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Assessing translocation success and long-distance homing in riverine turtles 10 years after a freshwater oil spill

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Abstract

Wildlife translocation is often used as a mitigation strategy for construction projects and other disturbances to habitat. In 2010, one of the largest freshwater oil spills in the United States occurred in the Kalamazoo River in Michigan, when over 3.2 million L of diluted bitumen crude oil impacted nearly 56 km of riverine habitat. During 2010 and 2011 cleanup efforts, 686 northern map turtles (*Graptemys geographica*) were captured from oil-impacted stretches of the river, cleaned, rehabilitated, and translocated 2.5–84.3 km from their original capture location. The goal of this translocation effort was to release turtles within the same watershed, but away from ongoing cleanup operations, so individuals could potentially return to their original home range after it had been cleaned of oil and restored. In this study, we evaluated the success of translocation as an emergency mitigation strategy for freshwater turtles by quantifying recapture probability and homing by northern map turtles translocated varying distances from their home ranges. During subsequent years of survey up to 10 years post-spill, 230 of the translocated turtles were recaptured, of which 104 exhibited homing by returning to their original home ranges. Turtles translocated to sites nearest their original capture location had a higher probability of recapture and homing than those translocated further away. Females had a higher probability of returning to original home ranges than males when translocated greater distances. In addition, four females and one male are known to have traveled >50 km between capture and release locations, which to our knowledge is the greatest travel distance recorded for any freshwater turtle species in the United States. Our results demonstrate that riverine turtles have considerable homing ability when displaced long distances, which has important implications for design and success of translocation projects.

KEYWORDS

anthropogenic impacts, freshwater, *Graptemys*, mitigation, northern map turtle, oil spill, relocation

1 | INTRODUCTION

Wildlife translocation is becoming an increasingly common conservation and mitigation practice to reduce the impacts of anthropogenic activities across taxa. Conservation-driven translocations often aim to augment, re-establish, or re-introduce a population to areas from which they have been extirpated or are in decline, while mitigation-driven translocations try to reduce wildlife mortality directly caused by human activities (e.g., development, pollution) by relocating individuals or populations away from an area that is or will become uninhabitable (Craven et al., 1998; Sedon et al. 2014; Germano et al., 2015). There have been notable translocation success stories, such as successful re-establishment of a black bear population in Arkansas (Smith & Clark, 1994), but there have also been translocations that failed to achieve their goals. For example, thousands of kangaroo rats were translocated in various parts of California, but no individuals appear to have survived 1-year post-release (Shier & Swaisgood, 2012). Failure of translocations most often result from improper planning and management, unsuitable habitat at the release site, and disease transfer (e.g., case studies; Soorae, 2018; Soorae, 2021). Therefore, substantial planning, pilot studies, and use of best practices are critical to maximize the likelihood of a translocation effort's success.

Mitigation translocations are often regarded by the public as a humane and effective solution to human-wildlife conflict, leading to them becoming even more commonplace than conservation-driven translocations (Bradley et al., 2020; Massei et al., 2010). If mitigation translocation strategies are to be successful conservation tools, it is critical that we find species-specific methods to maximize benefits relative to cost. In particular, the goals of a specific translocation effort should be established a priori to inform the post-release monitoring strategy in determining if those goals were met. Inadequate post-release monitoring or metrics of success can erroneously lead to labeling an effort as "successful" when in fact it was unsuccessful, potentially leading to replicated failures (Fischer & Lindenmayer, 2011; Wolf et al., 1998). Mitigation translocations often have poorly documented outcomes due to lack of monitoring or publicly accessible results (Nash et al., 2020; Silcock et al., 2019; Taylor et al., 2017). In mitigation translocations with documented outcomes, most often have high failure rates (Sullivan et al., 2014), especially in reptile and amphibian species where translocations of all types have resulted in successful outcomes only 41% of the time (Germano & Bishop, 2009). Typically, data for conservation translocations involving reptile species are available in primary literature, while the data for mitigation-based reptile translocations are often inaccessible, nonexistent, or lack measurable objectives (Armstrong & Seddon, 2008; Germano et al., 2015; Taylor et al., 2017). Moreover, mitigation translocation projects typically include insufficient monitoring to ascertain their long-term success, especially in long-lived species such as many reptiles (Sullivan et al., 2014). Insufficient monitoring, coupled with reluctance to report failed translocation efforts, has likely led to a high frequency of failure in mitigation translocation projects for reptiles (Germano et al., 2015).

Translocated reptiles appear to suffer high mortality rates relative to resident individuals due to increased stress, susceptibility to disease, and the fact that many reptiles exhibit strong site fidelity and homing ability (Cornelis et al., 2021). Site fidelity and homing ability can lead to aberrant movement patterns in translocated reptiles, which can increase negative human–wildlife interactions and decrease survival if individuals are unable to find critical resources, such as hibernacula, in their new environment (Brown et al., 2008; Harvey et al., 2014; Sullivan et al., 2014). Species with strong homing ability and a high degree of site fidelity may also be poor candidates for translocation because individuals may attempt to return to their original home area, which may have become uninhabitable (Dodd Jr. & Seigel, 1991; Germano & Bishop, 2009; Sosa & Perry, 2013). In turtles, translocated individuals of species that exhibit strong site fidelity have been found to "wander" more, have larger home ranges, and have increased mortality compared to resident turtles, presumably a result of translocated individuals trying to return to their original home range (Cook, 2004; Hinderle et al., 2015; Rittenhouse et al., 2007). The high failure rate of many translocation efforts, particularly those involving reptiles, has led to the suggestion that regulation of translocation efforts should be changed to match conservation outcomes (Germano et al., 2015). However, regulation of mitigation translocations can be difficult, as these may be conducted as emergency responses to large-scale disturbances such as chemical spills. In such situations, translocations are generally a last resort, wherein the risks associated with moving individuals outweigh the costs of losing the entire population. Although emergency translocations admittedly have very limited time available for decisions on experimental design, all such efforts should include post-release monitoring, which can serve as a learning opportunity to improve success and regulation of future translocation efforts in similar situations.

