volponi, 2018) in R (R Core Team Version 4.2.2 2022) to calculate the total distance traversed during the active season, the straight-line distance between the start and end point of the seasonal trajectory (start-to-end distance), and the sinuosity of the movement path. Sinuosity is a measure that calculates the tortuosity of a random movement path (Benhamou, 2004). The trajr package returns a sinuosity index between 0 and 1, where values closer to zero signify a straighter, more direct path and values closer to one signify a highly sinuous, more meandering path (McLean and Skowron Volponi, 2018). We used the corrected sinuosity index, which is appropriate for movement paths with unequal step-lengths (Bovet and Benhamou, 1988; McLean and Skowron Volponi, 2018). We also calculated three measures of net displacement. For the net displacement measures, we calculated the distance from their release point to the last location before their first winter, to the last location before their second winter, and to the centroid of the 100% MCP home range. We chose these three measures of net displacement because we were interested in how far snakes dispersed from the release location by the end of the season and how far from the release location they settled and established home ranges.

We used mixed effects models to analyze our movement data using the 'lme4' package (Bates et al., 2015) in R version 4.2.2 (R Core Team, 2022). We analyzed eight different model sets, including one for each of the following home range estimations or movement metrics: 100% MCP, 95% MCP, 95% a-LoCoH, total distance traversed, start-to-end distance, sinuosity, net displacement from release to first winter, and net displacement from release to centroid of the 100% MCP home range. There were too few datapoints to calculate the net displacement from release to second winter for analysis with mixed effects models, so we included summary statistics for this metric instead. For each model set, we tested six models with each of the following variables as a fixed effect: 'site' (a predictor splitting

the individuals into three groups of wetland residents at wetland donor site, canal residents at canal donor site, or recipient translocated to recipient site), ‘translocated’ (a binary predictor grouping all residents from both sites together and considering only whether a snake was translocated or not), ‘SVL’, ‘year’, a model including both ‘translocated’ and ‘year’ as an additive model, and the intercept-only ‘null’ model. For the three home range estimation model sets, we tested an additional seventh model with ‘rice’ (binary variable separating the wetland donor site and recipient site from the canal donor site) as a fixed effect. All models included snake ‘id’ as a random effect to account for non-independence in snakes that were radio-tracked in multiple years. We plotted the residuals versus expected values and examined QQ-plots to check for normality. To meet the assumption of normality, we log-transformed all movement metrics and home range estimates before statistical analysis. We used an information theoretic approach to evaluate model support, using AIC_c to correct for sample size and reported unaltered p-values and assessed significance at $\alpha = 0.1$ to minimize Type II errors. Our sample size was limited due to the species’ rarity and protected status; rather than increase sample size, we increased the alpha level of the test to increase statistical power (Lakens, 2022). Increasing the alpha level increases the probability of making a Type I error, which should be carefully considered (Cascio and Zedeck, 1983; Miller and Ulrich, 2019; Mudge et al., 2012). However, in conservation projects, the risk of committing a Type II error and possibly overlooking important differences in the metrics of interest may have conservation implications for a species that is often more costly than committing a Type I error (Field et al., 2004). In such cases, increasing the alpha level is justified when increasing the sample size is not an option (Baguley, 2004; Field et al., 2004).

3. Results

3.1. Home range size

We collected 2362 total resightings from 50 individual snakes over the course of the project from June 2018 – August 2021. From the 50 total snakes, there were 31 with at least 20 locations; these snakes were included in home range analysis. Of these 31 snakes, seven snakes had at least 20 locations in two different years and both years were included in the analysis, providing 38 total estimates. The home ranges averaged 12.0 ha for 100% MCP (95% CI: 3.2, 20.8 ha), 9.6 ha for 95% MCP (95% CI: 1.0, 18.3 ha), and 2.2 ha for 95% a-LoCoH (95% CI: 0.9, 3.5 ha). By all metrics, home ranges were largest on average at the canal donor site, followed by the recipient site, and then the wetland donor site (Table 1; Supplemental Figs. 1–3).

Translocated snakes had smaller home ranges compared with resident snakes overall in the 100% and 95% MCP estimations, but not in the 95% a-LoCoH estimation (Table 1). There were five snakes for which we had home range estimates before and after translocation; both the 100% and 95% MCP home range estimates were smaller after translocation, whereas the 95% a-LoCoH home range size estimate did not change appreciably after translocation (Table 1).

