

# Modeling strategies and evaluating success during repatriations of elusive and endangered species

B. Folt<sup>1</sup> , C. P. McGowan<sup>2</sup>, D. A. Steen<sup>3</sup>, S. Piccolomini<sup>4</sup>, M. Hoffman<sup>5</sup>, J. C. Godwin<sup>4</sup> & C. Guyer<sup>4</sup>

<sup>1</sup> Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL, USA

<sup>2</sup> U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences, Auburn University, Auburn, AL, USA

<sup>3</sup> Georgia Sea Turtle Center, Jekyll Island Authority, Jekyll Island, GA, USA

<sup>4</sup> Department of Biological Sciences and Auburn University Museum of Natural History, Auburn University, Auburn, AL, USA

<sup>5</sup> The Orianne Center for Indigo Conservation, Central Florida Zoo and Botanical Gardens, Sanford, FL, USA

## Keywords

detection probability; extinction; *Drymarchon couperi*; eastern indigo snake; population model; reintroduction; wildlife management.

## Correspondence

Brian Folt, School of Forestry and Wildlife Sciences, Auburn University, 602 Duncan Drive, Auburn, AL 36849, USA.  
Email: brian.folt@gmail.com

Editor: John Ewen

Associate Editor: Benedikt R. Schmidt

Received 18 March 2019; accepted 16 August 2019

doi:10.1111/acv.12537

## Abstract

Wildlife repatriation is an important tool to decrease extinction risk for imperiled species, but successful repatriations require significant time, resources and planning. Because repatriations can be long and expensive processes, clear release strategies and monitoring programs are essential to efficiently use resources and evaluate success. However, monitoring can be challenging and surrounded by significant uncertainty, particularly for secretive species with extremely low detection probability. Here, we simulated how alternative repatriation strategies influence repatriation success for the eastern indigo snake *Drymarchon couperi*, a federally-Threatened species that is currently being repatriated in Alabama and Florida. Critically, we demonstrate how observed population growth can differ from true population growth when detection probabilities are low and mark-recapture analyses are not an option. Specifically, we built a stochastic stage-based population model to predict population growth and extinction risk under different release strategies and use information from ongoing repatriations to predict success and guide future releases. Because *D. couperi* is difficult to monitor, we modeled how detection probability influenced perceptions of abundance and population growth by monitoring programs. Simulated repatriation strategies releasing older, head-started snakes in greater abundance and frequency created wild populations with decreased extinction risk relative to scenarios releasing fewer and younger snakes less frequently. Ongoing repatriations currently have a 0.23 (Alabama) and 0.61 (Florida) probability of quasi-extinction, but extinction risk decreased to 0.07 and 0.10 at sites upon achieving the targeted number of releases. Abundances observed under realistic detection thresholds for *D. couperi* did not always predict true population growth; specifically, we demonstrate that monitoring programs during repatriations of secretive species may indicate that efforts have been unsuccessful when populations are actually growing. Overall, our modeling framework informs release strategies to maximize repatriation success while demonstrating the need to consider how detection processes influence assessment of success during conservation interventions.

## Introduction

Wildlife repatriations (*sensu* Dodd & Seigel, 1991) have become an important conservation and restoration tool to increase the number of populations and decrease extinction probability of imperiled species, while also restoring ecosystem function at recipient sites (Soulé *et al.*, 2003; Seddon *et al.*, 2014). However, repatriations are difficult, laborious

and expensive processes, and success is not guaranteed (Dodd & Seigel, 1991). To increase the probability of success, researchers planning repatriations should carefully consider project objectives, purposes and limitations, and, when possible, use stochastic population models with relevant uncertainties to evaluate how potential management strategies might influence the long-term viability of repatriated populations (Seddon, Armstrong & Maloney, 2007; Converse &

Armstrong, 2016). After implementing a repatriation strategy in the field, post-release monitoring (Ewen & Armstrong, 2007; Sutherland *et al.*, 2010; Nichols & Armstrong, 2012; Gitzen *et al.*, 2016) is essential to assess the success of any repatriation program and inform future release decisions and projects. Effective monitoring processes can measure demographic rates of released individuals and assess whether the population is growing and at acceptably-low risk of local extinction, given the objectives (Converse & Armstrong, 2016). Because resources invested during one phase of the repatriation process (i.e. production and release of animals) can limit resources invested in other phases (i.e. monitoring and project assessment), we envision modeling and monitoring as two linked activities, during which managers must decide on release strategies from translocated or captive-bred individuals, and on monitoring assessment of the population during and after releases have been implemented. In this way, strong release strategies and clear monitoring programs are essential to efficiently use resources and evaluate program success.