One such learning opportunity arose from the 2010 Kalamazoo River oil spill (MI, USA), during which emergency translocation efforts were undertaken for nearly 700 oiled northern map turtles (*Graptemys geographica*). On July 25 and 26, 2010, 3.2 million L (834,444 gallons) of diluted bitumen (dilbit) crude oil were released after a pipeline rupture (NTSB 2012). The U.S. Environmental

Protection Agency (EPA) later estimated that 4.5 million L (1,181,599 gallons) were recovered, which made the Kalamazoo River spill one of the largest inland oil spills in U.S. history (USEPA, 2016). Emergency cleanup and habitat restoration efforts began on July 28, 2010 and continued until June 2012, with additional targeted work continuing through 2014 (USEPA, 2016). As part of cleanup activities, approximately 5000 freshwater turtles, predominately northern map turtles, were captured, rehabilitated, and released (USEPA, 2016). Release of rehabilitated turtles was complicated by the conflicting goals of releasing animals back to their capture location as soon as they were cleared by veterinarians, while also endeavoring to protect them from additional oiling and ongoing disturbance from cleanup operations at their original capture locations. To avoid releasing rehabilitated turtles back into habitat where they may become reoiled, but also to allow these individuals to potentially return "home," the U.S. Fish and Wildlife Service (USFWS) and Michigan Department of Natural Resources (MDNR) translocated rehabilitated turtles to other areas within the Kalamazoo River watershed while remaining oil precluded release of turtles at their original capture locations.

The emergency mitigation translocation of nearly 700 northern map turtles following the 2010 Kalamazoo River oil spill provided a unique opportunity to assess: (1) the success of a mitigation translocation of freshwater turtles following a large-scale oil spill, using northern map turtles as a model species, and (2) the homing ability of northern map turtles when translocated varying distances from their original home ranges. It is important to note that, in the case of the Kalamazoo River oil spill, turtles only needed to be temporarily removed from their home area while oil was removed from the river, at which point it was again habitable for northern map turtles. The objectives of the present study were to use recapture records up to 10 years post-spill to assess the success of translocation to mitigate the effects of an oil spill on northern map turtles, and to quantify homing in northern map turtles that had been moved known distances from uninhabitable home areas. Our study provides novel insight into the effectiveness of translocation for mitigating the effects of an environmental disaster on a riverine turtle species.

2 | METHODS

2.1 | Study site

Our study site was ~50 km of Kalamazoo River channel impacted by the 2010 oil spill, from the confluence of Talmadge Creek to Morrow Lake (Calhoun and Kalamazoo counties, MI, USA; Figure 1). Two retired hydroelectric dams (spillways; 3.7- and 4.6-m tall) and a 1.4-km-long concrete channel within the study site could potentially limit movement of turtles (Fongers, 2008; Figure 1). An additional 4.3-m tall active hydroelectric dam and five smaller spillways are between the study site and translocation sites (two within tributaries and three upstream from the study site; Figure 1).

2.2 | Study species

Riverine turtles are vulnerable to floating dilbit when they surface to breathe and as they leave the water to bask. In river habitat, a portion of the spilled dilbit mixture can sink over time (Dew et al., 2015), so turtles may also be exposed to oil when submerged. Turtle rehabilitation efforts following the 2010 oil spill included all species found in the Kalamazoo River, although northern map turtles were the most abundant species captured and are the focus of this study (USEPA, 2016).

The northern map turtle inhabits medium to fast flowing rivers and streams as well as impoundments, lakes, and backwaters. They are typically dormant November–March, depending on local climatic factors. Northern map turtles are diurnal leaving the water daily to bask on rocks, woody debris, or banks (Lindeman, 2013). Females typically feed on mollusks, insects, and crayfish while males feed on smaller mollusks and insects (Richards-Dimitrie et al., 2013). Northern map turtles exhibit pronounced sexual dimorphism, with adult females growing to nearly twice the length of males (18.0–27.3 cm straight carapace length [SCL] vs. 9.0–15.9 cm SCL, respectively; Lindeman, 2013). Males of this population reach sexual maturity at 4–5 years, while females mature at 12–14 years.

2.3 | Emergency turtle rescue and translocation (2010–2011, 2013)

Immediately following the oil spill in July 2010, and extending into 2011, capture and translocation of northern map turtles in the Kalamazoo River was conducted by paid contractors, including JO, and was overseen by LW and the USFWS (USEPA, 2016). Additional targeted surveys were conducted in 2013. During this time, all aspects of wildlife rehabilitation and release (including permitting) were done under the supervision and direction of state (MDNR) and federal agencies (USFWS). No oversight from an Ethics Committee were required by the agencies directing the work. Surveys focused on capturing oiled turtles for rehabilitation and individually