The most parsimonious model for the 100% MCP was the model that included ‘site’ as a fixed effect, followed by the model that included ‘rice’ (ΔAIC_c of 2.11), with a combined AIC_{c_w} of 0.63 (Supplemental Table 1). The top two models for the 95% MCP model set also included the model with ‘site’, followed closely by the model that included ‘translocated’ (ΔAIC_c of 0.4), with a combined AIC_{c_w} of 0.64 (Supplemental Table 2). These two models were likewise the top models in the 95% a-LoCoH model set, but with the model that included ‘translocated’ being the top model, followed by the model that included ‘site’ (ΔAIC_c of 0.90), with a combined AIC_{c_w} of 0.56 (Supplemental Table 3). Home range size was significantly smaller at the wetland donor site compared to the canal donor site for the 100% MCP estimate (Coef: -1.11 , 95% CI: -2.21 , -0.01 , P-value: 0.06; Supplemental Fig. 1). There were no other statistically significant differences based on the fixed effects we tested in the home range estimates for either of the other two estimation methods (p-values ≥ 0.13 Supplemental Fig. 2&3).

The differences in home range size, shape, and overall space use among the three sites is best shown in plots of the home ranges. Estimates of home range area using the a-LoCoH estimator were smaller than MCP estimates in the canal donor site, and were restricted to irrigation canals (Fig. 1). In the wetland donor site, the a-LoCoH estimate and snake locations were more dispersed throughout the

Table 1

Average home range sizes (ha) in 100% and 95% minimum convex polygons (MCP) and 95% alpha-local convex hulls (a-LoCoH) of giant gartersnakes (*Thamnophis gigas*) in Sacramento County, California, USA, 2018–2021. Values in the parenthesis represent the 95% confidence intervals around the mean.

Group	n	100% MCP	95% MCP	95% a-LoCoH
Wetland Donor	17	3.8 (1.2 – 6.4)	2.3 (0.7 – 3.9)	1.1 (0.5 – 1.6)
Canal Donor	16	21.4 (1.4 – 41.4)	18.4 (–1.6 – 38.3)	3.2 (0.2 – 6.3)
Recipient	5	9.7 (3.6 – 15.8)	6.6 (2.7 – 10.5)	2.7 (1.6 – 3.9)
Residents	33	12.4 (2.2 – 22.5)	10.1 (0.2 – 20.0)	2.1 (0.6 – 3.6)
Translocated	5	9.7 (3.6 – 15.8)	6.6 (2.7 – 10.5)	2.7 (1.6 – 3.9)
Translocated- Before	5	20.9 (0.2 – 41.5)	15.0 (–5.8 – 35.7)	2.6 (–0.2 – 5.4)
Translocated- After	5	9.7 (3.6 – 15.8)	6.6 (2.7 – 10.5)	2.7 (1.6 – 3.9)



Fig. 1. Home range estimates using 100% and 95% Minimum convex polygons (MCP) and 95% alpha local convex hulls (a-LoCoH) for a snake (MB 13295) from the canal donor site in the Natomas Basin, Sacramento, CA, USA in 2021. The scale of the map is adjusted to best display the home-range estimates of interest. Note the scale may differ among figures. Map produced using maptools in R, Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community



Fig. 2. Home range estimates using 100% and 95% Minimum convex polygons (MCP) and 95% alpha local convex hulls (a-LoCoH) for a snake (MB 13299) from the wetland donor site in the Natomas Basin, Sacramento, CA, USA in 2021. The scale of the map is adjusted to best display the home-range estimates of interest. Note the scale may differ among figures. Map produced using maptools in R, Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

MCP (Fig. 2). We saw similar space use patterns for translocated snakes, with estimates before and after depending on the habitat type of the site from which snakes were removed. For example, a snake translocated from the canal donor site had larger MCP estimates before translocation to the recipient site, and the a-LoCoH estimates and snake locations were confined mostly to irrigation canals before translocation (Fig. 3A). After being translocated to the recipient site, the distribution of the snake locations and a-LoCoH estimate were more dispersed throughout the MCP, similar to what was seen at the wetland donor site (Fig. 3B).

