

## REVIEW

# A systematic review of snake translocations to identify potential tactics for reducing postrelease effects

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**Article impact statement:** Eight tactics are identified that practitioners ought to consider when planning snake translocations to increase odds of a positive outcome.

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## Abstract

Advancements in the field of reintroduction biology are needed, but understanding of how to effectively conduct translocations, particularly with snakes, is lacking. We conducted a systematic review of snake translocation studies to identify potential tactics for reducing postrelease effects. We included studies on intentional, human-mediated, wild–wild, or captive–wild translocations to any location, regardless of motive or number of snakes translocated. Only studies that presented results for at least 1 of 4 outcomes (movement behavior, site fidelity, survival, or population establishment) were included. We systematically searched 4 databases for published studies and used 5 methods to search the gray literature. Our search and screening criteria yielded 121 data sources, representing 130 translocation cases. We quantified the association between 15 translocation tactics and short-term translocation outcomes by calculating odds ratios and used forest plots to display results. Snake translocations involved 47 species (from mainly 2 families), and most were motivated by research, were monitored for at least 6 months, occurred in North America, and took place from the 1990s onward. The odds of a positive snake translocation outcome were highest with release of captive reared or juvenile snakes, release of social groups together, delayed release, provision of environmental enrichment or social housing before release, or minimization of distance translocated. The odds of a positive outcome were lowest when snakes were released early in their active season. Our results do not demonstrate causation, but outcomes of snake translocation were associated with 8 tactics (4 of which were strongly correlated). In addition to targeted comparative studies, we recommend practitioners consider the possible influence of these tactics when planning snake translocations.

## KEYWORDS

displacement, head starting, population augmentation, relocation, repatriation, reptile, snake rescue, transplantation

## Resumen

La biología de la reintroducción requiere de avances; sin embargo, hay muy poco conocimiento sobre cómo realizar efectivamente las reubicaciones, particularmente las de las serpientes. Revisamos sistemáticamente los estudios sobre reubicación de serpientes para identificar las potenciales maniobras de reducción del estrés postliberación. Incluimos estudios sobre las reubicaciones a cualquier localidad que hayan sido intencionales, mediadas por humanos, de ambiente silvestre a ambiente silvestre o de cautiverio a ambiente silvestre sin importar el motivo o el número de serpientes reubicadas. Sólo incluimos

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estudios que presentaran resultados para al menos 1 de los cuatro resultados posibles: conducta de movimiento, fidelidad al sitio, supervivencia o establecimiento poblacional. Buscamos sistemáticamente en cuatro bases de datos de estudios publicados y usamos cinco métodos para buscar en la literatura gris. Nuestros criterios de búsqueda y revisión resultaron en 121 fuentes de datos, las cuales representaron 130 casos de reubicación. Cuantificamos la asociación entre 15 maniobras de reubicación y los resultados a corto plazo de las reubicaciones mediante el cálculo de la razón de probabilidades y usamos diagramas de efecto para mostrar los resultados. La reubicación de serpientes incluyó a 47 especies (principalmente de dos familias) y la mayoría estuvo motivada por la investigación, fue monitoreada durante seis meses (al menos), se ubicó en América del Norte y ocurrieron a partir de la década de 1990. La probabilidad de que la reubicación de serpientes tuviera un resultado positivo fueron mayores con la liberación de serpientes criadas o juveniles, la liberación de grupos sociales en conjunto, la liberación retardada, el suministro de enriquecimiento ambiental o alojamiento previo a la liberación o la reducción de la distancia de reubicación. Esta misma probabilidad fue menor cuando las serpientes fueron liberadas tempranamente durante su temporada activa. Nuestros resultados no demuestran causalidad, pero los resultados de la reubicación de serpientes estuvieron asociados con ocho maniobras (cuatro de las cuales contaban con una correlación sólida). Además de los estudios comparativos focalizados, recomendamos que los practicantes consideren la posible influencia de estas maniobras cuando se planifiquen la reubicación de serpientes.

#### PALABRAS CLAVE

aumento poblacional, desplazamiento, inicio ventajoso, rescate de serpientes, repatriación, reptil, reubicación, trasplante

#### 【摘要】

重引入领域需要进一步发展,但如何有效进行生物迁移仍存在知识空缺,特别是对蛇类的迁移。我们对蛇类迁地研究进行了系统性综述,以确定减少释放后影响的潜在策略。我们收集了所有地区有意的、人类介导的、野生-野生及圈养-野生的迁地研究,无论动机或蛇的数量。只有包含四个结果(运动行为、位点保守性、存活率、种群建立情况)中至少一个的研究才被纳入分析。我们系统地搜索了四个数据库中已发表的研究,并用五种方法搜索了灰色文献,最终获得121个数据源,代表了130个迁地案例。我们通过计算优势比量化了15种迁地策略和短期迁地结果之间的关联,并用森林图展示了结果。我们发现,蛇类的迁移涉及47个物种(主要来自2个科),大多数发生在北美、在20世纪90年代以后、出于研究的动机,且监测了至少6个月。在释放人工饲养的蛇或亚成体蛇、同时释放社会群体、延迟释放、在释放前提供环境丰富或遮蔽物,以及尽量减少迁移距离的情况下,产生积极结果的几率最高。当在蛇的活动季节早期释放,产生积极结果的几率最低。我们的结果并不能证明因果关系,但发现蛇类迁移结果与8种策略有关(其中4种强相关)。除了有针对性的比较研究外,我们还建议保护实践者在规划蛇类迁地项目时考虑这些策略可能产生的影响。【翻译:胡怡思;审校:聂永刚】

**关键词:** 爬行动物, 迁地, 强制迁移, 重新安置, 遣返, 增加种群, 有利开端, 蛇类救援

## INTRODUCTION

Conservation translocations are intentional human-mediated movements of organisms motivated by the urge to generate positive population-level conservation benefits (IUCN/SSC, 2013). These types of plant or animal movements are central to the emerging field of reintroduction biology, which is the study and practice of establishing populations of organisms through conservation translocations, the postrelease management of those populations, and the improvement of reintroduction techniques

(Armstrong & Seddon, 2008; Seddon & Armstrong, 2016). In an era of global biodiversity crisis, critical assessments and rapid advancements are essential. Seddon and Armstrong (2016) proposed 2 key questions to address ongoing challenges pertaining to population establishment (small population paradigm [Caughley, 1994]): how is establishment probability affected by size and composition of the release group and how are postrelease survival and dispersal affected by prerelease management (i.e., preconditioning) and postrelease management? The authors posed these questions in reference to all life forms,

yet their guidance is equally relevant to specific imperiled groups of animals, such as reptiles.

Reptiles are declining globally (Böhm et al., 2013), nationally (Lesbarrères et al., 2014), and locally (Choquette & Jolin, 2018), catalyzing the need for conservation translocations of some species. Kingsbury and Attum (2009) note that biologists lack a thorough understanding of how to conduct effective conservation translocations of snakes, propose a set of questions similar to those of Seddon and Armstrong (2016), and recommend research to develop snake-specific techniques that improve orientation, decrease adjustment period, and increase overwinter survival. Similarly, but from a more general perspective, the International Union for the Conservation of Nature's Species Survival Commission (IUCN/SSC) (2013) recommends that practitioners determine the most appropriate life stage for translocation, investigate the efficacy of prerelease conditioning techniques, and determine correlates between prerelease behavior and postrelease survival. Unfortunately, the urgent nature of many conservation translocations often precludes well-controlled and replicated studies, leading to difficulties in interpreting results from individual cases, and subsequently, in summarizing collective progress toward effective snake translocations.