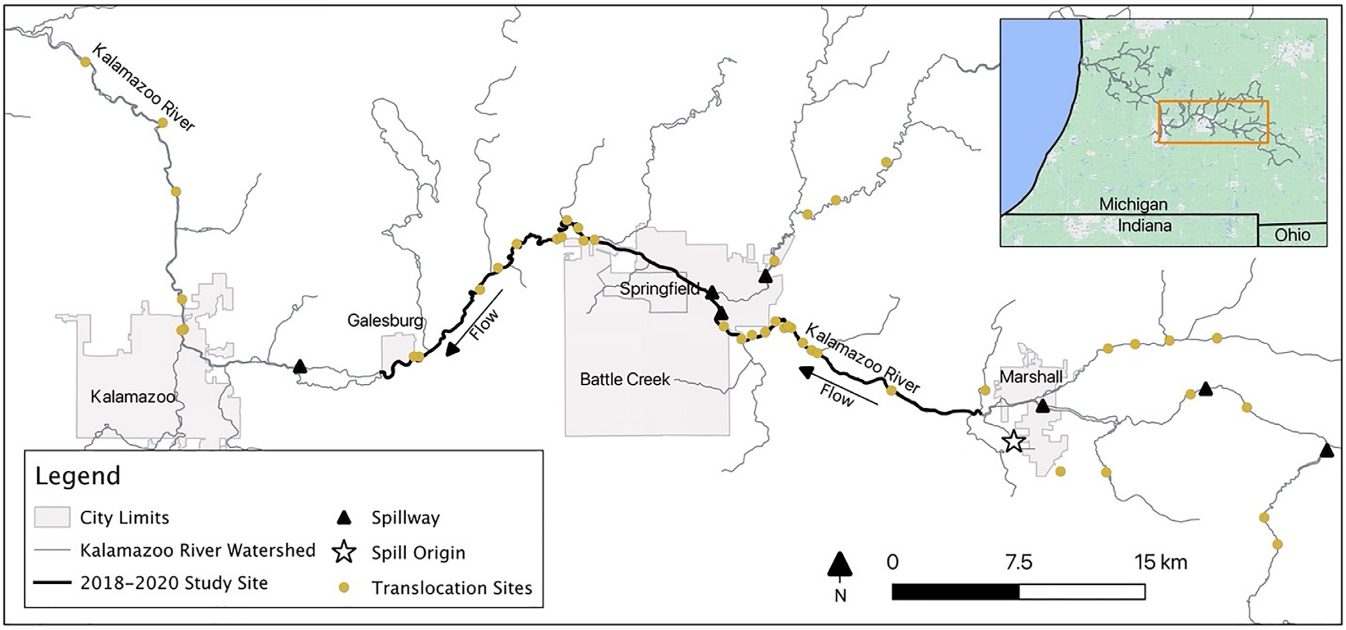

FIGURE 1 Study Site for the 2010–2011 translocations and 2018–2020 recapture surveys for northern map turtles (*Graptemys geographica*) in the Kalamazoo River, Calhoun and Kalamazoo counties, Michigan, following the Kalamazoo River oil spill on July 25 and 26, 2010. A total of 686 northern map turtles were translocated outside of their home range (based on mean stream home range lengths of each sex) at various distances at locations downstream and upstream in the Kalamazoo River and additional locations within tributaries.

identifying translocated turtles that had returned to the study site. During surveys in 2010–2011 and 2013, field crews captured turtles throughout the 50-km study site using dipnets from a boat (Lagler, 1943), hoop traps, and basking traps. Level of survey effort varied by day and year, with one to five boats surveying the study site each day. One survey day constituted a day in which at least one boat actively captured turtles within the study site. A total of 69 survey days occurred in 2010 (July–October), 97 in 2011 (April–October), and 60 in 2013 (July–October). Field crews recorded capture locations of all turtles with a handheld Global Positioning System unit (GPS; Garmin International Inc.) with an accuracy of <3 m. They measured each individual's SCL along the midline to the nearest mm, and mass to the nearest 0.1 g. When possible, sex was determined using secondary sex characteristics and age was estimated by the number of growth rings present on an individual scute (Ernst & Lovich, 2009; Lindeman, 2013). In 2010, field crews individually marked turtles >100 g with passive integrated transponder (PIT) tags (Avid Identification Systems, Inc.). Beginning on September 22, 2010 and continuing through 2013, instead of PIT tags, each newly captured individual was marked with a unique combination of notches filed along the marginal scutes; however, some individuals that were processed through the rehabilitation facility were marked with PIT tags (Cagle, 1939).

Turtles captured and released between July 29 and October 6, 2010 were temporarily housed in a rehabilitation facility for 2–21 days for cleaning, rehabilitation, and health monitoring. Rehabilitated turtles were released following a final veterinarian health assessment and confirmation they appeared free of oil. After October 6, 2010, newly captured individuals, turtles requiring additional cleaning, and turtles requiring continued health monitoring were housed over the winter in the rehabilitation facility to be released in spring 2011 (USEPA, 2016).

Because the translocation effort described here was an emergency mitigation translocation event in response to an environmental disaster, the immediate goal was to return healthy turtles to the wild as quickly as possible following capture, while also releasing them in locations that would minimize the potential for additional oiling and negative impacts from river channel cleanup operations. The secondary goal of this emergency mitigation effort was to translocate turtles to suitable habitat that was also physically connected to the area of original capture. If northern map turtles exhibit homing ability similar to several terrestrial turtle species (Hinderle et al., 2015; Rittenhouse et al., 2007; Sosa & Perry, 2013), releasing them at sites that were physically connected by river channel to their original home ranges should have allowed individuals to eventually return to their home ranges on their own. From July 31 to October 6, 2010, 601 northern map turtles (250 females and 351 males) were marked with PIT tags and translocated 2.5–84.3 km from their original capture location. Translocation sites were chosen by local agencies based on habitat suitability, the presence of local northern map turtles, distance from original capture site, and absence of oil and cleanup activities. Turtles were translocated between July 31 and 22 September, 2010 to 21 locations divided into three groups: tributaries of the Kalamazoo River (hereafter, *tributary*), Kalamazoo River channel downstream of the study site (*downstream*), and Kalamazoo River channel upstream from the study site (*upstream*). All translocation release sites were within the Kalamazoo River watershed and were interconnected via lotic habitat (Figure 1). On September 22, 2010, the study site was cleared by the EPA for release of rehabilitated turtles, so all subsequent releases of rehabilitated turtles occurred in the study site as near to turtles' original capture locations as possible (USEPA, 2016).

From April to June 2011, overwintered turtles were released at or near their original capture location. However, during this time, an additional 85 PIT tagged northern map turtles (42 females and 43 males) were translocated to locations within the study site due to continued cleanup work occurring at or near their original capture location. Translocation distances in 2011 ranged from 2.5 to 25.7 km, with all occurring within the study site.

2.4 | Post-spill monitoring and recapture surveys (2018–2020)

In 2018–2020, researchers from the University of Toledo conducted surveys at the study site to recapture northern map turtles that had originally been marked following the 2010 oil spill. The objectives of these surveys were to determine how many translocated turtles had