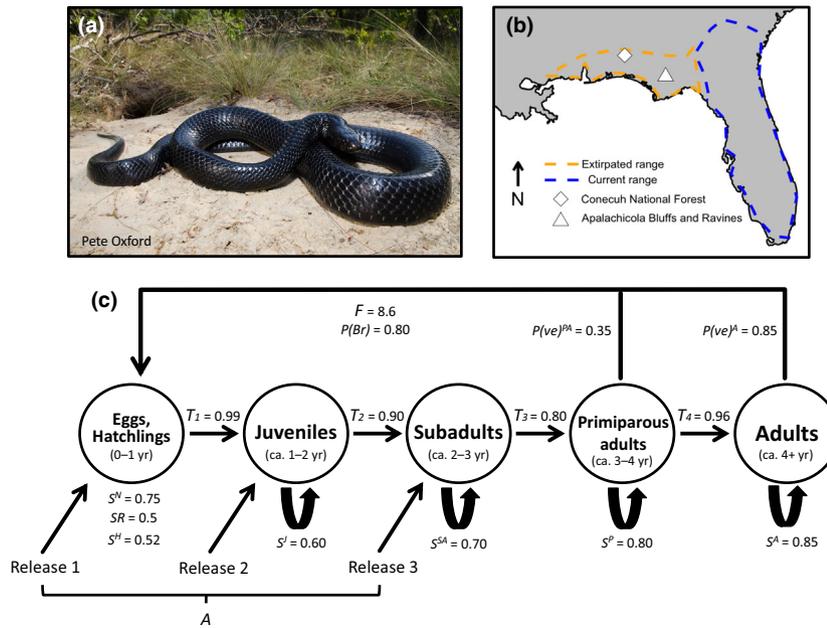
Monitoring for repatriation success can be a difficult task, particularly for species with life history and behavioral characteristics that obscure patterns of post-release population dynamics. For example, long-lived species with delayed sexual maturity may take years to begin recruitment, and signs of repatriation success may not be realized for long periods of time (Canessa *et al.*, 2016). For large predatory species with secretive life histories, populations may occur at low densities and individuals may be difficult to detect. For example, snakes are a diverse lineage of squamate reptiles that are extremely difficult to monitor for abundance because conventional sampling methods are associated with extremely low detection probabilities (Durso, Willson & Winne, 2011; Steen, Guyer & Smith, 2012) and progressive analyses that account for imperfect detection (Mazerolle *et al.*, 2007) fail to produce meaningful estimates of abundance (Steen, 2010). Furthermore, for species with seasonal shifts in habitat use and/or large home ranges, individuals may disperse from release sites either seasonally or permanently, becoming unavailable for detection at release sites. These situations provide challenges to repatriation projects because measurements of success can be uncertain or temporally delayed and managers may be reluctant to use repatriation as a strategy if success is difficult to evaluate.

The eastern indigo snake, *Drymarchon couperi* (see Folt *et al.*, 2019 for clarification of the content of this taxon), is a federally Threatened species that once ranged throughout the Coastal Plain of southeastern North America, from Georgia to Mississippi (Fig. 1). Closely associated with the longleaf pine ecosystem, *D. couperi* has declined both in geographic extent as well as perceived abundance and density, largely due to habitat degradation, road mortality, over-collecting for the pet trade and gassing of gopher tortoise burrows associated with rattlesnake roundups; consequently, the species has been extirpated from the western extent of its historic range (Enge *et al.*, 2013) and is rare elsewhere. The species' federal recovery plan (US Fish & Wildlife Service, 1982) suggests that the path to delisting of *D. couperi* will

likely depend on successful repatriation of the species into areas where the species was extirpated. Repatriation projects are currently underway in Conecuh National Forest (CNF), Alabama, and Apalachicola Bluffs and Ravines Preserve (ABRP), Florida; both result from a partnership between private and governmental agencies (e.g. Stiles *et al.*, 2013). The areas were selected as repatriation sites because the threats that led to extirpation of *D. couperi* are thought to have been alleviated at each site. For example, although both sites were heavily modified by silvicultural activities and fire suppression, the habitats have experienced considerable longleaf pine restoration in recent years, and both support populations of gopher tortoises whose burrows serve as essential overwintering habitat for *D. couperi* in the region (Hyslop *et al.*, 2014).

However, the life history of *D. couperi* presents several challenges to the repatriation process, particularly for researchers and decision makers charged with monitoring success of the repatriation. First, the species exhibits delayed maturation with high early life mortality (Hyslop *et al.*, 2012), thus potentially requiring significant time in captive rearing to head-start animals; head-starting creates production and cost limitations on the number of animals that can be released. Second, like many snakes, annual detection probability of individuals is low (0.16–0.23; Hyslop *et al.*, 2012) because individuals frequent subterranean retreats, such as tortoise burrows (Bauder *et al.*, 2017). Third, habitat use varies by season; individuals use gopher tortoise burrows on sandy, xeric ridgetops during winter, but largely shift to hydric bottomlands during the rest of the year (Hyslop *et al.*, 2014) where they are extremely difficult to monitor. Last, home ranges of *D. couperi* are among the largest of all North American snakes (Hyslop *et al.*, 2014; Folt *et al.*, 2018) and individuals released at recipient sites may disperse across the landscape in ways that make monitoring unfeasible. While radio-telemetry is a common tool used to monitor the survival and behavior of snakes, including *D. couperi* (Stiles *et al.*, 2013), this method is expensive to implement, cannot measure recruitment and population growth, and, importantly, accumulating evidence suggests that surgically implanted transmitters may have significant negative effects on individual survival (Rudolph *et al.*, 1997; Weatherhead & Blouin-Demers, 2004; Teixeira *et al.*, 2007). Additionally, analytical methods that account for imperfect detection (Mazerolle *et al.*, 2007) might also be an impractical solution for estimating abundance, because exceptionally low detection probabilities can cause such analyses to produce nonsensical results (Steen, 2010).

When life history features generate significant challenges to monitoring during repatriations (e.g. *D. couperi*), wildlife managers tasked with monitoring are largely left with simple, count-based survey metrics to assess abundance and evaluate repatriation success. However, partial observability will cause significant uncertainty when estimating abundance and making decisions (Nichols, 2019) about how to manage repatriations. Given low numbers of individuals observed during monitoring, wildlife managers may perceive populations to be at high risk of extinction and thus feel they are failing to



**Figure 1** (a) An eastern indigo snake *Drymarchon couperi*, basking outside of a gopher tortoise burrow. (b) *D. couperi* is a federally Threatened species that is currently being repatriated into the extirpated part of its historic range in Conecuh National Forest, Alabama, and Apalachicola Bluffs and Ravines Preserve, Florida (map adapted from Enge et al., 2013). (c) A hypothetical five-stage population model of females used to evaluate different management strategies to repatriate the species by releasing captive-bred individuals into the wild at different life stages. Model structure and parameters are as defined in the Methods section.

achieve management objections; managers may then be tempted to (1) invest more resources (i.e. animals) into repatriated populations to increase population growth, or (2) discontinue repatriation projects to save resources. Both of these actions would be undesirable if populations are actually growing and at low risk of extinction.