At least 4 literature reviews that provide general guidance on how to improve snake translocations have been published (Dodd & Seigel, 1991; Ewen et al., 2014; Germano & Bishop, 2009; Sullivan et al., 2014). Yet, results from divergent groups of herpetofauna, such as turtles, crocodylians, and frogs, may not provide meaningful answers to specific translocation questions targeting snakes (a monophyletic squamate group [Pyron et al., 2013]) because of their differing life-history characteristics (Fitzgerald et al., 2018). Furthermore, snake translocations represented an average of only 19% (range of 4–33%) of all translocation studies included in the 4 reviews, and 2 of these reviews did not include results of mitigation translocations (e.g., removing snakes from human–snake conflict situations or from development sites (Germano et al., 2015; but see Cornelis et al., 2021). A systematic review explicitly targeting snake translocations is urgently needed to allow for a reevaluation of the prior snake-specific recommendations (Kingsbury & Attum, 2009), to address the paucity of snake studies included in past reviews of herpetofauna translocations, and to inform the ongoing need to improve captive husbandry and release techniques (Germano et al., 2014). We conducted a systematic review of the literature on snake translocation projects to clarify semantics, summarize important contextual factors and translocation tactics, identify potential tactics for reducing postrelease effects, and outline key avenues for future research. We asked the following questions: What is the current contextual state of snake translocations? Which snake translocation tactics are most commonly used and how frequently are key outcomes reported? And, which snake translocation tactics are correlated with reduced postrelease effects on movement behavior, site fidelity, survival, and population establishment?

## METHODS

To guide our literature review, we first identified and defined contextual factors and translocation tactics suspected of influencing snake translocation outcomes. Concurrently, we identified translocation outcomes most relevant to snakes and defined criteria for translocations that were either effective at reducing postrelease effects for each short-term outcome or had achieved population establishment. Following clarification of semantics, we conducted a systematic literature search and then extracted, synthesized, and analyzed relevant data for each distinct translocation case.

### Identification of contextual factors

Relevant contextual factors were identified and summarized to describe the current state of snake translocations and to better understand their potential confounding influence on our dataset. We focused on 7 contextual factors based on their potential correlation with snake translocation outcomes, or their relevance to our tactic and outcome definitions: species translocated, funding source, hibernation ecology, translocation motive, translocation type, decade of translocation, and duration of postrelease monitoring (Appendix S1). We also identified 4 other contextual factors of interest: IUCN region (IUCN, 2019), monitoring method (radiotelemetry, mark–recapture, or occupancy surveys), whether postrelease monitoring included the hibernation period, and whether a control group was used.

### Identification of translocation tactics

We followed the Translocation Tactics Classification System (TTCS) (Batson et al., 2015) to guide the selection, definition, and organization of tactics we deemed relevant in the context of influencing snake translocation outcomes (Table 1; Appendix S1). Translocation tactics are strategies carried out by a practitioner with regard to release individuals (biological tactics) or a release site (environmental tactics). We chose relevant translocation tactics presented in the TTCS and added some of our own, based on specific recommendations by Kingsbury and Attum (2009) and Dickens et al. (2010), and following insights gleaned from reviews of other vertebrate translocations (Beck et al., 1994; Dickens et al., 2010; Ewen et al., 2014; Germano & Bishop, 2009; Germano et al., 2015; Harrington et al., 2013; Seddon & Armstrong, 2016; Sullivan et al., 2014; Tetzlaff et al., 2019). Our chosen snake translocation tactics ( $n = 15$ ) were organized into 6 tactical groups (from Batson et al., 2015): animal selection, animal preconditioning, animal release design, environmental preconditioning, environmental release design, and postrelease environmental management (Table 1). We used Batson et al.'s (2015) definitions for specific tactics and tactical options because they distinguished between individual translocation tactics more specifically than other authors (Appendix S1).

**TABLE 1** Fifteen biological and environmental translocation tactics that may affect outcomes of snake translocations based on the Translocation Tactics Classification System (Batson et al., 2015) and organized by tactical group

Snake translocation tactic	Associated tactical option (copied from Batson et al., 2015)	Rationale
Animal selection		
Captive reared	Experiential selection: deliberate selection of individuals or groups from multiple candidates based on prerelease experiences	Beck et al., 1994; Germano & Bishop, 2009; Harrington et al., 2013; Houde et al., 2015; Kingsbury & Attum, 2009
Animal preconditioning <sup>a</sup>		
Environmental enrichment provided in captivity (subset of captive reared tactic)	Experiential preconditioning: deliberate alteration of environmental characteristics of the source environment prior to release	Dickens et al., 2010; Kingsbury & Attum, 2009; Seddon & Armstrong, 2016; Sullivan et al., 2014; Tetzlaff et al., 2019
Social groups held together in captivity (subset of captive reared tactic)	Social preconditioning: deliberate alteration of social relationships between individuals prior to release	Dickens et al., 2010; Skinner & Miller, 2020
Minimized time spent in captivity (wild-caught snakes)	Physiological preconditioning: deliberate alteration of physiological traits in individuals prior to release	DeGregorio et al., 2017; Dickens et al., 2010
Animal release design		
Maximized number of individuals released	Population size: deliberate selection of number of individuals included in a translocated cohort	Beck et al., 1994; Dickens et al., 2010; Fitzgerald et al., 2018; Frankham et al., 2004; Germano & Bishop, 2009; Miller et al., 2014; Seddon & Armstrong, 2016; Seddon et al., 2014
Released juvenile age classes	Demographic composition: deliberate control of the demographic make-up of a translocated population or cohort	Germano & Bishop, 2009; Hodges & Seabrook, 2019; Kingsbury & Attum, 2009; Seddon & Armstrong, 2016; Sullivan et al., 2014
Released female-biased sex ratio	Demographic composition: See above	Fitzgerald et al., 2018; Kingsbury & Attum, 2009; Seddon & Armstrong, 2016; Spellerberg, 1975
Released social groups together	Social composition: deliberate control of the social make-up of a translocated population or cohort	Amarello, 2012; Dickens et al., 2010; Sullivan et al., 2014
Environmental preconditioning		
Causes of decline or threats abated at release site	Prerelease threat control: deliberate control of threats in the recipient environment prerelease	Dickens et al., 2010; Ewen et al., 2014; Fitzgerald et al., 2018; Germano & Bishop, 2009; Kingsbury & Attum, 2009; Spellerberg, 1975
Public outreach or education conducted with local community	Prerelease threat control: See above	Beck et al., 1994; Ewen et al., 2014; Harrington et al., 2013
Environmental release design		
Minimized distance translocated from capture site (wild-caught snakes)	Spatial configuration: deliberate control of number and configuration of release sites	Dickens et al., 2010; Sullivan et al., 2014
Maximized time span of releases	Temporal configuration: deliberate control of number and configuration of release events	Beck et al., 1994; Harvey et al., 2014

(Continues)

TABLE 1 (Continued)

Snake translocation tactic	Associated tactical option (copied from Batson et al., 2015)	Rationale
Released early in the active season	Release timing: deliberate control of the timing of a release events	Dickens et al., 2010; King et al., 2004; Spellerberg, 1975; Sullivan et al., 2014
Temporary confinement at release site <sup>b</sup>	Delayed or immediate release: deliberate inclusion, exclusion and design of a holding period immediately preceding release	Dickens et al., 2010; Fitzgerald et al., 2018; Germano & Bishop, 2009; Harrington et al., 2013; Spellerberg, 1975; Tetzlaff et al., 2019
Postrelease environmental management		
Supplementary resources provided at release site <sup>b</sup>	Postrelease resource augmentation: deliberate augmentation of resources within the recipient environment postrelease	Dickens et al., 2010; Harrington et al., 2013; Spellerberg, 1975; Tetzlaff et al., 2019

Note. Definitions of outcomes and tactics are in METHODS and Appendix S1, respectively.

<sup>a</sup>Antipredator training (e.g., situations in which researchers actively attempt to condition this specific behavior through predator exposures) was excluded from the list because it is not commonly used for reptiles (Tetzlaff et al., 2019).

<sup>b</sup>We followed Batson et al. (2015) by categorizing temporary confinement at release site and supplementary resources provided at release site tactics as environmentally focused tactics, as opposed to animal-focused tactics (but see Armstrong & Seddon [2008]; Harrington et al. [2013], and Tetzlaff et al. [2019]). Postrelease environmental management can be conducted under an adaptive management approach, wherein manipulations occur over space and time in response to population needs (Armstrong & Seddon, 2008).