3.2. Net displacement

For the 31 snakes for which we estimated home ranges, we also calculated three measures of net displacement. The average net displacement from the release location to the last location before the first winter was greatest at the canal donor site, followed by the

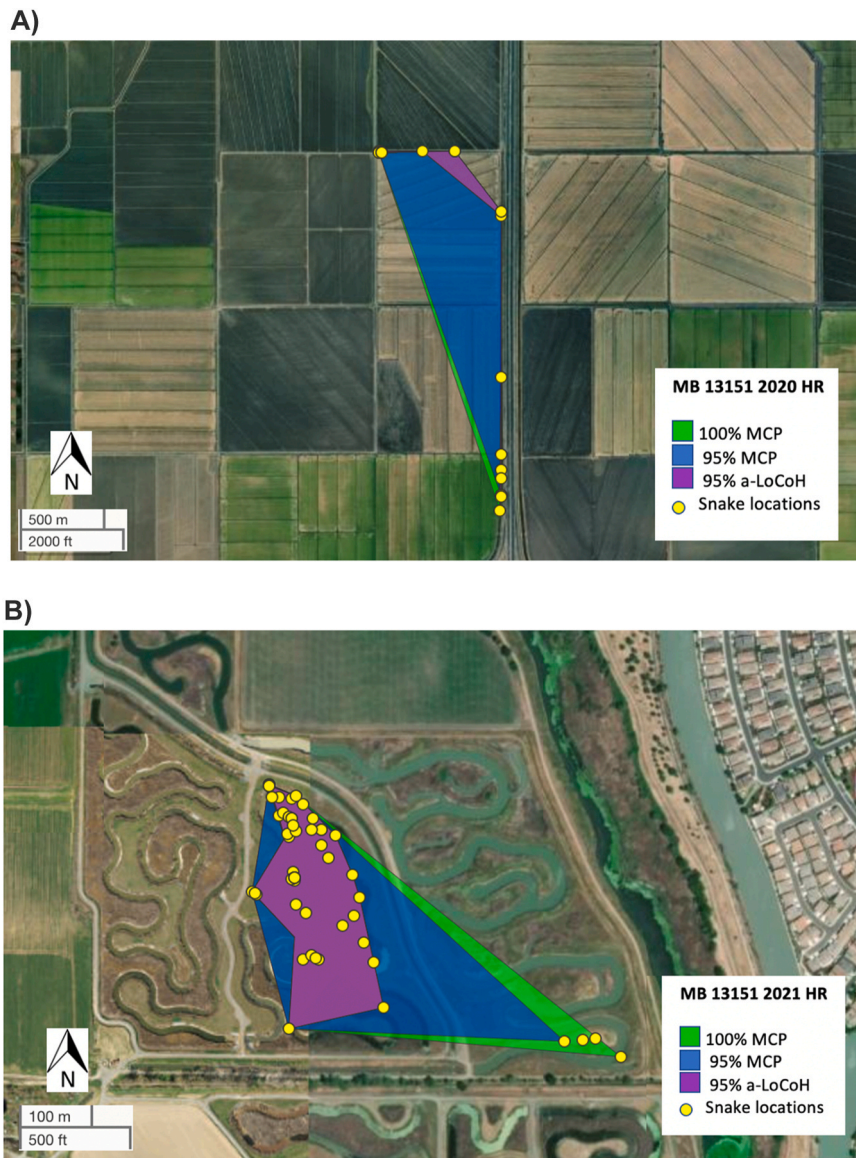


Fig. 3. Home range estimates using 100% and 95% Minimum convex polygons (MCP) and 95% alpha local convex hulls (a-LoCoH) for snake ‘MB 13151’ (A) from the canal donor site in 2020 before it was translocated and (B) from the wetland recipient site in 2021 after it was translocated. Both sites were in the Natomas Basin, Sacramento, CA, USA. The scale of each map is adjusted to best display the home-range estimates of interest. Note the scale may differ among figures and between panels. Maps produced using mapproj in R, Source: Esri, i-cubed, USDA, USGS, AEX, GeoEye, Getmapping, Aerogrid, IGN, IGP, UPR-EGP, and the GIS User Community

recipient site, and the wetland donor site (Table 2).