In this paper, we present a predictive population model to inform repatriation programs for *D. couperi* and other secretive species with low detection rates that cannot be monitored with conventional mark-recapture frameworks. Initially the repatriation programs for *D. couperi* in Alabama and Florida relied on a preliminary deterministic predictive analysis that recommended release of 300 head-started animals coupled with the choice that this be done at a rate of 30 individuals per year for 10 years to account for logistical issues associated with generating snakes in captivity (Godwin et al., 2011). Our model revisits that preliminary analysis by applying field- and laboratory-estimated demographic rates of *D. couperi* to project population dynamics with parametric uncertainty and temporal stochasticity under different repatriation scenarios and evaluates the likelihood of population establishment at repatriation sites. Specifically, we evaluate how age of animals released, number of individuals released and release program duration influence population growth and extinction probability by simulating and comparing population projections under different repatriation scenarios. Then, given the importance and difficulties of monitoring *D. couperi* for evaluations of repatriation success, we model how varying levels of detection probability influence observations of population growth and inferences

of repatriation success by wildlife managers. Finally, to demonstrate the utility of our model for evaluating current management plans, we project abundance and extinction probability of animals released as components of the two ongoing reintroductions in Alabama and Florida and model how many individuals wildlife managers might expect to observe, given limitations in monitoring and analytical efforts. Our model framework allows managers to project population growth and estimate extinction risk under alternative management scenarios and to understand how partial observability can influence observations of population growth for species that are difficult to detect.

## Materials and methods

### Management objectives and project summary

Predictive modeling for management decision-making first requires an explicit statement of project objectives so that alternative management actions can be assessed with respect to their purpose (Keeney, 1996). The federal recovery plan for *D. couperi* suggests that, in order to delist the species, viable populations need to be re-established in the western portion of the species’ historical range (Fig. 1; US Fish & Wildlife Service, 1982). The ultimate goals of repatriation efforts are to generate sustainable repatriated populations, achieve recovery criteria, delist the species and restore the species’ ecological role in Alabama and western Florida (US Fish & Wildlife Service, 1982). To effectively contribute to

management objectives, we view repatriation success as establishing a self-sustainable repatriated population with significantly low risk of extinction 30 year after initiating releases, which we define here as being < 0.10.

To work toward these criteria and objectives, a collaborative partnership (Supporting Information Appendix S1) was formed to generate captive stock of *D. couperi* and to release captive-bred individuals into recipient sites. The preliminary goal of releasing 30 snakes/year for 10 years was accepted as a target, with snakes obtained from eggs of wild-caught, gravid females from southeastern Georgia. Hatchlings from these eggs (hereafter, head-started snakes) generated the first 98 snakes used for repatriation as well as producing stock for the Orianne Center for Indigo Conservation, a captive-breeding facility used to generate remaining snakes available for conservation activities. After producing eggs for future captive stock, wild-collected females were released to their populations of origin.

To date, 154 head-started snakes have been released into CNF (Table 1), and current plans seek to release c. 150 additional snakes into CNF over the next 5 years. Some individuals of the first release cohorts were soft-released in pens (Stiles *et al.*, 2013), but the majority of individuals have been hard-released into tortoise burrows. Monitoring activities included radio-tracking the first 60 individuals released (2010–2013), conducting area-constrained searches at gopher tortoise burrows occupied by the initial cohorts of snakes during winter, and recording incidental sightings in the study area during all years. All released individuals were injected with passive integrative transponder tags for individual identification. Excluding individuals tracked by radio telemetry, 16 individuals were detected by researchers, wildlife managers or private citizens during 2014–2018. At ABRP, 12 and 20 individuals were hard-released during 2017 and 2018, respectively (Table 1), and all individuals were monitored by telemetry. While preliminary results indicated that some individuals were behaving similar to snakes from source populations (Stiles *et al.*, 2013; Steen *et al.*, 2016), whether the repatriation programs are on track to be successful, as defined above, has not been evaluated, largely because individuals have been difficult to monitor post-release. Given these limitations, the collaborator partnership managing *D. couperi* repatriations asked us to produce a model to guide release strategies and provide predictions for monitoring programs, given low detection rates.

### Predictive population model

We built a female-only, post-breeding-census, stage-structured, population model of *D. couperi* with five stages: hatchlings, juveniles, subadults, primiparous adults and adults (Fig. 1). We used the model to predict the future abundance of wild, repatriated individuals using a first-order Markovian process where abundance of stage *i* at time *t* was a function of abundance at time *t* – 1 with stochastically-generated population vital rates:

$$N_t^i = N_{t-1}^i \times S_{t-1}^i \times (1 - T_{t-1}^i) + N_{t-1}^{i-1} \times S_{t-1}^{i-1} \times T_{t-1}^{i-1}, \quad (1)$$

where *N* is abundance, *S* is the survival rate, *T* is a transition rate during each time step *t* (year) and life stage *i*.

To model fecundity and recruitment, we first accounted for the number of eggs (fecundity; *F*) produced by each stage (*i*) that bred in year *t* using a randomized Poisson draw:

$$F_t^i = \sum \text{Poisson}_i(N_t^i \times P(Br)_t, C_t), \quad (2)$$

where *P(Br)<sub>t</sub>* is the proportion of females that produced clutches of eggs and *C<sub>t</sub>* is the mean of the Poisson distribution of the estimated mean clutch size of females. We modeled the proportion of individuals that produced eggs in a given year as a function of a good-year/bad-year binomial probability dynamic, where a Bernoulli trial with a probability of success of 0.80 was used to determine if it was a good or bad year: during a good year, 100% of the individuals produced eggs, while only 75% of the population produced eggs during a bad year. While we do not have data on inter-annual variation in fecundity, we incorporated this parameter because it was a conservative assumption that would dampen population growth.