Although we initially included releases in suitable or similar environments as a tactic in the environmental selection tactical group (Appendix S1), this tactic was later removed from analyses due to inadequate data. Armstrong and Seddon (2008) promote the characterization of habitat at a release site based on presence of features necessary for survival and reproduction, as opposed to simply presence of specific vegetation types. Only about one half of our cases included enough information to gauge presence or absence of relevant habitat features at release sites. We therefore assumed all translocations were to sites with reasonable habitat quality and acknowledge that negative outcomes could have occurred due to poor-quality habitat.

### Identification of translocation outcomes

We focused our investigation on 3 short-term outcomes (movement behavior, site fidelity, and survival) (Appendix S1) that are considered part of the population establishment phase (Armstrong & Seddon, 2008; IUCN, 2013; Seddon & Armstrong, 2016). Short-term outcomes were chosen due to the temporary nature of most postrelease monitoring regimes for animals (e.g., <1 year on average [Tetzlaff et al., 2019]), the frequency with which these outcomes are reported (Harrington et al., 2013; Tetzlaff et al., 2019), the difficulty of measuring most long-term outcomes (Chauvenet et al., 2013; Seddon et al., 2014), and because postrelease effects (i.e., short-term increases in mortality or dispersal above normal associated with the translocation process [Armstrong et al., 2017]) have been detrimental in some snake reintroductions (Kingsbury & Attum, 2009). Animal health, welfare, or stress levels were excluded as outcomes because they are rarely reported (Harrington et al., 2013). We initially included one long-term outcome, population establishment, in our data collection because it is a major goal of translocation projects (Chauvenet et al., 2013; Ewen et al., 2014) (Appendix S1); however, it was rarely reported in the literature.

### Definition of postrelease effects

We assumed postrelease effects on short-term survival when  $\leq 50\%$  of snakes survived within 1 year after translocation. Given that the average annual survival rate in wild snakes is  $>50\%$  (Pike et al., 2008), then a survival rate for translocated snakes below this rate was presumed to be influenced by postrelease effects (Appendix S1). Similarly, we assumed postrelease effects on short-term site fidelity when  $\leq 50\%$  of snakes remained at the release site within 1 year after translocation because only snakes remaining at the release site can contribute to the local population (Appendix S1). Next, we assumed postrelease effects on short-term movement behavior when translocated snakes had larger home ranges or movement distances than nontranslocated conspecifics (Appendix S1). We assumed that a lack of postrelease effect on survival, site fidelity, or movement behavior was indicative of positive translocation outcomes. In some cases, only a portion of released snakes were monitored (e.g., via radiotelemetry), and those outcomes were based on a subsample of released snakes. We did not assess cases for which only recapture rates (e.g., snakes monitored using mark–recapture methods) were reported because of the confounding of survival and site fidelity and to avoid comparing outcomes generated using dissimilar monitoring techniques.

### Literature searches

We conducted systematic literature searches in 4 academic databases (Scopus, Web of Science, ProQuest, and Google Scholar). We also conducted supplementary searches for gray literature to ensure a comprehensive search strategy that maximized the inclusion of peer-reviewed and unpublished sources on snake translocations. Supplementary searches were conducted to address the bias in the peer-reviewed literature toward publishing results from successful translocations

(Miller et al., 2014; Paez, 2017). Accordingly, our potential data sources were varied and included articles in peer-reviewed journals, book chapters, conference proceedings, undergraduate and graduate theses and dissertations, reports by government and nongovernment agencies, herpetological newsletters, and unpublished data summaries. Although we identified a planned protocol for searching, screening, and data extraction (including detailed definitions and criteria) a priori, the protocol was not peer reviewed, registered, or published beforehand (see Haddaway et al., 2020), and some definitions needed to be adjusted during data extraction in response to the varying levels of detail presented in all sources.

Literature searches occurred from January to December 2020. We followed search strategy and selection protocols based on the PICO (population, intervention, comparator, outcome) framework (e.g., Slodowicz et al., 2019). We identified preliminary search terms by reading reintroduction and translocation review papers, particularly those focused on herpetofauna (e.g., Armstrong & Seddon, 2008; Dodd & Seigel, 1991; Ewen et al., 2014; Germano & Bishop, 2009; Germano et al., 2014). Our search terms were grouped into the PICO categories and then assessed individually for their relevance to the research topic (Appendix S2). Terms in each category were linked by the Boolean operator *OR*, whereas terms in separate categories (i.e., population, intervention, and outcome) were linked by the Boolean operator *AND* (Appendix S3). After preliminary searches (i.e., benchmarking in Web of Science), terms that were irrelevant, too vague, or redundant were removed from the search string, and exclusion terms were added using the Boolean operator *NOT* (Appendices S3 & S4). To increase comprehensiveness and relevance of the search string, preliminary search outputs were compared with a reference list of peer-reviewed snake translocation publications previously prepared by J.C. and with journal articles found incidentally during supplementary searches. The search string was refined as necessary.

Search options differed between databases and resulted in differences between fields searched (Appendix S3). The full search string was used in 3 databases (2 of which used category filters [e.g., Slodowicz et al., 2019]), whereas a simplified version of the search string was used in Google Scholar due to a more limited search interface (Appendix S3). Although searches in Google Scholar are not entirely repeatable (i.e., retrieved articles are not exactly the same or in the same order during subsequent searches) due to its broader search scope (i.e., full article), it was an effective database for capturing sources not available in the other databases. For the Google Scholar search, the first 150 hits were included and an incognito window was used to prevent previous search history from affecting the search.

We used 5 methods in our supplementary searches to retrieve additional sources not found during the database searches (Appendix S5). These sources were identified for possible inclusion by comparing their title, abstract, or both with our PICO criteria and were included for screening at the full text phase. Sources resulting from supplementary searches yielded a significantly different representation of publication types than the database searches (Fisher's  $p < 0.001$ ) and substantially

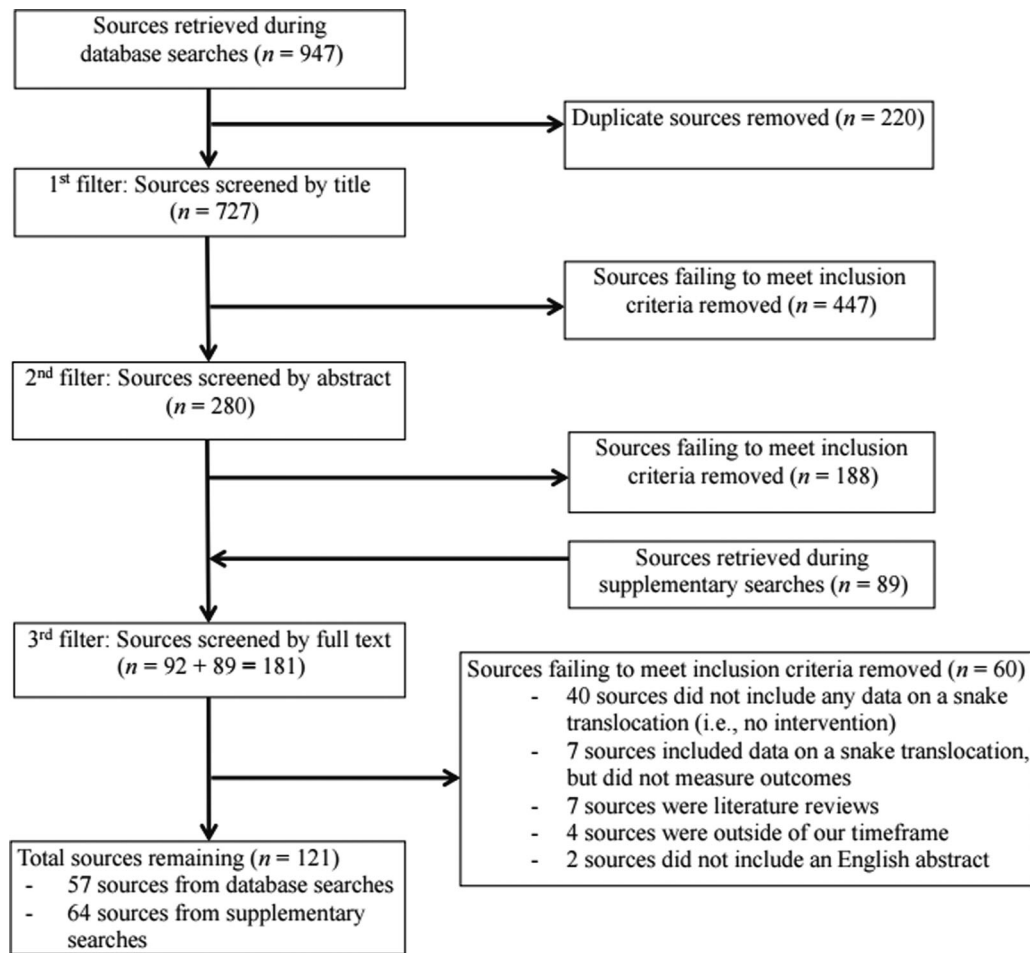
**TABLE 2** Number of sources and source types retrieved during a systematic review of the literature on snake translocations