Resident snakes overall had a greater net displacement from the release location to the last location before the first winter than translocated snakes, and the net displacement before the first winter was greater before translocation than after (Table 2). The null model was the most parsimonious model for net displacement from the release to the first winter, with the model including ‘site’ as the next most parsimonious model ($\Delta AICc$ of 1.38; Supplemental Table 4). There was a significant difference in the net displacement before the first winter among the three sites overall ($P = 0.03$), with the net displacement at the wetland donor site being smaller than at the canal donor site ($P = 0.07$) in post-hoc pairwise comparisons (Supplemental Figure 4).

The net displacement from release to the centroid of the snake’s home range was greatest at the canal donor site, followed by the recipient site, and then the wetland donor site (Table 2). Resident snakes overall had a greater net displacement from the release location to the centroid than translocated snakes. Translocated snakes also had a greater net displacement from the release location to the centroid of their home range before translocation than after (Table 2). The model including ‘site’ as a fixed effect was the most parsimonious for the net displacement from the centroid of the home range model set (Supplemental Table 5). The net displacement

Table 2

Net displacement between the release point and the last location before the first overwintering period and net displacement from the release point to the centroid of the home range (HR) for giant gartersnakes (*Thamnophis gigas*) in Sacramento County, California, USA, 2018–2021. Values in the parentheses represent the 95% confidence interval around the mean.

Group	n	Release to First Winter (m)	Release to HR Centroid (m)
Wetland Donor	17	125.9 (71.6 – 180.3)	96.5 (53.8 – 139.1)
Canal Donor	5	341.1 (204.2 – 478.1)	392.7 (219.2 – 566.2)
Recipient	16	266.8 (80.6 – 452.9)	184.1 (7.3 – 361.0)
Residents	33	230.3 (150.2 – 310.3)	240.1 (140.4 – 339.8)
Translocated	5	266.8 (80.6 – 452.9)	184.1 (7.3 – 361.0)
Translocated- Before	6	326.9 (46.1 – 607.7)	330.0 (54.9 – 605.2)
Translocated- After	5	266.8 (80.6 – 452.9)	186.2 (7.3 – 361.0)

Table 3

Average sinuosity, start-to-end distance, and total distance traversed over seasonal movement paths of giant gartersnakes (*Thamnophis gigas*) in Sacramento County, California, USA, 2018–2021. The values in the parentheses represent the 95% confidence interval around the mean. Sinuosity values range from 0–1 with the curvature of the movement path increasing as values approach one.

Group	n	Sinuosity	Start-end Distance (m)	Total Distance (m)
Wetland Donor	50	0.32 (0.20 – 0.44)	97.81 (71.5 – 124.2)	783.2 (567.7 – 998.8)
Canal Donor	40	0.15 (0.10 – 0.20)	387.6 (265.25 – 509.88)	2187.1 (1691.1 – 2683.2)
Recipient	19	0.19 (0.14 – 0.24)	309.9 (181.7 – 438.08)	1292.9 (773.6 – 1812.2)
Residents	90	0.24 (0.17 – 0.31)	226.6 (163.2 – 290.0)	1393.5 (1105.4 – 1681.6)
Translocated	19	0.19 (0.14 – 0.24)	309.9 (181.7 – 438.1)	1292.9 (773.6 – 1812.2)
Translocated- Before	22	0.15 (0.12 – 0.19)	273.8 (144.8 – 402.8)	1601.8 (1024.2 – 2179.4)
Translocated- After	19	0.19 (0.14 – 0.24)	309.9 (181.7 – 438.1)	1292.9 (773.6 – 1812.2)

from the release locations to the centroid of the home range was smaller at the wetland donor site than the canal donor site (Coef: -0.52 , 95% CI: -0.81 , -0.24 , $P = 0.003$; Supplemental Figure 5). There were five snakes that were tracked through an additional season, giving us net displacements from the release to the second winter. The average net displacement from their release location to the last location before the second winter was 145.6 m (95% CI: 1.0, 290.1 m). There were too few individuals with net displacements through the second winter to compare among sites or between treatments.

3.3. Movement analyses

For the movement metric analysis, we were able to include data from all 50 snakes that were tracked. With several snakes radio-tracked across multiple years, we were able to calculate 109 measurements of each: total distance traversed, start-to-end distance, and sinuosity. The total distance traversed was greatest in the canal donor site, intermediate in the recipient site, and lowest in the wetland donor site (Table 3).