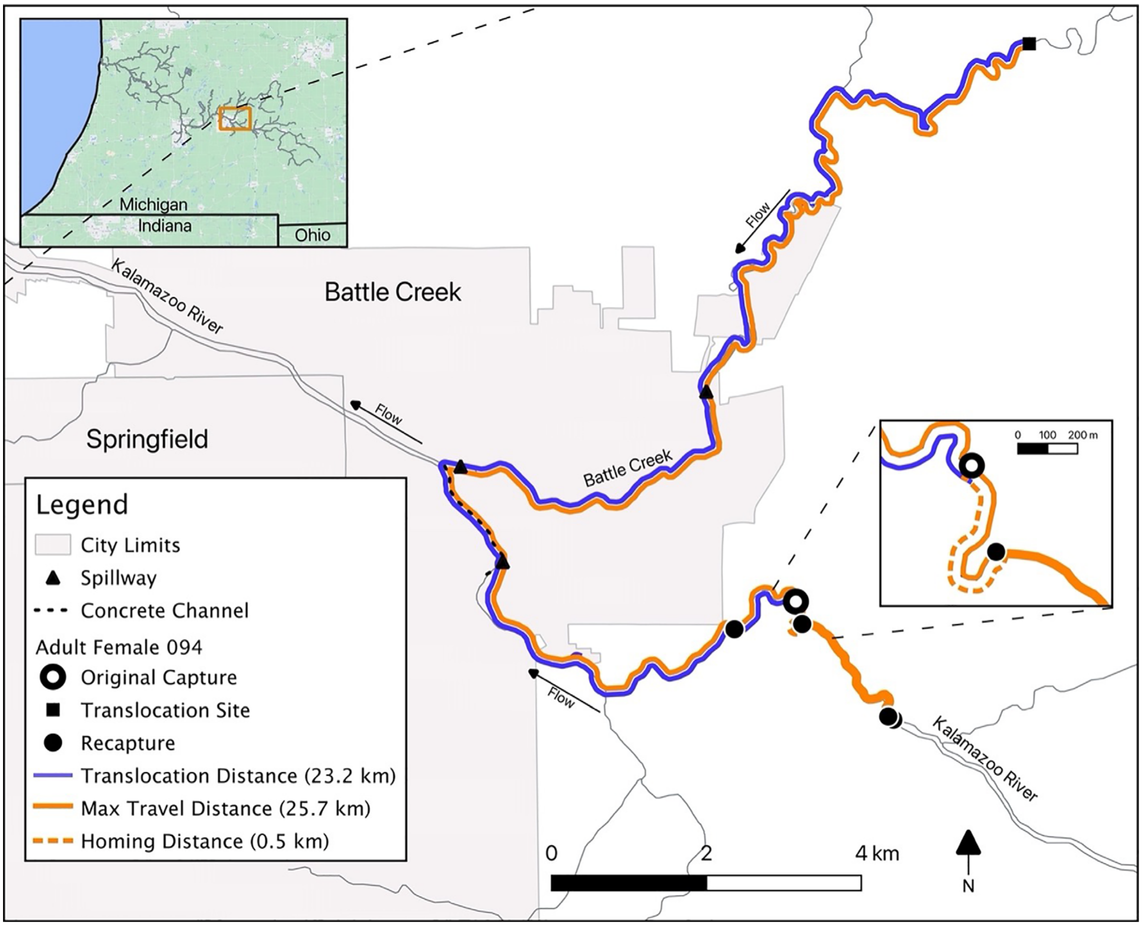

FIGURE 2 Translocation distance (i.e., distance between an individual's original capture location and its translocation site), travel distance (i.e., maximum distance between an individual's translocation site and subsequent recapture locations), and homing distance (i.e., minimum distance between an individual's original capture location and subsequent recapture locations) for a representative adult female northern map turtle (*Graptemys geographica*) translocated following the Kalamazoo River oil spill of 2010 in Calhoun County, Michigan. This individual traveled around multiple spillways and through a concrete channel, before being recaptured ~0.5 km from the original capture location.

returned to the study site as a measure of the overall translocation effort's success, and to quantify homing ability of translocated turtles. Data collection in 2018–2020 followed the same methods as those used in 2010–2011. That is, during each survey day, we captured turtles throughout a portion of the 47.0 km of the study site, from the confluence of Talmadge Creek to East Michigan Avenue, using dipnets from a boat or kayak (Lagler, 1943), hoop traps, basking traps, and by hand while snorkeling (Marchand, 1945). Level of survey effort varied by day and year, with one to three boats surveying the study site on each survey day. A total of 62 survey days occurred in 2018 (May–September), 117 in 2019 (April–October), and 57 in 2020 (April–October). We recorded capture location of each individual with a handheld GPS unit (Garmin International Inc.) with an accuracy of <3 m. We recorded the same morphological measurements as in 2010–2011, and we used the same sex characteristics to determine sex and age. We identified any previously marked individual by PIT tag or unique shell notches and recorded these individuals as recaptures.

2.5 | Data analysis

We used R 3.6.3. (R Core Team, 2020) to conduct all statistical analyses, and the Riversdist package to calculate distances, all distance pathways remaining entirely within the river channel (Tyers, 2017). For all analyses, we used only individuals that were presumed to have been translocated to an unfamiliar location outside of their original home range. To determine whether an individual had been translocated outside its original home range, we used previously estimated mean stream home range lengths for this population, 2.4 km for males, and 4.6 km for females, based on radio-telemetry locations throughout an entire year (Otten, 2022). In this study, we considered *translocation distance* to be the distance between an individual's original capture location and its translocation release location (Figure 2). We calculated translocation distance by determining the shortest distance between points while staying entirely within the river channel. Therefore, any male turtle with a translocation distance >2.4 km and any female with a translocation distance >4.6 km was assumed to have been translocated to an unfamiliar area and was included in subsequent analyses.

To evaluate the success of the mitigation translocation conducted as an emergency response to the 2010 Kalamazoo River oil spill, we determined the number of individuals translocated in 2010 or 2011 that were subsequently recaptured in the study site during each survey year. We

TABLE 1 Total number of female and male northern map turtles (*Graptemys geographica*) translocated in 2010–2011 following the Kalamazoo River oil spill, that were recaptured (Recap) in subsequent surveys during 2010, 2011, 2013, and 2018–2020.

		2010		2011		2013		2018		2019		2020		Total individuals	
	Translocated	**Recap**	**Homed**	**Recap**	**Homed**	**Recap**	**Homed**	**Recap**	**Homed**	**Recap**	**Homed**	**Recap**	**Homed**	**Recap**	**Homed**
Female	292	29	2	58	31	6	2	4	4	19	15	16	11	87 (29.8%)	48 (16.4%)
Male	394	66	15	101	39	10	6	7	3	13	7	9	5	143 (36.3%)	56 (14.2%)
Total	686	95	17	159	70	16	8	11	7	32	22	25	16	230 (33.5%)	104 (15.2%)

Note: Homed individuals were those turtles that were recaptured within previously calculated stream home range size for this population (i.e., 2.4 km of their original capture location for male or 4.6 km for females). An individual may have been counted in multiple years for recaptures and homed turtles if it was captured during those years.

TABLE 2 Total number of individual female and male northern map turtles (*Graptemys geographica*) that were translocated, recaptured, and successfully returned (i.e., homed) to their original home area from three different translocation site types (e.g., downstream, upstream, and tributary) following the Kalamazoo River oil spill on July 25 and 26, 2010.

		Downstream	Upstream	Tributary	Total individuals
Female	Translocated	143	74	75	292
	Recaptured	60	14	13	87
	Homed	28	10	10	48
Male	Translocated	227	90	76	394
	Recaptured	104	29	10	143
	Homed	33	20	3	56

Note: Downstream included sites where turtles were translocated within the Kalamazoo River downstream of the study site, upstream included sites where turtles were translocated within the Kalamazoo River upstream of the study site, and tributary included translocation sites where turtles were released within tributaries that were directly connected to the Kalamazoo River via lotic habitat. Recaptured turtles occurred between 1 day and 10 years after release while homed turtle captures occurred between 23 days and 10 years after release.