Source type*	Number from database searches	Number from supplementary searches	Total sources
Journal article	43	7	50
Government or nongovernmental report (GL)	1	24	25
Thesis (GL)	9	8	17
Conference proceeding or presentation (GL)	1	9	10
Newsletter article (GL)	2	8	10
Book chapter	1	4	5
Unpublished data summary (GL)	0	4	4
Total sources	57	64	121

\*Gray literature (GL) as defined by greynet.org. Newsletter article includes sources published in periodicals that are not available in Web of Science or Scopus and not searchable on [www.journalguide.com](http://www.journalguide.com). Unpublished data summaries were provided by 3 researchers directly or indirectly. Seven published journal articles found during supplementary searches were not captured during database searches because these were unavailable in Web of Science and Scopus ( $n = 6$ ) or did not include an abstract ( $n = 1$ ). Conference proceedings and books in Web of Science were only available from 1990 to present and 2005 to present, respectively.

increased our source material from the gray literature (Table 2). Although technically not systematic in its approach, we believe our supplementary search methods are generally repeatable by experts because ~80% of the sources included in our study are publicly accessible online, in books, or through an institutional library (Appendix S5). Further, the inclusion of a large number of cases from the supplementary searches potentially increased representation of failed translocations, mitigation translocations, older studies, and long-term studies (Appendix S6).

The time span of sources included in our literature search was 1970–2019 (50 years). This time frame was chosen to coincide with the introduction of radiotelemetry techniques used to investigate snake ecology and behavior in the early 1970s (Újvári & Korsós, 2000) and captures the first published study on a snake translocation monitored through radiotelemetry (force feeding and abdominal implantation [Fitch & Shirer, 1971]). The time frame also overlapped with herpetofauna translocation reviews conducted by others, which is acceptable because snake translocations made up a small proportion of all reptile and amphibian translocations in previous review papers (4% [1 of 25] in Dodd & Seigel [1991], 13% [5 of 40] in Ewen et al. [2014], 25% [23 of 91] in Germano & Bishop [2009], and 33% [1 of 3] in Sullivan et al. [2014]). Only sources with at least the title and abstract in English were included because English is the dominant language of documents indexed in Web of Science and Scopus (Vera-Baceta et al., 2019).



**FIGURE 1** Screening process for a systematic review of the literature on snake translocations and the number of sources included in each stage

## Study inclusion criteria and article screening

All sources were compiled and organized using RefWorks. Duplicates were removed to create the main search record. Study inclusion and exclusion criteria were developed following the PICO framework, and all sources identified during literature searches were screened for relevance against these criteria (Appendix S2). Review articles were excluded during the abstract or full-text screening stage and were used as part of supplementary searches (Appendix S5). In general, sources were screened by title, then by abstract, and finally by full text (sources retrieved during supplementary searches were screened directly at full-text stage) (Figure 1). Title screening was generally completed following application of population-level PICO criteria, to avoid rejecting relevant articles too early, followed by intervention and outcome-level criteria at the abstract and full-text screening phases. To maintain consistency and avoid potential response biases, sources were screened independently by J.C. and J.G. These authors discussed inconsistencies until a mutually agreed upon decision was made to exclude or include a particular source based on the established PICO criteria. Sources of broad relevance at any stage (e.g., fauna, reptiles) were included in the subsequent stage or stages. We retained

sources that were not translocation studies themselves only if they included relevant details on a translocation presented in another source.

Our search and screening criteria yielded 121 unique sources (57 from database searches and 64 from supplementary searches) (Figure 1; Table 2). Journal articles and book chapters made up the majority of sources from the database searches (77%), whereas gray literature made up the majority of sources from the supplementary searches (83%). Among all sources, we identified 130 independent snake translocation cases (i.e., sampling units). A snake translocation case was considered an independent event for the purpose of analysis (regardless of the number of snakes in the translocated group) if one or more of these variables was distinct from other cases: release site, authors, species, study question or purpose, or translocation method or tactic. When multiple sources provided data on the same translocation case, these data were combined to yield a more complete picture of that case; however, it was still treated as single sampling unit. Alternatively, a single source may have provided data on multiple independent cases. For example, if a translocation study compared outcomes of 2 groups of snakes released using different tactics (e.g., delayed release group vs. immediate release group), we considered each

group to represent an independent case (i.e., 2 cases from one source). In such instances, we assumed the outcomes of one treatment group did not significantly alter the outcomes of the other treatment groups. We considered 2 or more treatment groups from a single study as independent cases because our goal was to determine which tactics were correlated with a lack of postrelease effects (e.g., survival >50%) and because many cases (42%) were not part of a comparative study but did report on translocation outcomes.

## Data extraction

For each independent snake translocation case, we assigned a unique identification code and name, recorded citation, title, and publication type of source or sources, included a one-sentence summary of purpose and methods, and organized relevant data based on 3 broad categories: contextual factors, translocation tactics, and translocation outcomes. Data categories were further subdivided for the purposes of record keeping (e.g., 15 data columns for the translocation tactics category). Data were systematically extracted by J.G., who independently scanned each source and transcribed detailed information relevant to the context, tactics used (Table 1), and outcomes measured for each case. Most data subcategories for tactics and outcomes were identified a priori, whereas some contextual factors were identified and recorded later in the extraction process. Data were compiled in a spreadsheet and were subjected to quality control (opportunistic for contextual factors; systematic for tactics and outcomes) by J.C. prior to synthesis and analysis in an effort to reduce errors. A basic critical appraisal plan was conceptualized at this stage (outcome level [Appendix S6]) and completed after the analyses to look for potential sources of bias. It did not involve scrutinizing sources beyond initial inclusion criteria.

## Statistical analyses

To measure the association between each translocation tactic and translocation outcome, we calculated odds ratios (ORs) (program R epitools package, `oddsratio` function), and results were displayed using forest plots. ORs (Szumilas, 2010) are frequently used in the medical literature, but they are a sound approach for comparing proportions in ecological studies (e.g., Jones & Peery, 2019; Rita & Komonen, 2008). Translocation tactics for each case were standardized into a binary data format based on whether a particular tactic was clearly used (i.e., used or not used [Appendix S1]). Some tactics were not applicable to certain cases (coded as NA, which program R equates with a blank cell) (Appendix S1), and these were excluded from analyses as appropriate. If the use of a tactic was not indicated in source material, it was assumed to have not been used. Outcomes for each case were also standardized into a binary data format based on the average results for the translocated group of snakes (i.e., yes for positive outcomes, no otherwise [see METHODS]) (Appendix S1). No binary outcomes were identified if telemetry data were unavailable, results

were not quantified or unclear, or if an outcome was not measured (also coded NA), and cases with no results for an outcome were excluded from that particular analysis. A different subset of cases was included in each analysis (due to inconsistent data availability for each case); therefore, relationships between tactics and outcomes may not be representative of all snake translocations as synthesized (Tables 3 & 4).