Resident snakes overall had a larger total distance traversed than translocated snakes (Table 3). The total distance traversed decreased after translocation (Table 3). The most parsimonious model for the total distance traversed included 'site' as a fixed effect (Supplemental Table 6). Total distance traversed was lower at the wetland donor site (Coef: -0.95 , 95% CI: -1.41 , -0.49 , $P < 0.001$) than at the canal donor site (Supplemental Figure 6). The total distance traversed increased over the years (Coef: 0.24 , 95% CI: 0.00 , 0.48 , $P = 0.05$).

The distance between the start-to-end distance of the snakes' trajectories followed a similar pattern as with the total distance traversed across the three sites. Start-to-end distance was highest at the canal donor site, intermediate at the recipient site, and lowest at the wetland donor site (Table 3). Resident snakes overall had a smaller start-to-end distance than translocated snakes. The start-to-end distance was greater after translocation than before (Table 3). The most parsimonious model for start-to-end distance was the model that included 'site' as a fixed effect, followed by the 'null' model (Supplemental Table 7). Start-to-end distance was smaller at the wetland donor site compared with both other sites (wetland donor – canal donor Coef: -0.48 , 95% CI: -0.86 , -0.10 , $P = 0.01$,

wetland donor – recipient Coef: -0.47 , 95% CI: -0.89 , -0.04 $P = 0.03$; Supplemental Figure 7).

Snakes from the canal donor site had the lowest average sinuosity, snakes from the recipient site had an intermediate average sinuosity, and snakes from wetland donor site had the highest sinuosity (Table 3). Resident snakes overall had a higher sinuosity measure on average than translocated snakes (Table 3). The sinuosity of translocated snakes before and after translocation was similar, but slightly higher after translocation than before (Table 3). The most parsimonious model for sinuosity included ‘site’ as a fixed effect (Supplemental Table 8). The sinuosity measure was greatest at the wetland donor site (Coef: 0.61 , 95% CI: 0.37 , 0.86 , $P < 0.001$), followed by the recipient site (Coef: 0.36 , 95% CI: 0.08 , 0.63 , $P = 0.04$; Supplemental Figure 8), indicating that snakes took more meandering paths at the two wetland sites compared with the canal donor site.

4. Discussion

Monitoring home range and animal movement after translocation provides important insights into how translocated animals acclimate and respond to their new environments (Knowlton and Graham, 2010; Thalmann et al., 2015). The results of our study are consistent with those seen in other studies that have found a change in home range size and movement distances after translocation (Barve et al., 2013; Butler et al., 2005; Farnsworth et al., 2015; Plummer and Mills, 2000; Tuberville et al., 2005). However, unlike many of these studies, we did not see a universal increase in home range size after translocation, instead seeing only an increase in some, but not all, movement metrics examined. The variable responses in movements after translocation may stem from the fact that the habitat type in which snakes were found—rice agriculture or wetland—had a major influence on snake home range size and movement patterns here.

Snake home ranges were smaller for translocated snakes than residents on average for 95% and 100% MCP, but results depended on the habitat type of the resident site. Home range size and movement distances were consistently largest at the canal donor site compared with the two wetland sites. Human modified landscapes like agriculture often create fragmented habitat patches interspersed with unsuitable matrix habitat that poses barriers to movement or that channels wildlife movements (Fischer and Lindenmayer, 2006). Habitat patches in agricultural landscapes are also typically more linear in shape (Forman, 1995), which was true in the present study. Rice grows seasonally at the canal donor site, with emergent vegetation covering the fields from mid-July to September (Halstead et al., 2019). Although rice fields may provide foraging opportunities and additional movement corridors for giant gartersnakes, the majority of persistent habitat lies in linear irrigation canals (Halstead et al., 2019), which was evident in the snake locations and home range maps of rice agriculture snakes; although the MCP home range estimates encompassed rice fields, snake locations and the a-LoCoH estimates were largely restricted to irrigation canals. The width and length of linear habitat influences the movement and home range sizes of animals living in these environments (Sommaro et al., 2010). A study of corn mice (*Calomys musculus*), for example, found that mice in narrower habitats had greater movement distances and had to extend their foraging trips, whereas animals living in more two-dimensional landscapes could forage in multiple directions (Sommaro et al., 2010). In some cases, wildlife in fragmented habitats may occupy smaller home ranges or reduce movements in disturbed landscapes (Doherty et al., 2019, 2021; Marshall et al., 2020). In other cases, however, modified landscapes and their dispersed resources may cause animals to travel farther in habitat patches or move among multiple patches to meet their needs (Young et al., 2018), a scenario that likely unfolded at the canal donor site in the present study.