The number of hatchlings was determined by:

$$N_t^H = F_t^i \times P(\text{ve})_t^i \times S_t^E, \quad (3)$$

where *N<sup>H</sup>* is abundance of hatchlings (*H*), *F* is the mean number of eggs in a clutch from equation (2), *P(ve)* is the proportion of viable eggs within a clutch and *S<sup>E</sup>* is the survival rate of eggs, each in year *t*. Because captive husbandry data indicate that clutches laid by primiparous females tend to be dominated by unviable eggs, we modeled *P(ve)* as

**Table 1.** Number of individuals released during repatriation efforts for *Drymarchon couperi* in Conecuh National Forest, Alabama, and Apalachicola Bluffs and Ravines Preserve, Florida during 2010–2018

Release site	Sex	Year										Total
		2010	2011	2012	2013	2014	2015	2016	2017	2018		
Alabama	Females	8	11	14	3	–	3	–	13	9	61	
	Males	9	19	17 <sup>a</sup>	17 <sup>a</sup>	–	6	–	14	10	92	
Florida	Females	–	–	–	–	–	–	–	4	8	12	
	Males	–	–	–	–	–	–	–	8	12	20	

Sex was undetermined for two individuals in 2012 and one individual in 2013 in Alabama (<sup>a</sup>), and we categorized those individuals as males.

decreased for primiparous females relative to females with experience breeding.

During simulations, we modeled survival rates, the proportion of breeding females, the proportion of viable eggs and sex ratios as population-level, beta-distributed, random variables using mean and standard deviation estimates to calculate shape parameters for beta distributions using the method of moments (Fig. 1; Morris & Doak, 2002). We modeled survival estimates as increasing probabilities across stages using estimates of apparent survival from southern Georgia source populations (Hyslop *et al.*, 2009, 2012) and estimates of survival of radio-telemetered snakes released in CNF (Stiles, 2013); each survival estimate was modeled with  $SE = 0.10$ . To accommodate variation in growth where individuals may not transition out of stages each year, we modeled transition rates between stages as varying between 0.80–0.99 (Fig. 1; Supporting Information Appendix S2). We modeled productivity (fecundity;  $F$ ) with a mean of 8.6 eggs per female with a Poisson-distributed random variable for all breeding stages, but we modeled the proportion of viable eggs,  $P(ve)$ , as less for primiparous females [ $P(ve)^{PA} = 0.35$ ; 0.05 SE] than adult females [ $P(ve)^A = 0.85$ ; 0.05 SE; Wines *et al.*, 2015]. Our productivity parameters assume that fecundity of released individuals will operate similarly to what we have observed among wild-caught and captive-raised females. We modeled the proportion of females within release cohorts and hatchlings (sex ratio) as 0.50 (0.04 SE) to remove males and followed Hyslop *et al.* (2012) by modeling mean egg survival within nests ( $S^N$ ) as 0.75 (0.15 SE). For the survival parameters in the model, we applied the parametric uncertainty simulation structure described by McGowan, Runge & Larson (2011) that first selects a mean survival value for each replicate of the simulation and then uses that mean to draw a survival value for each year in the replicate.

To prevent exponential population growth, we incorporated density-dependence by modeling subadult survival ( $S^{SA}$ ) as a function of total population abundance: if the population exceeded ceilings of 100 and 150 females,  $S^{SA}$  dropped to a mean of 0.40 and 0.20 respectively. We set population ceiling thresholds at 100 and 150 females, given the approximate number of females observed in reference populations in Georgia (Stevenson *et al.*, 2009; Hyslop *et al.*, 2012).

### Incorporating management actions

For life stages being used as release propagules for repatriation, we extended equation (1) to accommodate the release of captive-bred individuals:

$$N_t^i = N_{t-1}^i \times S_{t-1}^i \times (1 - T_{t-1}^i) + N_{t-1}^{i-1} \times S_{t-1}^{i-1} \times T_{t-1}^{i-1} + NR_{t-1}^{i-1} \times S_{t-1}^{i-1} \times T_{t-1}^{i-1}, \quad (4)$$

where NR is the number of females released. Releases of captive-bred animals were incorporated into the projection model by adding individuals to the hatchling ( $NR_t^H$ ), juvenile ( $NR_t^J$ ),

or subadult age classes ( $NR_t^{SA}$ ). We started each simulation with zero individuals in the population and added captive-bred individuals into the population. Because there is annual uncertainty in the number of snakes available for release due to variability in captive productivity, we used the uniform distribution bounded by 80 and 120% of the specified management target for release.

Captive-bred individuals that are released into the wild may go through an acclimation period following release while they establish a home range, learn to forage, thermoregulate and seek to avoid predation (i.e. post-release effects; Armstrong & Reynolds, 2012). Because individuals in this period may experience decreased survival relative to wild individuals in the same stage (Snyder *et al.*, 1996; Cayuela *et al.*, 2019), we modeled released individuals to have decreased annual survival relative to wild animals during the first year following release:

$$SR_t^i = S_t^i \times A_t, \quad (5)$$

where SR is the survival rate of released individuals in stage  $i$  during year  $t$  and  $A$  is the acclimation effect in year  $t$  for all life stages.

### Observation uncertainty

To model how detection influences our ability to monitor population growth, we implemented an observation function in the model that output count data under different detection probabilities:

$$No_t^i = \sum \text{Binomial}(N_t^i, p_t), \quad (6)$$

where  $No_t^i$  is the number of snakes at stage  $i$  observed at time  $t$ , which is the sum of a set of independent Bernoulli trials in which each individual in the population  $N_t^i$  is detected or not given a specified probability of  $p$  (i.e. a binomial probability trial) at time  $t$ . The function simulates the detection probability of individuals present at release sites during 3-month survey intervals implemented in other monitoring programs for *D. couperi* (Hyslop *et al.*, 2012) and allows the population model to predict abundance observed after a detection process during monitoring at release sites.