Binary data for each tactic were plotted in 2-way contingency tables against the binary yes–no outcomes for all relevant cases (15 tactics and 3 outcomes = 45 tables). Each translocation case was assumed to be an independent replicate for each relevant tactic; a case may have used multiple tactics, and was therefore included in multiple analyses for the same outcome. Sample sizes for each analysis reflected the number of translocation cases, not the number of snakes translocated. The OR for each paired tactic and outcome represented the odds that a particular tactic (e.g., release of juvenile age class) was associated with a positive outcome (e.g., survival >50%) divided by the odds that the tactic was associated with a negative outcome (e.g., survival ≤50%). Predictions for each paired tactic and outcome ( $n = 45$ ) were generated independently by J.C. and J.G. a priori (Appendix S7), and then inconsistencies ( $n = 6$ ) were discussed until all predictions were mutually agreed upon.

ORs, 95% CIs, and  $p$  values were calculated in R for each paired tactic and outcome with 2 methods: unconditional maximum likelihood estimation with one fixed margin (Wald) and small sample-adjusted unconditional maximum likelihood estimation (small). The Wald and small methods use normal approximation for confidence intervals and allow for the Haldane–Anscombe correction (i.e., the addition of 0.5 to all cells of those  $2 \times 2$  tables containing at least 1 “zero cell”). Results are reported only for the small method because it accounts for small samples and returns conservative results (Ruxton & Neuhauser, 2013). We report  $p$  values from the Fisher’s exact test (FET) because it is recommended for small sample sizes (e.g., when some expected numbers in a table are <1) and is more conservative than the 2 other  $p$  values resulting from the small method (Campbell, 2007; McDonald, 2014). Although FET was designed for studies with fixed margins, it provides more conservative estimates for studies such as ours with no fixed margins (i.e., when neither of the total values of the rows or columns in a contingency table are fixed as part of the experimental design [McDonald, 2014]). An FET requires the assumption that the individual observations (in this case, each translocation case) are independent (McDonald, 2014). A Bonferroni correction was applied to detect false positives (Appendix S6).

## RESULTS

### Synthesis of contextual factors

In our cases, 47 species of snakes were translocated, with a bias toward vipers and colubrids and 3 species (Table 3; Appendix S8). Translocations occurred in 17 countries, across 7 regions (IUCN [2019] regions); the majority were reported



**TABLE 3** Summary of main contextual factors among all snake translocation cases ( $n = 130$  or relevant subsample of cases) included in a systematic literature review of such translocations\*

Snake translocation contextual factor	Proportion of cases (number of cases, total number of cases)
Translocations of viperids or colubrids	0.88 (114, 130)
Translocations of eastern massasauga ( <i>Sistrurus catenatus</i> ), eastern indigo snake ( <i>Drymarchon couperi</i> ), or timber rattlesnake ( <i>Crotalus borridus</i> )	0.32 (41, 130)
Translocations in North America and the Caribbean IUCN region	0.78 (101, 130)
Translocations in either the 1990s, 2000s, or 2010s	0.74 (99, 133)
Outcomes monitored using radiotelemetry	0.60 (78, 130)
Outcomes monitored using mark–recapture	0.52 (68, 130)
Outcomes monitored using occupancy	0.11 (14, 130)
Control group monitored (resident or nontranslocated)	0.48 (63, 130)
Motivated by research	0.57 (74, 130)
Motivated by conservation	0.32 (41, 130)
Motivated by mitigation	0.12 (15, 130)
Translocations to sites occupied by conspecifics	0.65 (84, 130)
Conservation translocations to sites unoccupied by conspecifics (i.e., reintroductions)	0.93 (38, 41)
Translocations of populations that undergo seasonal hibernation	0.85 (111, 130)
Monitoring of populations that undergo seasonal hibernation overlapped hibernation period	0.79 (88, 111)
Monitoring occurred for >6 months	0.83 (107, 129)
Monitoring occurred for >12 months	0.64 (83, 129)
Government funded	0.43 (134, 313)
Nongovernmental or private organization funded	0.32 (101, 313)
University, zoo or aquarium, or unspecified funder	0.28 (78, 313)

\*Some cases included multiple methods to monitor outcomes. For translocation decade, 3 cases spanned 2 periods. Populations that undergo seasonal hibernation included snakes in milder temperate zones that seek specific underground shelters in winter but remain active on warm days. One case did not specify length of monitoring. Source of funding based on total number of funders and funders were not specified in 12 cases.

**TABLE 4** Prevalence of 15 snake translocation tactics among all translocation cases ( $n = 130$  or relevant subsample of cases) included in a systematic literature review of snake translocations

Snake translocation tactic <sup>a</sup>	Proportion of cases using the tactic <sup>a</sup> (number of cases, total number of cases)
Captive reared <sup>b</sup>	0.51 (44, 87)
Environmental enrichment provided in captivity	0.30 (13, 44)
Social groups held together in captivity	0.41 (18, 44)
Minimized time spent in captivity	0.35 (30, 85)
Maximized number of individuals released	0.44 (38, 87)
Released juvenile age classes	0.70 (91, 130)
Released female-biased sex ratio	0.16 (14, 87)
Released social groups together	0.32 (41, 130)
Causes of decline or threats abated at release site	0.58 (63, 109)
Public outreach or education for local community	0.42 (46, 109)
Minimized distance translocated	0.19 (16, 85)
Maximized time span of releases	0.45 (30, 66)
Released early in the active season	0.42 (47, 111)
Temporary confinement at release site	0.12 (15, 130)
Supplementary resources provided at release site	0.12 (15, 130)

<sup>a</sup>Definitions of each tactic and, if applicable, descriptions of relevant subsamples are in Appendix S1.

<sup>b</sup>The majority (92%) of cases with captive reared snakes involved translocations of colubrids or viperids; however, colubrids dominated the subsamples of cases with either environmental enrichment in captivity (92%) or social groups in captivity (78%).

from the North America and the Caribbean region. Translocations occurred in each decade from the 1960s to the 2010s; most occurred from the 1990s onward. Translocations were monitored predominantly with radiotelemetry or mark–recapture; however, a control group was not consistently used. Research was the dominant translocation motive. Mitigation and conservation were secondary motives in 38% and 34% of research translocations, respectively. Most snake translocations were monitored for at least 6 months (median = 24.0 months; range = 0.5–324.0 months) from first translocation to cessation of all monitoring activities. Snake translocations were funded by governments, nongovernmental and private organizations, universities, and zoos and aquariums (mean = 2.6 funders/case; range = 1–10) (Table 3).

### Synthesis of translocation tactics

Three or 4 translocation tactics, on average, were used per case (range = 0–10; mean = 4; median = 3). Of the cases using captive reared snakes, an average of 5 tactics were used per case (including captive reared) (range of number of tactics = 2–9). The 3 most common translocation tactics were release of juve-

**TABLE 5** Translocation outcomes synthesized as part of a systematic review of the literature on snake translocations

Translocation outcome	Positive cases (%)*	Negative cases (%)	Total applicable cases	Proportion of total applicable cases by taxonomic group (colubrid, viperid, other)
Movement behavior	37 (55)	30 (45)	67	0.30, 0.58, 0.12
Site fidelity	31 (63)	18 (37)	49	0.33, 0.55, 0.12
Survival	42 (62)	26 (38)	68	0.34, 0.56, 0.10

\*Cases without postrelease effects (see METHODS).

nile snakes (70% of all cases), choosing a release site where the causes of decline or threats were abated (58% of relevant cases), and release of captive reared snakes (51% of relevant cases). The 3 least common tactics were release of female-biased cohorts (16% of relevant cases), provisioning of supplementary resources at the release site (12% of all cases), and temporary confinement of snakes at the release site (i.e., delayed release) (12% of all cases) (Table 4).