Just one study has previously compared home range size of giant gartersnakes in rice agriculture versus wetland habitat (Valcarcel, 2011). In that study, snakes living in rice agriculture had smaller, less variable home ranges compared to those in wetlands—contrary to what the author had predicted (Valcarcel, 2011). In contrast to their results, snakes in the wetland donor site in the present study had the smallest home ranges, moved the shortest distances by all measures, and had the most sinuous, non-linear movements. This result is more in line with expectations when individuals live in productive habitats (Todd and Nowakowski, 2021), as home range size is often tied to the availability of resources (Mitchell and Powell, 2004; Powell, 2000; Schoener, 1981). Studies of other species have likewise found that animals in more resource-dense landscapes generally have smaller home ranges (Börger et al., 2008; Haskell et al., 2002; Schoepf et al., 2015). In fact, prey abundance data from the three study sites over the period studied here found that the wetland donor site had the highest catch-per-unit-effort of fish and the most stable capture rates of frogs (Nguyen et al., 2023). Abundant prey may in part explain why home ranges and movements were smallest at the wetland donor site here.

The age of the managed wetland sites may also play a role in the differences we observed between the wetland donor site and the recipient site specifically. Despite both sites being restored managed marshes, the wetland donor site was built in 2002 compared with the recipient site, which was completed in 2016 (AECOM, 2016). A review of mitigation bank wetlands in the US also found that, over time, the vegetation composition trends toward characteristics more like natural wetlands (Spieles, 2005). Other studies have found similar results that older wetlands had greater aboveground plant biomass than more recently restored wetlands (Ballantine and Schneider, 2009) and vegetation reaches a state of equilibrium after the 20-year mark at which point mitigation wetlands more closely resemble natural reference wetlands (Atkinson et al., 2005; Balcombe et al., 2005; Stefanik and Mitsch, 2012). Existing literature on species richness and ecosystem function of restored wetlands is more variable. Some studies suggest that species richness is not always greater in older wetlands (Campbell et al., 2002; Meli et al., 2014) or that richness increases rather quickly following restoration and resembles reference sites after five years for vertebrate species (Moreno-Mateos et al., 2012). Other studies contradict these results, instead finding older restored wetlands support greater species richness of birds and fish (VanRees-Siewert and Dinsmore, 1996; Rewa, 2007) or that although species richness may reach maximum values in the first three to seven years, they don't stabilize until closer to 12–13 years (Strand and Weisner, 2013). Scientists have also highlighted that species richness is not necessarily equivalent to ecosystem function (Callaway, 2005; Zedler, 2000). Therefore, the age difference of the donor and recipient wetland could have contributed to the lower capture rates of fish and frog species at the recipient site, which in turn may underlie the difference in home

range and movement metrics between the two sites. Additionally, the shape of the two wetland habitats varied between the two wetland types. The donor wetlands were more circular in shape with more contiguous habitat that sometimes branched into a few channels—as is typical of traditional marsh environments—whereas the recipient site had wetlands that were designed as a series of sinuous canals with fewer circular features. It is likely that the age of the sites, overall structure of the landscape, and resource availability all influenced space use.

Home ranges of translocated individuals were smaller after translocation than before in both of the MCP estimations, and similar (2.6 ha before and 2.7 ha after) in the 95% a-LoCoH estimation. All five translocated snakes for which we had before and after home range estimates originated from the canal donor site, so the reduction in home range size observed in the MCP estimates, but not the a-LoCoH estimate, probably reflects the change in habitat type from canal habitat before translocation to wetland habitat after. MCP measurements are often influenced by the outermost points in a data set, whereas a-LoCoH estimates can be optimized to better fit linear landscapes and those with existing barriers to movement (Getz et al., 2007). This was evident in our study, where MCP estimation methods performed well in the wetland sites but seemed to overestimate space use in the canal sites. Snakes living in a canal environment may have larger MCP estimates from using areas across the full extent of a long, linear canal or from making occasional forays into adjacent perpendicular canals. However, the lack of noticeable increase in the 95% a-LoCoH after translocation suggests that the core area used by translocated snakes after release remained similar to the core area used in their origin site regardless of the shift in habitat types. Given the difference in interpretation of MCP and a-LoCoH, future studies should consider using both methods and including multiple estimates to ease comparisons with existing literature to provide the greatest insights into the ecology of the species and study areas.