### Evaluating management actions

To better understand how different release strategies influence success during *D. couperi* repatriations, we modeled 12 strategies differing in snake release age (hatchlings, juveniles, subadults), release program duration (annual releases for 5- and 10-year programs) and annual release size (15 individuals/year vs. 30 individuals/year). For each repatriation strategy, simulations predicted abundance, population growth ( $\lambda$ ), observed population growth ( $\lambda_o$ ), and extinction risk for a 30-year period. We evaluated extinction risk with a quasi-extinction probability ( $P_e$ ), where  $P_e$  was estimated by the proportion of simulations resulting in less than five females alive at the end of the simulation period. To more

fully understand the relationship between release propagule pressure, program duration and  $P_e$ , we also simulated population projections under a wider range of potential management actions [all combinations of release size (2–300 females/year) and program duration (1–20 years)] and estimated  $P_e$  under each scenario. We visualized the results of these additional simulations using three-dimensional surface plots.

To understand extinction risk associated with ongoing repatriation efforts, we estimated  $\lambda$ ,  $\lambda_o$  and  $P_e$  in CNF and ABRP by performing two population projections for each site by simulating: (1) the exact number of females released at sites to date (Table 1), and (2) releases to date along with planned future releases during the next 6 years (CNF) and 10 years (ABRP) to achieve a goal of releasing 150 females at both sites. Because >90% of individuals were released *c.* 2 years after the hatch year and had not reproduced, we modeled all released females as subadults during simulations.

To model post-release acclimation and detection effects, we modeled  $A = 0.50$  decrease of stage-specific survival and  $p = 0.20$  in all models. These parameters assume that released individuals experience a 50% decrease in survival during the first-year post release and that individuals have a 20% chance of being observed during a given year. However, because we do not know the true effects of  $A$  or  $p$ , we used the repatriation scenario with greatest population growth and tested the sensitivity of model predictions and assessments of success to uncertainty in acclimation ( $A = 0.0, 0.20, 0.40, 0.60, 0.80$ ) and detection ( $p = 0.05, 0.15, 0.25, 0.35$ ; following estimates from Hyslop *et al.*, 2012). Because hatchling releases might have lower  $A$  than juvenile or subadult releases, we also sought to understand how  $P_e$  is influenced by variation in  $A$  among different release stages. Each scenario was replicated 1000 times with the statistical Program R (R Core Team, 2018). See Supporting Information Appendix S2 for our R code.

## Results

Model outputs from the 12 repatriation scenarios varied in estimates of  $\lambda$ ,  $\lambda_o$  and extinction risk. Subadult releases generally generated larger populations with decreased extinction probability relative to juvenile and hatchling release scenarios (Table 2; Fig. 2). Scenarios with smaller release size and duration experienced 1.5–2 times greater extinction risk than larger and longer release programs for each release stage. After the 30-year projection period, the scenario with the lowest quasi-extinction risk was 30 subadults/year for 10 years ( $P_e = 0.11$ ), while the highest extinction probability was 15 hatchlings/year for 5 years. Simulations of all combinations of release propagule pressure and program duration also predicted decreased extinction probability when releasing subadults compared to hatchlings and juveniles (Fig. 3). Model predictions for ongoing repatriations in Alabama and Florida (Fig. 4) suggested that extinction risk was relatively high for repatriation projects to date (Alabama:  $P_e = 0.23$ ; Florida:  $P_e = 0.61$ ; Table 3); however, when including

planned future releases, extinction risk decreased to  $\leq 0.10$  for both populations.

Observed population growth was less than  $\lambda$  in all repatriation scenarios (Table 2). However, in eight of 12 scenarios,  $\lambda_o$  was so low as to suggest declining populations, even though populations were growing. When simulated at varying levels of  $p$ , observed abundance was always much lower than actual abundance and was highly dependent on sampling probability of the binomial function (e.g. Fig. 4). Model predictions for ongoing repatriations in Alabama and Florida also suggested that populations are growing ( $\lambda > 1$ ), but that  $\lambda_o$  was considerably less than  $\lambda$  (Table 3). Repatriation success metrics were sensitive to  $A$ .  $\lambda$  varied little in response to changes in  $A$  (Table 4), but  $P_e$  increased greatly during simulations with increased  $A$  (Fig. 5).