## Synthesis of translocation outcomes

Relevant data were available to evaluate at least one short-term translocation outcome in 58% of cases ( $n = 76$ ), whereas outcomes were not determined in 42% of cases (54 cases that presented mark–recapture data only or in which radiotelemetry was used but provided insufficient data). Out of the cases with relevant data ( $n = 76$ ), we were able to evaluate posttranslocation movement behavior (hereafter movement), site fidelity (hereafter fidelity), and survival outcomes in 88%, 66%, and 89% of cases, respectively (Table 5), whereas all 3 outcomes could only be gauged in 54% of cases ( $n = 41$ ). Other short-term outcomes we identified incidentally were broadly categorized as, but not limited to, the following: mark–recapture rates, time between recaptures, exposure frequency, hibernation ingress or egress dates, habitat use or behavior, and growth or body condition. Less than one third (31%) of all cases monitored translocated snakes for over 3 years (regardless of monitoring methods used), and 28% of cases met all the criteria for us to evaluate population establishment. We were able to evaluate both short- and long-term outcomes in only 5% of cases. As a result, the population establishment outcome was excluded from further analyses.

## Correlates of positive translocation outcomes

The odds of a positive movement outcome were highest (and strongly associated) with the use of one of 4 translocation tactics: releasing captive reared snakes ( $n = 39$ ,  $p < 0.001$ , OR = 17.14 [95% CI: 3.89–177.42]), releasing juvenile snakes ( $n = 67$ ,  $p < 0.001$ , OR = 8.46 [2.07–70.97]), releasing social groups together ( $n = 67$ ,  $p = 0.001$ , OR = 4.71 [1.86–16.11]), and temporary confinement of snakes at the release site ( $n = 67$ ,  $p = 0.002$ , OR = 6.55 [1.29–88.88]) (Figure 2). The odds of a positive fidelity outcome were highest with the tactic of releasing captive reared snakes ( $n = 32$ ,  $p = 0.049$ , OR = 3.89

[1.04–28.71]) (Figure 3). Finally, the odds of a positive survival outcome were highest with the use of one of 3 translocation tactics: housing captive reared snakes in social groups ( $n = 26$ ,  $p = 0.036$ , OR = 4.81 [1.06–55.51]), providing environmental enrichment to captive reared snakes ( $n = 26$ ,  $p = 0.051$ , OR = 3.81 [0.99–30.56]), and minimizing distance translocated for wild snakes ( $n = 42$ ,  $p = 0.037$ , OR = 3.82 [0.73–56.28]) (Figure 4). Conversely, the odds of a positive survival outcome were lowest with the tactic of releasing snakes early in the active season ( $n = 62$ ,  $p = 0.038$ , OR =  $3.70^{-1}$  [0.27; 0.11–0.95]) (Figure 4). None of the significant relationships between tactics and the site fidelity or survival outcomes were particularly strong (Appendix S6).

Cases with positive movement outcomes that used either of 3 tactics, releasing social groups together ( $n = 22$ ), releasing juvenile age classes ( $n = 14$ ), or temporary confinement at release sites ( $n = 9$ ), were biased toward captive reared snakes (77%, 93%, and 78%, respectfully) and 2 species (eastern massasauga [*Sistrurus catenatus*] and smooth green snake [*Opheodrys vernalis*]) (50%, 57%, and 44%, respectfully). Further, 95% of cases in which captive reared snakes were used and that had either positive movement or fidelity outcomes ( $n = 20$  and 15, respectfully) used at least one of the 3 tactics listed above.

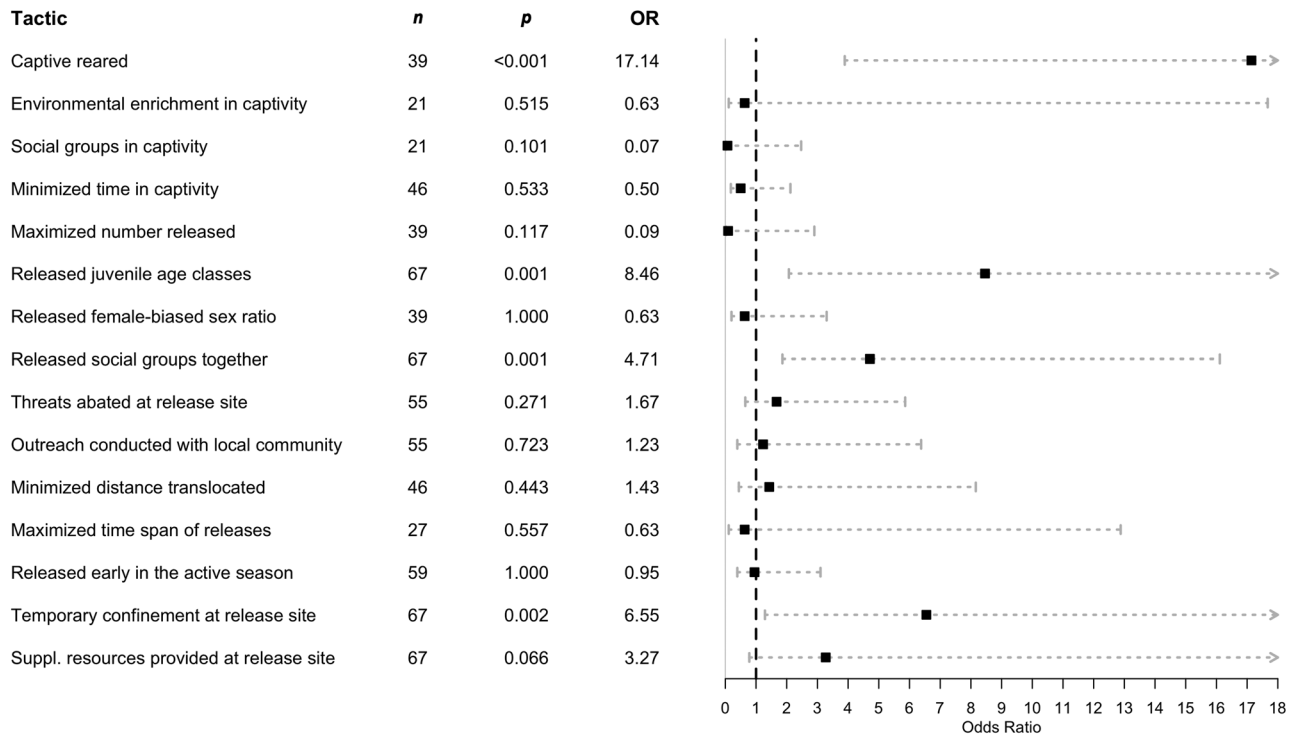
Cases with positive survival outcomes that did not use the tactic of releasing early in the active season ( $n = 20$ ) were dominated by translocations of vipers or colubrids that were released from midsummer to fall (75%; the remainder involved releases throughout the active season). All cases that minimized translocation distance (i.e., short distance translocations [SDT]) and presented sufficient outcome data had positive survival outcomes ( $n = 8$ ), whereas almost half (41%) of the cases that did not minimize translocation distance (i.e., long-distance translocations [LDT],  $n = 34$ ) had negative outcomes. Of the cases with positive survival outcomes that provided environmental enrichment to captive reared snakes ( $n = 8$ ), most provided a simulated hibernation period (75%) or involved colubrids (88%). Of the cases with positive survival outcomes that housed captive reared snakes in social groups ( $n = 7$ ), most also translocated snakes in social groups (86%).

## DISCUSSION

### Animal selection and preconditioning

Translocations of captive reared snakes were 17.1 times more likely to have had a positive movement outcome and

## Translocation Tactics and Movement Behaviour



**FIGURE 2** Odds ratios (OR) (95% confidence interval) for each of 15 translocation tactics and positive movement behavior outcomes for translocation cases identified in a systematic review of the literature on snake translocations. We calculated the OR for each tactic using a relevant subset of cases from a larger database ( $n = 130$ ).