Many studies have found an increase in exploratory movements after animals are translocated (Butler et al., 2005; Germano and Bishop, 2009; Hinderle et al., 2015). We also saw increases in some of the metrics we studied, including start-to-end distances and the net displacement between the release location and the first winter in translocated snakes compared to snakes in the resident sites overall. Often, these movements and home ranges tend to decrease with time after release as animals become familiar with their new habitats (Farnsworth et al., 2015; Pille et al., 2018; Tuberville et al., 2005). The similarity of the start-to-end distance before and after translocation and the decrease in total distance traversed and net displacements is promising and suggests that any increased exploratory movements after translocation did not exceed typical movements at donor sites. Translocated snakes had smaller total distances traversed relative to resident snakes overall, although the distances moved by residents is likely inflated by residents from the canal donor site. Translocated snake movements were greater than those of resident snakes in the donor wetland site across all metrics, suggesting that exploratory movements after translocations or existing differences in resource distribution and other site characteristics discussed above could still be influencing the differences among wetland sites. Had we been able to track translocated snakes for more than one year after release, we may have seen a further decrease in movements as has been seen for many other species (Fryxell et al., 2008; Scillitani et al., 2012; Smedley et al., 2019; Werdel et al., 2021).

Aside from exploratory movements, many wildlife also display homing behaviors and may attempt to move back to previous habitat (Germano and Bishop, 2009; Hinderle et al., 2015; Mack and Berry, 2023; Miller et al., 1999; Sullivan et al., 2004). We saw no evidence of this in our study based on the similarity in movement values before and after translocation. Additionally, the net displacement from the release location to the first winter location and to the centroid of the home range were smaller after translocation than before. We would expect the displacement values to be larger after translocation if animals had been attempting to find previous habitat. We also did not observe any snakes emigrating from the recipient site after translocation (Nguyen et al., 2023).

4.1. Conclusions

Overall, the results of our study demonstrate that site-level differences—whether it be the structure of the landscape, the availability or distribution of prey, or both—and translocation itself both influence the home range sizes and movements of giant gartersnakes. This is supported by the results of our mixed effects models. The variable ‘site’ was in the top two models for nearly all model sets and ‘translocated’ was in the top two models for the 95% MCP and 95% a-LoCoH. The fact that translocated snakes had smaller home ranges and movements than did snakes in the canal donor site is encouraging because it suggests snakes did not behave much differently than resident snakes in canal habitats. Additionally, the lack of major differences before and after translocation is promising for the applicability of translocations for giant gartersnakes in the future. However, the greater movements and home ranges at the recipient site compared with the wetland donor site may indicate snakes either weren’t fully settled into the recipient site at the time of our study or that there are site-level differences between these two managed wetland sites that caused the observed differences.

For species like giant gartersnakes that will likely require translocation to meet long-term recovery goals, understanding the potential costs and benefits of translocation will be critical to inform species recovery. Although increased movement after translocation can have serious implications for survival and establishment, if the differences before and after are similar, or if the differences decrease after an initial exploratory period, the cost of translocation may be worth the potential benefits of reconnecting populations genetically and of reintroducing populations to restored habitat. Our study also highlights the complex interactions between the act of translocation and the underlying landscape and site differences that can influence wildlife movement and space-use. Understanding movement ecology in different situations can inform which animals to translocate, from which sites animals should be taken, and where to translocate them to maximize the likelihood of success. With the vast number of species that have experienced habitat loss, especially those living in modified landscapes like giant gartersnakes, careful consideration of animal movement in existing habitats and after translocation will be important to ensure populations receive the highest possible benefits from translocation efforts.

Declaration of Competing Interest

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Data Availability

Data will be made available on request.

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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; MOU CDFW SC-10779; UC Davis IACUC #20405; USGS WERC IACUC #WERC-2014-01.

Declaration of interests

We have no declarations of interest to make other than disclosing our funding sources which are included in the acknowledgements.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02789](https://doi.org/10.1016/j.gecco.2023.e02789).

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