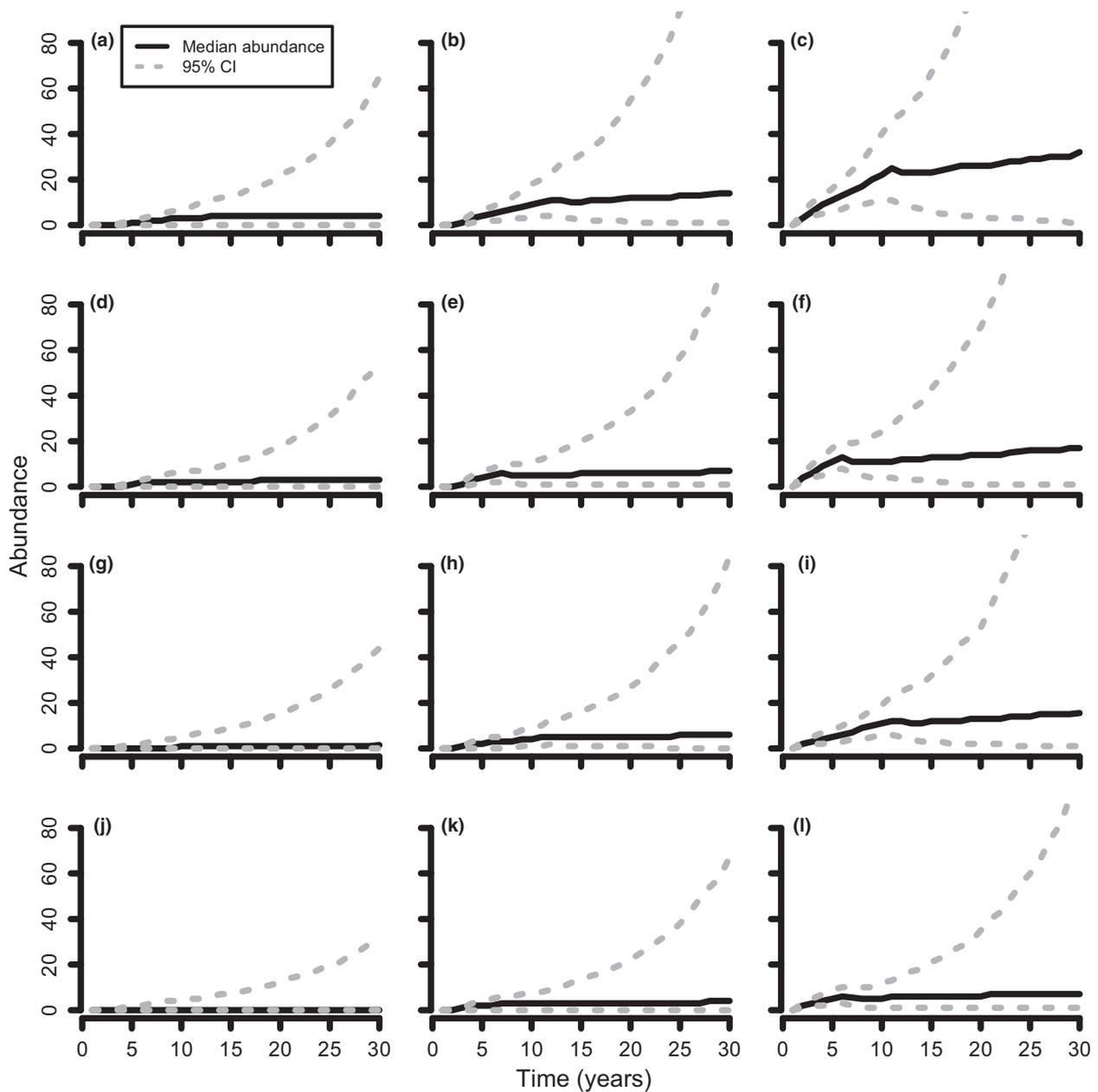
## Discussion

Our model predicted high probability of success for multiple management actions to repatriate *D. couperi*, including ongoing management plans in Alabama and Florida. Strategies releasing older, head-started snakes in greater abundance and frequency generated population outcomes characterized by greater population size and lower extinction risk compared to scenarios releasing fewer, younger snakes less frequently; these release programs provide the best opportunity for wildlife managers to accomplish the objective of repatriating *D. couperi*. Similarly, simulated outcomes for ongoing repatriations in Alabama and Florida also underscored the importance of releasing a large number of individuals to sufficiently decrease extinction risk: current efforts releasing 64 females in Alabama experience more-than-doubled extinction

**Table 2.** Total number of females released, true population growth ( $\lambda$ ), observed population growth ( $\lambda_o$ ), and probability of quasi-extinction ( $P_e$ ) for simulated repatriation strategies varying in the release age, size, and duration of eastern indigo snakes, *Drymarchon couperi*

Release age	Release size	Release duration (year)	Total females released	$\lambda$	$\lambda_o$	$P_e$
Hatchlings	30	10	150	1.05	0.71	0.51
Hatchlings	30	5	75	1.05	0.98	0.63
Hatchlings	15	10	75	1.07	0.95	0.73
Hatchlings	15	5	37	1.07	0.99	0.84
Juveniles	30	10	150	1.05	1.00	0.23
Juveniles	30	5	75	1.02	0.97	0.38
Juveniles	15	10	75	1.02	0.90	0.42
Juveniles	15	5	37	1.00	0.79	0.58
Subadults	30	10	150	1.04	1.00	0.11
Subadults	30	5	75	1.00	1.00	0.20
Subadults	15	10	75	1.03	1.00	0.20
Subadults	15	5	37	1.00	0.90	0.33

Release size is snakes per year and includes males and females.  $\lambda$  and  $\lambda_o$  were modeled for all reproductive individuals with sampling probability ( $p$ ) of 0.2 in each scenario. The scenario with lowest  $P_e$  involved releasing 30 subadults/year for 10 years.