TABLE 3 Top five generalized linear model with a binomial distribution describing probability of recapture and probability of homing for northern map turtles (*Graptemys geographica*) translocated after the Kalamazoo River oil spill on July 25 and 26, 2010.

Type	Rank	Model[a]	*K*[b]	Δ AICc	*w*[c]	Log-likelihood
Probability of Recapture	1	Translocation km × Sex + Site	6	0.00	0.40	−351.38
	2	Translocation km × Site + Sex	7	1.28	0.21	−351.00
	3	Translocation km + Site	4	1.36	0.20	−354.09
	4	Translocation km + Sex + Site	5	2.27	0.13	−353.53
	5	Translocation km × Site	6	3.8	0.06	−353.27
	12	null	2	162.27	0.00	−437.57
Probability of Homing	1	Translocation km × Sex	4	0.00	0.44	−131.67
	2	Translocation km × Sex + Site	6	1.25	0.23	−130.19
	3	Translocation km + Sex	3	1.60	0.20	−133.50
	4	Translocation km + Sex + Site	5	2.97	0.10	−132.11
	5	Translocation km × Site + Sex	7	7.10	0.02	−131.77
	12	null	2	23.21	0.00	−158.37

[a] Predictor variables for each model. Translocation km is the river-distance between original capture location and translocation site. Site categories included a tributary connected to the Kalamazoo River, or downstream or upstream of the original capture location within the Kalamazoo River.

[b] Number of parameters.

[c] Akaike weight.

pooled all recaptures regardless of year and used a χ^2 proportion test to compare recapture rates between males and females. We modeled recapture probability using a generalized linear model with a binomial distribution and a logit link function, with translocation distance, sex, and translocation site (i.e., downstream, upstream, and tributary), and all two-way interactions as predictor variables (Table S1; Neter et al., 1996). Recapture probability models were ranked, and the best-supported model was chosen using Akaike's Information Criterion adjusted for small sample sizes (AICc; Anderson & Burnham, 2002). If ΔAICc <2, we assumed there was no difference between alternative models.

We calculated homing distance for each translocated turtle that was subsequently recaptured. We defined *homing distance* as the distance between an individual's original capture location and its subsequent recapture location; for individuals with multiple recaptures, we retained only the single, minimum distance for analysis. We used homing distance to determine whether an individual was recaptured within its potential home range (Figure 2): that is, if an individual's homing distance was less than the mean stream home range length for that sex, we categorized the individual as having homed.

We used a χ^2 proportion test to compare differences in homing rates between males and females, and to compare homing rates among the three translocation sites (i.e., downstream, upstream, and tributary). We modeled homing (i.e., whether or not a recaptured individual

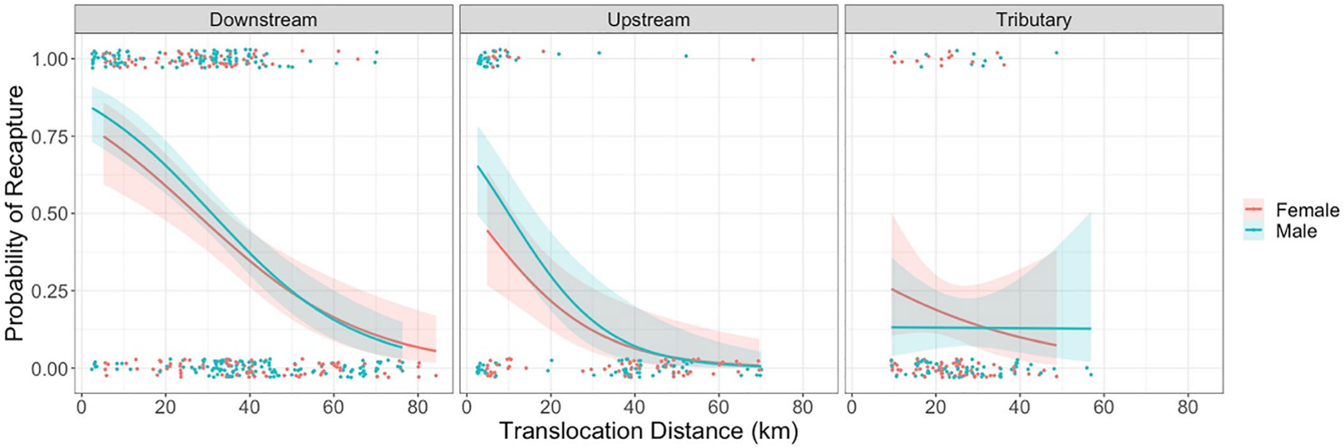

FIGURE 3 Probability of recapture by translocation distance in female (red) and male (blue) northern map turtles (*Graptemys geographica*) based on translocation site (i.e., downstream, upstream, and tributary) following the Kalamazoo River oil spill on July 25 and 26, 2010. Results are predicted by general linear models, with shading representing 95% confidence intervals. Individuals that were recaptured during subsequent surveys had a recapture probability of 1.0, while those not recaptured had a recapture probability of 0.0.

returned to its original home range following translocation) using a generalized linear model with a binomial distribution and a logit link function, modeled with translocation distance, sex, and translocation site, and all two-way interactions, as predictor variables (Table S1; Neter et al., 1996). Homing models were ranked, and the best-supported model was chosen as described above.

For each translocated individual that was subsequently recaptured, we calculated *travel distance*, which was defined as the distance between its translocation site and subsequent recapture location (Figure 2). For individuals with multiple recaptures, we calculated travel distance for each recapture event and retained only the single, maximum distance for each individual in analysis, which was considered the maximum known distance the individual had traveled. We used a *t*-test to compare male and female travel distances. Finally, we used analysis of variance (ANOVA) to compare travel distances among individuals released at three translocation sites (i.e., downstream, upstream, and tributary). When ANOVA results were significant, we used Tukey's HSD test for pairwise comparisons between sites.

3 | RESULTS

3.1 | Recapture

Overall, 686 northern map turtles were translocated to unfamiliar locations following the 2010 Kalamazoo River oil spill (601 in 2010 and 85 in spring 2011). We recaptured 230 (33.5%) of the 686 during subsequent surveys (Tables 1 and 2). Similar proportions of translocated males were recaptured (143 of 394; 36.3%) compared to females (87 of 292; 29.8%; $\chi^2 = 3.18$, d$f = 1$, $p = .07$). Most recaptures of translocated turtles occurred in 2011 (159 of 230; 69.1%; Table 1). A total of 82 individuals were recaptured in multiple years: 63 in two different years of this study, 13 in 3 years, 5 in 4 years, and 1 male in 5 years.