3.9 times more likely to have had a positive fidelity outcome than similarly motivated translocations of wild snakes. Regardless, we could not exclude the possibility that positive movement and fidelity outcomes (e.g., due to reduced movements) were at least partially the result of snakes being in poor body condition. For example, captive rearing can contribute to unintended changes in morphology or behavior of snakes (e.g., Degregorio et al., 2013, 2017; Ryerson, 2020) that may negatively affect short-term survival after release.

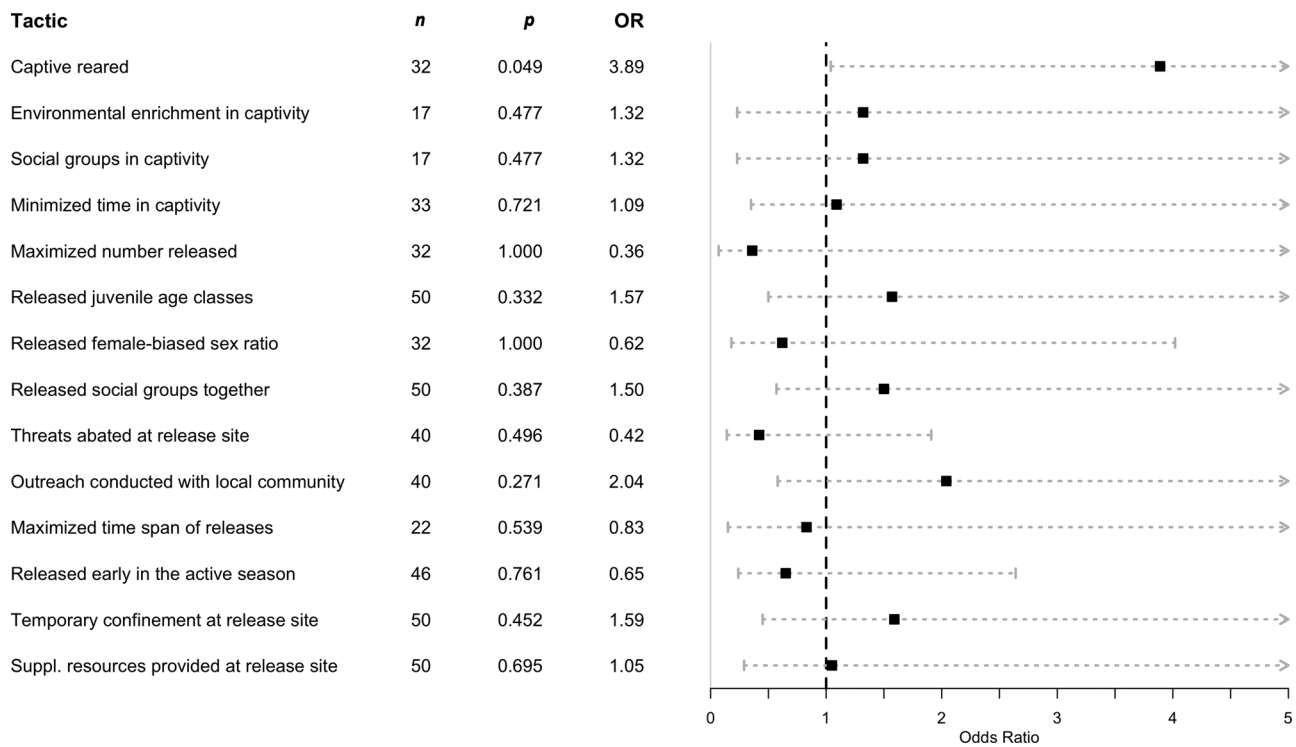
Our results suggest that cases of captive reared snakes that were provided environmental enrichment or communal housing in captivity prerelease were 3.8 and 4.8 times more likely, respectfully, to have had a positive survival outcome than translocations not using these tactics. Recent investigations with both captive garter snakes (Skinner & Miller, 2020) and wild rattlesnakes (Amarello, 2012) identified distinct patterns of social interaction between individual snakes. Perhaps the provisioning of captive snakes with the opportunity to interact with conspecifics reduces chronic stress (Dickens et al., 2010) or familiarizes them with scent trails (Mason & Parker, 2010), resulting in improved survival prospects after release. Although our definition of enrichment was broad (Appendix S1), results from 3 comparative studies with colubrids suggest that the provisioning of naturalistic conditions in captivity does not improve short-term survival outcomes postrelease (Degregorio et al., 2017; Roe et al., 2015), but that providing a simulated overwintering period might (Roe et al., 2015; Sacerdote-Velat

et al., 2014) (Appendix S9). In any event, the perceived benefits from release of captive reared snakes should be weighed against potential costs of disease transmission to wild counterparts (Jacobson, 1993; Schumacher, 2006).

### Animal release design

Regardless of source, translocations involving the release of social groups together or of predominantly juvenile snakes were 4.7 and 8.5 times, respectively, more likely to have had a positive movement outcome than translocations involving releases of snakes singly or nonjuvenile-biased translocations, respectfully. These results are consistent with recommendations by others (Cornelis et al., 2021; Germano & Bishop, 2009; Hodges & Seabrook, 2019; Sullivan et al., 2014), who suggest that translocations may be improved if social groups are moved together or if younger individuals are released (for species with strong homing tendencies because these have not yet established home ranges). In *Vipera berus*, neonate and juvenile snakes had little or no homing instinct for hibernation sites, but by the time they became subadults (2-year-olds), wintering areas became fixed (i.e., the site selected the second winter was returned to annually [Hodges & Seabrook, 2019]). Although we did not find a significant association between fidelity or survival and the tactic of releasing juvenile snakes, 4 comparative snake translocation studies provide preliminary evidence to suggest translocating older juveniles may improve survival posttranslocation (Bieser,

Translocation Tactics and Site Fidelity



**FIGURE 3** Odds ratios (OR) (95% confidence interval) for each of 15 translocation tactics and positive site fidelity outcomes for translocation cases identified in a systematic review of the literature on snake translocations. We calculated the OR for each tactic using a relevant subset of cases from a larger database (*n* = 130). Results for minimized-distance-translocated tactic are irrelevant because no cases with short-distance translocations were used in the site fidelity analysis (Appendix S1).

2008; King et al., 2004; Roe et al., 2015; Stiles, 2013) (Appendix S9).

**Environmental release design**

Short-distance translocations of wild snakes were 3.9 times more likely to have had a positive survival outcome than long-distance translocations of wild snakes. Although few cases used the tactic (*n* = 8) compared with cases that did not (*n* = 34), our results are consistent with results and recommendations in other reviews (Cornelis et al., 2021; Sullivan et al., 2014). Also, 4 comparative snake translocation studies provide evidence suggesting that wild subadult and adult rattlesnakes translocated short distances have higher survival rates, or survive for longer, in the short term than rattlesnakes translocated long distances (Black, 2019; Brown et al., 2008; Corbit, 2015; Sealy, 1997) (Appendix S9). We encountered some apparent confusion in the literature around the concepts of SDT and LDT, and we echo the recommendation by Corbit (2015) for a standardized definition of movement distances that are relative to an individual’s home range size.