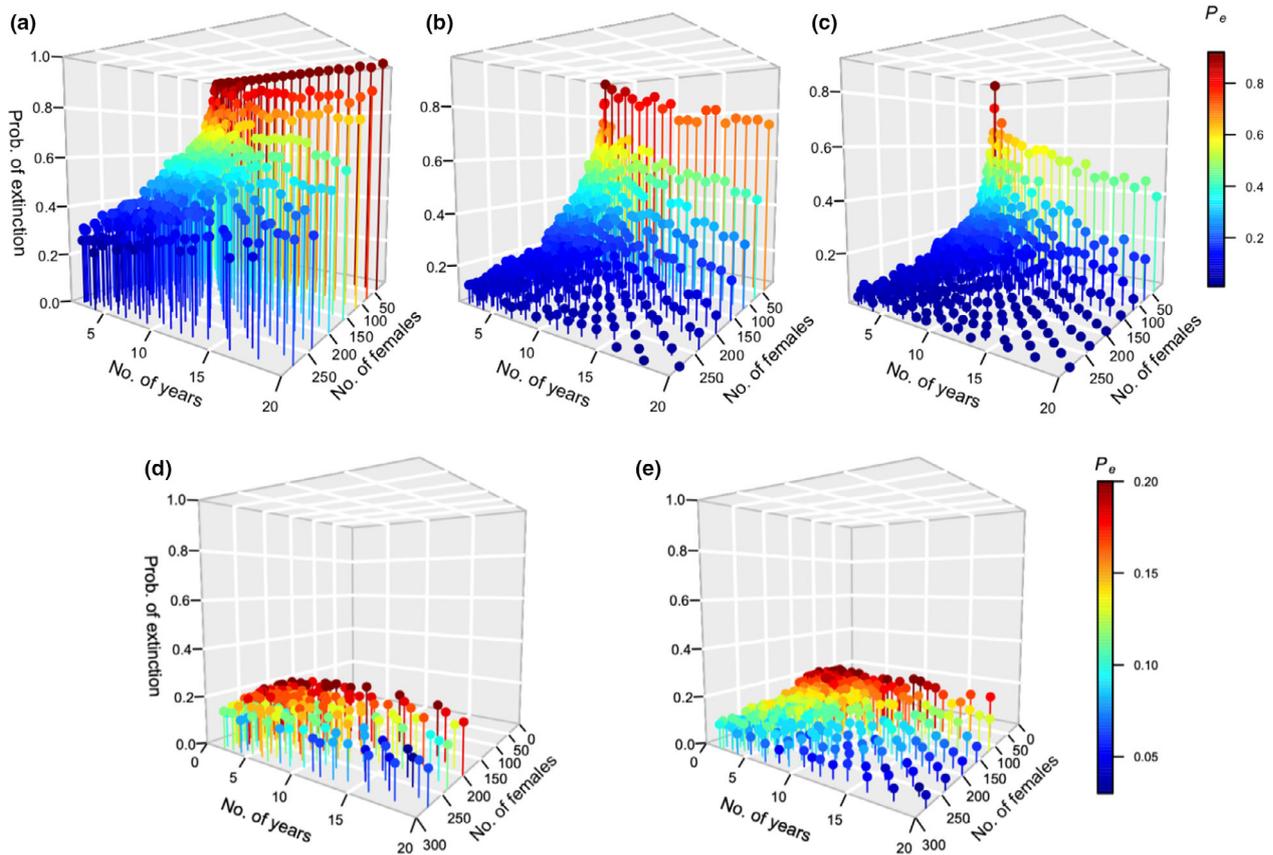


**Figure 2** Simulated population growth of *Drymarchon couperi* under 12 repatriation scenarios varying in release age, release size, and release duration. Panel columns illustrate models releasing hatchlings (left), juveniles (center), and subadults (right). (a–c) 30 individuals/year for 10 years; (d–f) 30 individuals/year for 5 years; (g–i) 15 individuals/year for 10 years; (j–l) 15 individuals/year for 5 years. Graphs illustrate the median ( $\pm 95\%$  CI) abundance of all reproductive adults (primiparous adults, experienced adults).

risk relative to simulations that include releasing *c.* 150 females at similar rates. A thorough approach in evaluating release strategies may be to first identify acceptable extinction probabilities and subsequently find the optimal release strategy that meets those criteria (Gregory & Keeney, 2002; Gregory & Long, 2009). If, for example, we accept 0.10 as an acceptable minimum risk for extinction, then repatriation efforts should focus on releasing a minimum of 150 juvenile females or 100 subadult females during a 5- to 10-year

period (Fig. 3), and ongoing repatriations need to release the targeted number of females (150) to achieve this level of extinction risk. Scenarios releasing hatchlings never met this threshold, even when the acclimation effect was removed from the model.

Although all scenarios, on average, resulted in growing populations, abundance and  $\lambda_o$  observed after a detection process were always less than true abundance and  $\lambda$ , and, in some situations,  $\lambda_o$  was low enough to suggest declining

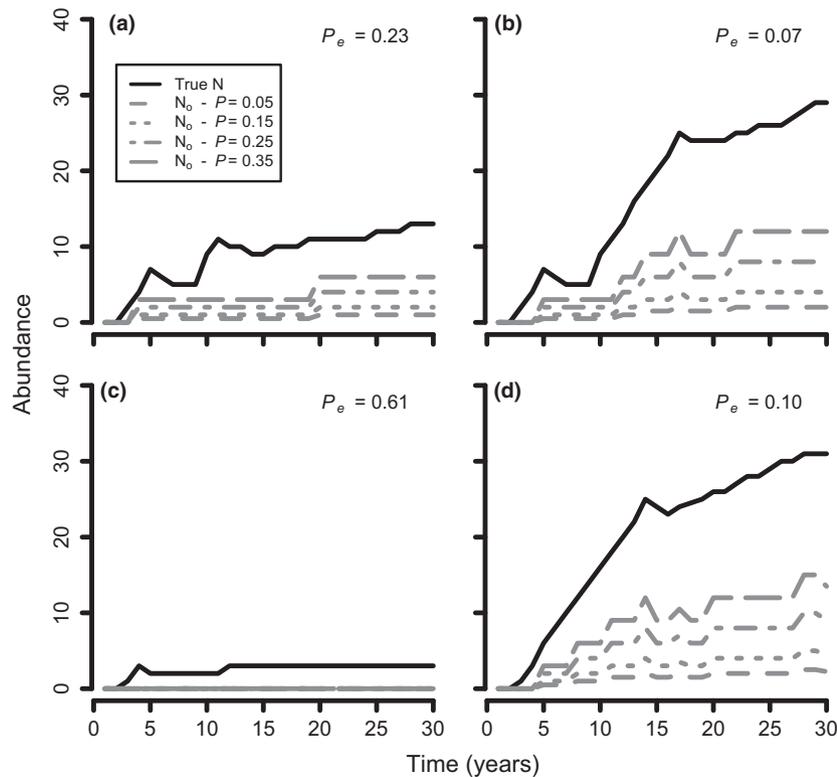


**Figure 3** Three-dimensional relationship between release program duration (years), release propagule pressure (total number of females released), and resulting probability of quasi-extinction ( $P_e$ ) for simulated population repatriations of *Drymarchon couperi*. Top-row: simulations releasing hatchlings (a), juveniles (b), and subadults (c). Bottom-row: simulations releasing juveniles (d) and subadults (e) that resulted in  $P_e < 0.20$ ; coloration of  $P_e$  is re-scaled for panels d and e.

populations, even though true population dynamics were growing (i.e. false negatives; Table 2). For example, when releasing 30 subadults/year for 10 years with a sampling probability of 0.15, 25% of replicates observed zero individuals in the fifth year, and the percentage of replicates observing zero individuals was 8–16% for all 30 years of the simulation, despite population growth in those simulations. In these cases, even with a substantial repatriation effort and a growing wild population, there was still a considerable chance that no individuals would be detected at the release site in the fifth year and years beyond. Similarly, projections of ongoing repatriations suggested that populations may be small after 30 years (*c.* 30 females), and detection processes may cause monitoring efforts to fail to observe population growth. Thus, low detection probability in monitoring contexts can give rise to situations in which wildlife managers realize false perceptions of repatriation failure.