The strongest predictors of an individual being recaptured were translocation site and translocation

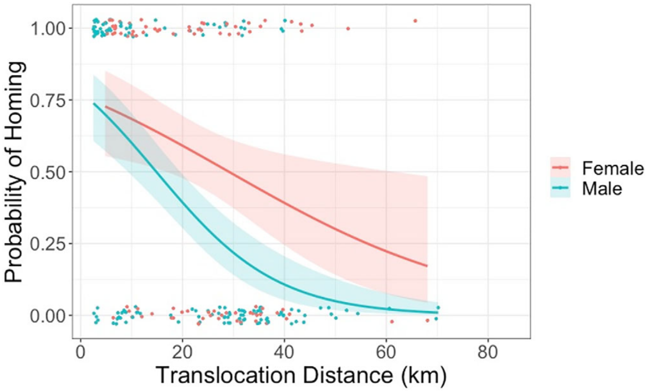

FIGURE 4 Probability of homing by translocation distance of female (red) and male (blue) northern map turtles (*Graptemys geographica*) following the Kalamazoo River oil spill on July 25 and 26, 2010. Results are predicted by the general linear models, with shading representing 95% confidence intervals. Individuals that were recaptured within the mean stream home range length (i.e., 2.4 km of their original capture location for males and 4.6 km for females) were defined as having homed, and therefore had a homing probability of 1.0, while those not recaptured within those distances had a homing probability of 0.0.

distance × sex interaction. Two additional models were also within two ΔAICc: the model including sex and translocation distance × site interaction, and the model including translocation distance and site (Table 3). The probability of recapture decreased with increasing translocation distance ($b = -0.05$, SE $= 0.01$, $z = -5.76$, $p < .01$; Figure 3), and recapture probability was highest from turtles translocated downstream of their original capture location (Figure 3).

3.2 | Homing

Homing was confirmed for 104 (45.2%; 48 females and 56 males) of the 230 northern map turtles recaptured in this study (Tables 1 and 2). That is, these 104 individuals had been translocated outside their original home ranges following the oil spill but were subsequently recaptured within 2.4 km (for males) or 4.6 km (for females) of their original capture location. Overall, 15.2% of translocated turtles were confirmed via recapture records to have homed, with 66% of these confirmations made in 2011 (i.e., within 1 year of the start of the spill response, and during ongoing habitat restoration efforts). We found that a higher proportion of recaptured females homed (55.2% of recaptured females and 16.4% of all translocated females) compared to males (39.2% of recaptured and 14.2% of all translocated males; $\chi^2 = 5.60$, d$f = 1$, $p < .02$; Table 2). Additionally, more recaptured turtles translocated upstream homed (69.8%) compared to turtles translocated to tributaries (56.5%) or downstream locations (37.2%; $\chi^2 = 15.91$, d$f = 2$, $p < .01$; Table 2). However, very few individuals translocated upstream greater than 20 km were recaptured (Figures 3 and 5).

The best-supported model predicting homing by translocated individuals included translocation distance × sex interaction. Two additional models were also within two ΔAICc: the model including translocation site and a translocation distance × sex interaction, and the model including translocation distance and sex (Table 3). The top three models predicted that probability of homing decreased as translocation distance increased ($b = -0.04$, SE $= 0.02$, $p = .02$ [top model]; Figures 4 and 5), while the top two models also predicted the probability of homing from greater translocation distances to be higher for females than for males ($b = -0.04$, SE $= 0.02$, $p = .05$ [top model]; Figures 4 and 5).

3.3 | Travel distance

Females traveled significantly farther ($n = 87$, 16.2 ± 15.8 km) than males ($n = 143$, 11.6 ± 12.2 km) after being translocated ($t_{148} = 2.31$, $p = .02$; Figure 6). In particular, two subadult females (8 and 10 years of age) traveled the farthest of any turtle in this study (65.9 and 72.4 km upriver, respectively), while the longest recorded travel distance by a male was 55.7 km upriver (Figure 6). We found differences among translocation sites in travel distance following translocation ($f_2 = 6.49$, $p < .01$), wherein turtles translocated to tributaries moved significantly farther ($n = 23$, 21.3 ± 8.4 km) than those translocated downstream ($n = 164$, 13.5 ± 14.7 km) or upstream ($n = 23$, 8.8 ± 10.4 km). In addition, we found that manmade obstacles may pose little

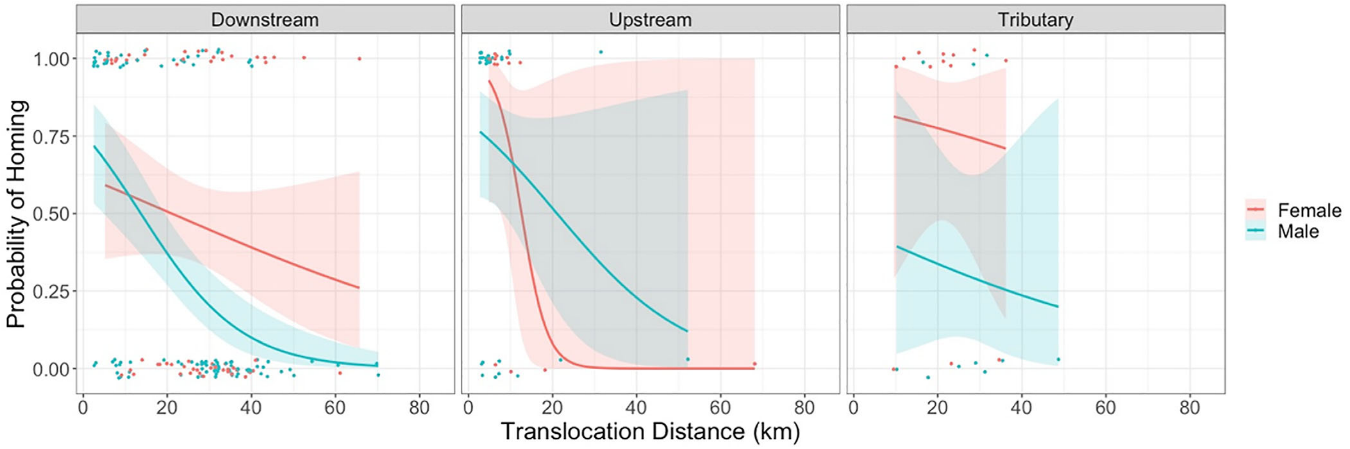

FIGURE 5 Probability of homing success by translocation distance in female (red) and male (blue) northern map turtles (*Graptemys geographica*) based on translocation site (i.e., downstream, upstream, and tributary) following the Kalamazoo River oil spill on July 25 and 26, 2010. Results are predicted by general linear models, with shading representing 95% confidence intervals. Individuals that were recaptured within the mean stream home range length (i.e., 2.4 km of their original capture location for males and 4.6 km for females) were defined as having homed, and therefore had a homing probability of 1.0, while those not recaptured within those distances had a homing probability of 0.0.