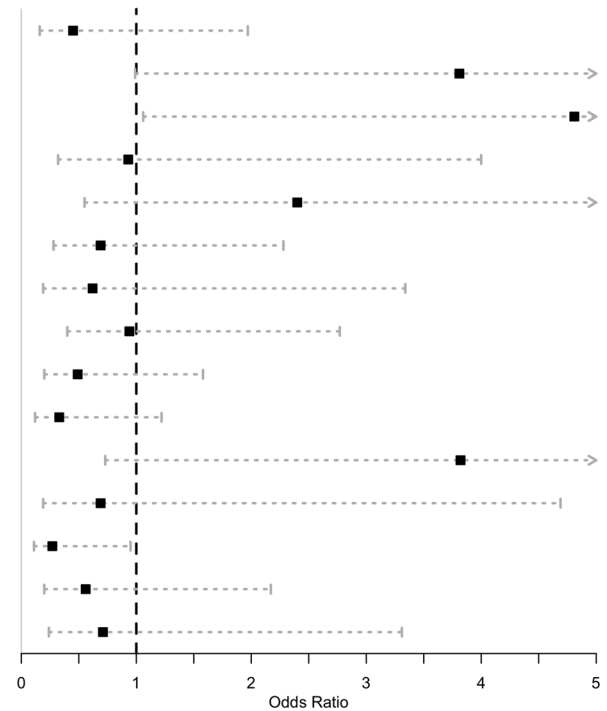
Translocations of hibernating snakes that took place predominantly in the early part of the active season (e.g., spring months) were 3.7 times more likely to have a negative sur-

vival outcome than translocations that did not explicitly use this tactic. This result was counter to our predictions as well as recommendations by others (Appendices S1 & S7). Regardless, 3 comparative translocation studies provide preliminary evidence that temperate rattlesnakes and garter snakes released in summer (July–August in the Northern Hemisphere) had lower mortality rates than snakes released in March through April (Jungen, 2018; King & Stanford, 2006) or September (King et al., 2004) (Appendix S9).

Translocations wherein snakes were temporarily confined at release sites (i.e., delayed release) were 6.6 times more likely to have had a positive movement outcome, than translocations with an immediate release. Although relatively few cases used the delayed release tactic (*n* = 9) compared with cases that did not (*n* = 58), our results are consistent with recommendations in 2 herpetofauna-focused literature reviews (Fitzgerald et al., 2018; Germano & Bishop, 2009). We gauged positive outcomes in reference to movement metrics of non-translocated resident snakes. Interestingly, 2 comparative studies with captive and wild (LDT) rattlesnakes both found no difference in movement metrics between snakes that were exposed to either an immediate release or held in pens for 1–2 weeks (Bieser, 2008; Josimovich, 2018; Appendix S9). Tetzlaff et al. (2019) suggest that delayed releases might be most beneficial for reducing movement in reptiles if held for much longer periods

## Translocation Tactics and Survival

Tactic	<i>n</i>	<i>p</i>	OR
Captive reared	42	0.518	0.45
Environmental enrichment in captivity	26	0.051	3.81
Social groups in captivity	26	0.036	4.81
Minimized time in captivity	42	1.000	0.93
Maximized number released	42	0.210	2.40
Released juvenile age classes	68	0.783	0.69
Released female-biased sex ratio	42	1.000	0.62
Released social groups together	68	1.000	0.94
Threats abated at release site	59	0.297	0.49
Outreach conducted with local community	59	0.135	0.33
Minimized distance translocated	42	0.037	3.82
Maximized time span of releases	33	1.000	0.69
Released early in the active season	62	0.038	0.27
Temporary confinement at release site	68	0.540	0.56
Suppl. resources provided at release site	68	1.000	0.71



**FIGURE 4** Odds ratios (ORs) (95% confidence interval) for each of 15 translocation tactics and positive survival outcomes for translocation cases identified in a systematic review of the literature on snake translocations. We calculated the OR for each tactic using a relevant subset of cases from a larger database ( $n = 130$ ).

than 2 weeks (e.g., 4–12 months in geckos and tortoises). Finally, although reviews of wildlife translocations suggest delayed releases can provide health and survival benefits for some animals (Dickens et al., 2010; Harrington et al., 2013; Tetzlaff et al., 2019), direct evidence for this in snakes is limited and conflicting (Josimovich, 2018; Sacerdote-Velat et al., 2014; Appendix S9).

## Population establishment

Although population establishment was excluded from our analyses due to limited data, some additional discussion of this topic is warranted. The fact that this long-term outcome could be evaluated in less than one third of all cases is primarily the result of it only being applicable to conservation and research–conservation translocations (Appendix S1), which eliminated 47% of cases upfront. Second, almost one half (46%) of the remaining applicable cases could not be evaluated as a result of an insufficient time spent monitoring translocations postrelease (Appendix S1). Regardless, and compared with the frequency with which we were able to evaluate short-term outcomes, the long-term monitoring data required to adequately evaluate population establishment of snake conservation translocations were generally lacking.

## Monitoring translocation outcomes

The importance of radiotelemetry for evaluating short-term outcomes of snake translocations is apparent, given its use in a large proportion of translocation cases, and its ability to provide direct measures of movement, fidelity, and survival outcomes that are comparable across studies. Benefits of radiotelemetry, however, should be carefully weighed against constraints on snake size and monitoring duration imposed by technological limitations, as well as the invasiveness of surgical implantation (e.g., Lentini et al., 2011; but see Lutterschmidt et al., 2012). Although mark–recapture methods were common among snake translocations, they present clear limitations regarding the direct estimation of short-term outcomes (e.g., distinguishing between mortality and lack of site fidelity in snakes that are not recaptured) and may be more suitable for evaluating long-term outcomes (see below). Occupancy surveys, although rarely used overall, were a common method among cases that evaluated population establishment. Presuming surveys are designed to detect individuals or signs of reproduction, are timed appropriately, and incorporate detection probabilities; occupancy surveys could be used to evaluate long-term binary translocation outcomes (see population establishment in Appendix S1). Evaluation of long-term population trajectory,

however, would require the addition of mark–recapture methods (Rodda, 2012), assuming generally low snake capture rates can be overcome.

## Limitations

Our current understanding of snake translocations and the use of various translocation tactics stem largely from a small number of published studies on colubrids or viperids, which hibernate seasonally, from one region (North America and the Caribbean) that occurred over the last 30 years. Therefore, insights gleaned from our review should be used with caution when applied to other genera from other regions. Further, our results do not represent an exhaustive overview of all snake translocations because results of many translocations are not published (Miller et al., 2014), and our review was limited to publications written in English. Nonetheless we believe we succeeded in assembling the largest collection of snake translocation studies (wherein monitoring was conducted) in a single review.

Additional limitations of a case–control study such as ours are imposed by the way outcomes are defined, data are extracted, coding is done, and results are analyzed. Alternative conclusions may have been generated had we chosen to analyze different outcomes, included outcomes from mark–recapture studies, or defined outcomes differently (Appendix S6). It is possible that some data in our sources were missed, that transcription errors occurred during data extraction, and that false presumptions were made when details were not clearly presented. Although 55% of our sources were from the gray literature, a rich source of data known to benefit systematic reviews (Paez, 2017), it is likely that some of our source material omitted relevant descriptive information (e.g., publications in peer-reviewed journals, wherein brevity is favored). We often assumed that a tactic was not used if it was not explicitly mentioned in source material, which would have biased our results toward false negatives, thus providing greater confidence when associations were observed. Our results showed correlations between translocations with positive outcomes and the use of certain translocation tactics; however, they do not demonstrate causation. Our findings nonetheless point to worthwhile avenues for additional comparative research on snake translocations.

## Future research

Kingsbury and Attum (2009) recommended that conservation efforts test a variety of methods to reduce postrelease effects, which were considered to be the main factors limiting effectiveness of snake reintroductions. Our results indicated that future comparative research on snake conservation translocations should specifically investigate the following: effect of prerelease conditioning (artificial hibernation and social housing) on postrelease survival of captive reared snakes; effect of age class on postrelease site fidelity and survival (e.g., late vs. early juveniles; adult vs. juvenile LDT); effect of release timing (seasonality) on postrelease survival; and effect of the length and

type of delayed release on movement behavior. Future comparative research on snake translocations should explicitly aim to avoid the prominent issues of confounding variables (lack of standardization), small sample sizes, and lack of replication. Future snake translocations (comparative or otherwise) should consider incorporating the methods necessary to evaluate both short- and long-term outcomes. Finally, a review of the snake translocation literature published in other languages (Amano et al., 2016) or that synthesizes results of mark–recapture research would complement our study.

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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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