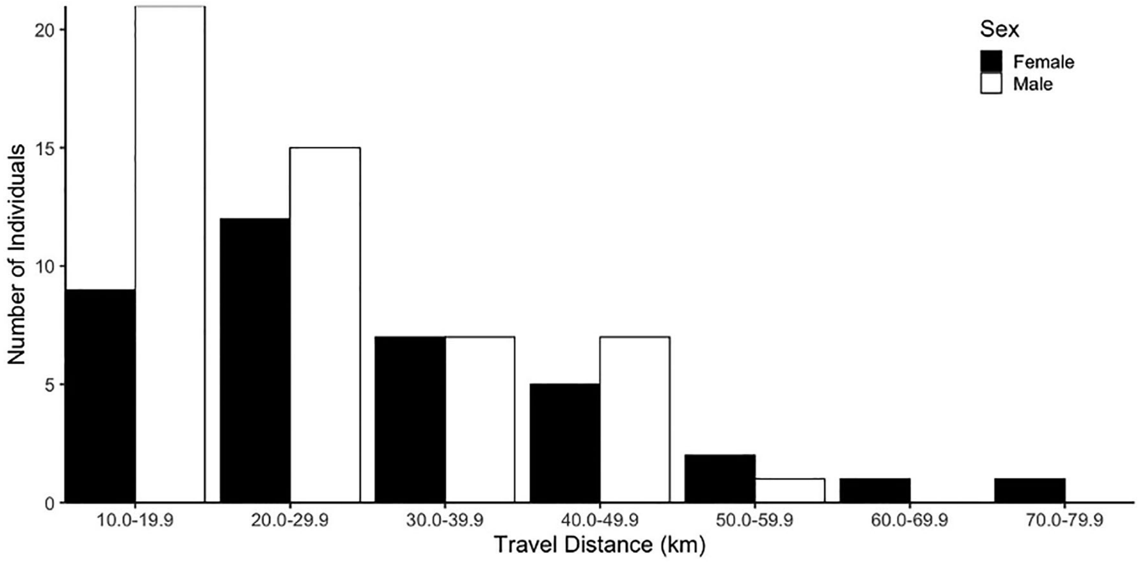

FIGURE 6 Maximum distances traveled by individual female and male northern map turtles (*Graptemys geographica*) following translocation due to the Kalamazoo River oil spill on July 25 and 26, 2010. Travel distance was calculated as the shortest distance between translocation site and any subsequent recapture location while staying entirely within the river channel. Maximum travel distances were calculated from recaptures occurring between 23 days and 10 years after release date.

to no barrier to travel for some individuals, as we observed that both sexes passed around or across spillways when traveling both upriver and downriver, as well as through the 1.4 km long concrete channel. Nearly, equal numbers of both sexes traveled upriver (22 females and 20 males) and downriver (11 females and 10 males) around at least one spillway following translocation.

4 | DISCUSSION

Predicting the success of a translocation project is challenging, as site-specific characteristics and species-specific behaviors may interact in complex ways to influence the overall outcome. In environmental disasters such as the 2010 Kalamazoo River oil spill, crisis-driven decisions such as whether and how to conduct translocations of impacted species may be poorly informed if there are few published reports detailing what was and was not successful in the past. In particular, determining a species' ability to home and the factors that influence homing can increase the effectiveness of translocation projects. Here, we demonstrated that 33% of northern map turtles translocated following the 2010 Kalamazoo River oil spill survived to be recaptured in subsequent surveys up to 10 years later. Moreover, 45% of these recaptured individuals homed back to their original capture site. While both sexes exhibited homing when translocated short distances from their capture location, homing probability decreased with increased translocation distances, although females were more likely to home from greater distances than were males. An important consideration for future translocation efforts, however, is that the considerable distances over which northern map turtles traveled in this study, as well as their ability to return to their original home ranges, means that translocated individuals of both sexes are likely to attempt to return to the area from which they were moved. Homing may be beneficial in situations where habitat has been temporarily rendered unsuitable, but it could be detrimental to a translocated population if the original home area is no longer habitable, or impermeable travel barriers exist to individuals attempting to return home.

In turtles, homing has been documented in the context of natal philopatry (Bowen et al., 2004; Freedberg et al., 2005; Valenzuela, 2001), nest site fidelity (Freedberg et al., 2005; Moore et al., 2020; Tucker & Lamer, 2008), hibernaculum fidelity (Graham et al., 2000; Sweeten, 2008), and experimental translocation (Attum et al., 2013; Attum & Cutshall, 2015; Otten & VanDeWalle, 2014; Roth & Krochmal, 2015). Evidence from these studies generally supports substantial capacity for homing under natural conditions or when individuals are translocated short distances (i.e., <5 km). Our study expands the spatial scale at which homing in turtles has been assessed and demonstrates that turtles can home over substantially greater distances than previously reported (i.e., >20 km in this study), and moreover can maneuver around manmade obstacles such as spillways. We confirmed that 15.2% of all translocated turtles subsequently returned home over a wide range of translocation distances, which is comparable to homing rates recorded in other turtle translocation studies. In particular, 11.8% of Alabama map turtle (*G. pulchra*) translocated 24 km returned after 1–3 years (Shealy, 1976), and 19.1% of desert tortoises translocated up to 5 km returned within 180 days (Hinderle et al., 2015).

In species with strong site fidelity, individuals attempting to return to their home areas after being translocated over longer distances would likely incur higher energetic costs and greater exposure to human threats, both of which likely increase mortality rates, compared to individuals translocated over shorter distances (Dickens et al., 2010; Finn & Stephens, 2017; Sullivan et al., 2014). Potential links to familiar feeding grounds, hibernacula, or mating opportunities may drive both sexes to travel long distances to return to their original home range. However, in our study, these resources were presumably readily available at all translocation release sites, as the observation of other northern map turtles was a pre-requisite for an area to be approved as a translocation site. Therefore, a lack of resources at the translocation sites was unlikely to drive homing in the translocated turtles. Instead, many translocated turtles that we later recaptured were likely attempting to return to familiar home ranges. The distances traveled by many translocated turtles, and the physical obstacles they overcame, were likely energetically expensive and may have increased turtles' exposure to anthropogenic threats.

Although limited, survey effort occurred upriver and downriver of eight translocation sites (four in the tributary of Battle Creek and four in the upstream Kalamazoo River area). During 2018 and 2019, 50 survey days occurred over a 28.3 km stretch of Battle Creek. A portion of the tributary was surveyed during each survey day, including at least two translocation sites during each survey. Only one marked turtle was captured, an individual that had traveled from a release location on the Kalamazoo River. No individuals released at any of the four tributary translocation sites were recaptured within the tributary. Additionally, in 2020, 9.1 km of the Kalamazoo River containing four upstream translocation sites were surveyed 10 days. No marked turtles were captured during upstream surveys. No surveys occurred downstream of the study site where downstream translocation occurred.

Our results show that both sexes exhibit strong site fidelity after being translocated. In particular, three females and four males were recaptured <20 m from their original capture location after having been translocated >20 km following the oil spill. However, we observed differences in homing between the sexes based on translocation distance; namely, females were more likely to home from greater translocation distances than were males. Our results are consistent with other turtle translocation studies in that homing differs between sexes (Field et al., 2007; Nussear et al., 2012; Smar & Chambers, 2005). Taken together, studies on homing in turtles suggest that translocation projects should consider differences in homing between sexes, particularly in species with pronounced sexual dimorphism such as *Graptemys* species, where females are on average larger so longer travel distances may be expected. In addition, we found that female northern map turtles traveled significantly farther than males following translocation, including the longest recorded movement of any freshwater turtle species in the United States, wherein a subadult female (15.6 cm SCL) traveled 72.4 km upriver and around a 4.3-m tall active hydroelectric dam following translocation. A second subadult female (14.0 cm SCL) traveled 65.9 km upriver and around 2 spillways after being translocated. That both these long-distance homing movements occurred in subadults suggests that home range and ultimately homing ability develops in turtles before they reach sexual maturity. Similarly, the smallest male that successfully homed in this study was approximately 1 year old (5.9 cm SCL).

Although we observed no significant difference in the proportion of females and males that homed, any between-sex differences in homing and travel distances could result from females having strong fidelity to nesting sites. Female map turtles often travel long distances to nest in the same location from one year to the next (Freedberg, 2020; Freedberg et al., 2005; Nagle & Russell, 2020). In particular, female sea turtles migrate hundreds to thousands of kilometers among breeding, foraging, and nesting grounds, and exhibit natal philopatry to the beaches at which they hatched (Bowen et al., 1992; Plotkin, 2003). Alternatively, the greater distances over which female northern map turtles homed in our study may be due to females' increased physical ability to travel long distances compared to males, as females are substantially larger and likely stronger swimmers (Bodie & Semlitsch, 2000; Jones, 1996; Pluto & Bellis, 1986). Our results are consistent with other northern map turtle studies in which females were found to travel greater distances than males (Carriere et al., 2009; Pluto & Bellis, 1988).

We were unable to determine how quickly individuals returned to their original home ranges because our study design depended on incidental recaptures of marked turtles, and we did not physically track translocated individuals following their release. In other turtle species, homing occurred almost immediately in individuals translocated <2 km (Hinderle et al., 2015; Smar & Chambers, 2005). Based on incidental recapture data in 2010, we documented 17 individuals homing an average of 11.1 days after translocation. However, in a separate study, we radio-tracked female map turtles in this population to nesting sites and found that they regularly travel several kilometers in a single day, indicating that individuals may have the ability to home almost immediately if translocated near their original capture location. Here, most turtles that successfully homed were recaptured within a year of being translocated, and while some individuals were not recaptured until the 2018–2020 study period (i.e., 8–10 years after translocation), we presume they were present near their original home range but were not detected in earlier years of the study. We recommend that, during the design phase of translocation projects, managers should carefully consider where and when translocated individuals are to be released, particularly in the context of whether the goal of the project is to allow individuals to return to original capture locations, or to retain them permanently in the area to which they will be translocated.

Finally, as a caveat, we likely underestimated overall homing rate due to undetected mortalities or individual variation in home range size and detection rate. Female stream home range size ranged from 1.1 to 17.5 km, while that of males ranged from 0.5 to 6.4 km (Otten, 2022). Therefore, it is possible that individuals with relatively large home ranges may have actually returned to their original home range following translocation, but if we recaptured them farther from their original capture location than the population mean home range length, we would have classified them as not having homed. We have previously estimated that annual detection rates of both adult females and males in this population are ~66%, and annual mortality rates are <5% for adult females and <10% for adult males (Otten, 2022; Otten et al., 2022). Therefore, these detection rates likely mean that some translocated turtles that returned to their original home range were undetected, and therefore that our estimate of homing is conservative. Finally, any turtles that died after translocation would still have been included in our analyses as available for recapture, despite actually having been removed from the study population. Such undetected mortalities would have led us to underestimate the frequency of homing in this population.

Overall, our results demonstrate that if the goal of a mitigation-driven translocation project is for individuals to remain at the site to which they are translocated, the success of the effort may be impeded by individuals' homing behavior and their ability to move large distances out of a translocation site after release. Future research should determine the navigational mechanisms involved in homing, and whether hard versus soft release strategies change the likelihood of individuals attempting to home. Additionally, it is important to reiterate the importance of post-translocation monitoring regimes, conducted at a temporal scale appropriate for the species, to accurately assess the long-term success of translocation efforts. In situations where translocation is used as an emergency mitigation measure, responsible parties should demonstrate the effectiveness of translocation as a tool to achieve conservation outcomes. This process should involve transparency, clear conservation-oriented goals, follow-up monitoring and surveys, and data made publicly available; however, in the instance of rare or sensitive species, specific locality data may need to be obscured. This framework would ultimately provide future emergency or mitigation-driven translocations insight into potential success or failure.

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DATA AVAILABILITY STATEMENT

Data are available on request from the lead author, Joshua Otten (joshua.otten1@gmail.com).

ETHICS STATEMENT

All research was conducted in accordance with Michigan Department of Natural Resources scientific collection permits and University of Toledo's Institutional Animal Care and Use Committee (protocol # 108797).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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