A large and growing body of literature has used population modeling and mark-recapture analyses to predict and measure  $\lambda$  during repatriations (reviewed in Armstrong & Reynolds, 2012). While modeling and monitoring are widely accepted as a critical component of the repatriation process (Gibbs, 2000; Nichols & Armstrong, 2012), cryptic species

such as snakes are extremely difficult to monitor and we still lack effective methods to estimate abundance (Steen, 2010; Steen *et al.*, 2012) and evaluate repatriation success for species like *D. couperi*. If few or no individuals are encountered in the wild following releases, managers may observe  $\lambda_0$  that is substantially lower and not representative of true  $\lambda$ . In such situations, managers may perceive repatriations to be failing and therefore be tempted to (1) increase the numbers of individuals being released, or (2) cease an ongoing repatriation effort and reallocate resources. However, our modeling results suggest that infrequent observations of individuals and low population growth are largely expected and should not be interpreted to mean the repatriation is failing. We demonstrated here that *a priori* modeling of expected population counts given a detection process can help evaluate success under realistic monitoring expectations and warn wildlife managers of false perceptions of repatriation failure. Because population size for *D. couperi* will be difficult to estimate at repatriation sites, we suggest wildlife managers should look for corroborative information to determine whether populations are experiencing growth, such as increasing geographic range of individuals detected across the landscape.



**Figure 4** Population projections of true abundance ( $N$ ) and observed abundance ( $N_o$ ) after different levels of detection probability ( $p$ ) for *Drymarchon couperi* repatriations in Conecuh National Forest, Alabama (CNF), and Apalachicola Bluffs and Ravines Preserve, Florida (ABRP). Top-row: population projections in CNF, given the (a) current number of released snakes (157 snakes over 9 years), and (b) current and planned releases (~300 snakes over 15 years). Bottom-row: projections in ABRP given the (c) current number of release snakes (34 over 2 years), and (d) current and planned future releases (~300 snakes over 12 years).  $P_e$  is the probability of quasi-extinction, or the proportion of simulated populations with <5 females at year 30.

**Table 3.** Number of females released, population growth ( $\lambda$ ), observed population growth ( $\lambda_o$ ), probability of extinction ( $P_e$ ), and median abundance ( $N$ ) for simulated population repatriations of *Drymarchon couperi* in Alabama (AL) and Florida (FL)

Site	Releases	Females released	$\lambda$	$\lambda_o$	$P_e$	$N$
AL	Current	62	1.02	0.92	0.23	12
	Current + futures	149	1.07	0.91	0.07	29
FL	Current	12	1.00	0.65	0.61	3
	Current + futures	150	1.07	0.98	0.10	31

Two release program simulations were performed for each site: one projecting the population given the number of females released to date (current; Table 1), and another including future releases (current + futures) to achieve a target of c. 150 females released per site during the next 6–10 years.  $\lambda_o$  was calculated after a detection process ( $p = 0.15$ ).

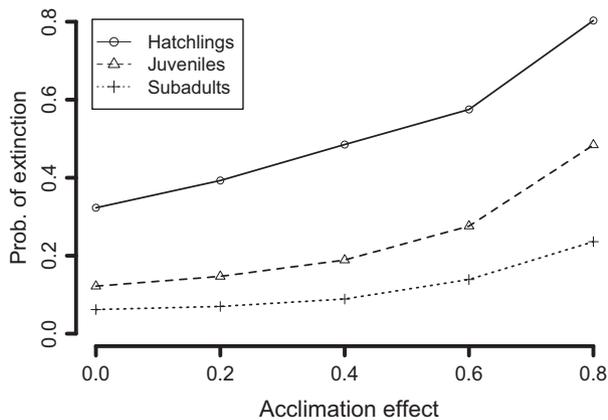
Repatriation scenarios for *D. couperi* that released older, head-started subadults had greater population growth and decreased extinction risk when compared to scenarios releasing younger hatchlings and juveniles. Subadult releases performed best because subadults have higher survival, are closer to the age of sexual maturity, and reach sexual

**Table 4.** True population growth ( $\lambda$ ), probability of extinction ( $P_e$ ), and per cent changes in  $\lambda$  and  $P_e$  for repatriated populations of *Drymarchon couperi* under different levels of the post release acclimation effect ( $A$ ) when releasing 30 subadults/year for 10 years

$A$	$\lambda$	Per cent change in $\lambda$	$P_e$	Per cent change in $P_e$
0.00	1.037	–	0.062	–
0.20	1.039	0.20	0.070	12.90
0.40	1.039	0.26	0.089	43.55
0.60	1.037	–0.01	0.139	124.19
0.80	1.036	–0.02	0.236	280.65

Per cent changes are relative to simulations with  $A = 0$ .

maturity more quickly than younger life stages (Hyslop et al., 2012; Canessa et al., 2015). In this sense, our modeling exercise supports the value of head-starting as a useful tool to increase probability of success during repatriations; because populations repatriated with subadults begin reproducing more quickly, such scenarios also experience the added benefit of decreased monitoring costs required to observe recruitment. It may also be important to consider that captive head-starting is a cost to captive-rearing facilities



**Figure 5** Probability of quasi-extinction ( $P_q$ ) as a consequence of variation in acclimation effects on survival ( $A$ ; a proportional decrease in survival) of released snakes during repatriations of *Drymarchon couperi*. Simulated results illustrated here were generated from scenarios releasing 30 individuals/year for 10 years with hatchling, juvenile, or subadult age classes.

and may increase negative acclimation effects on releases to the wild if, for example, (1) captive individuals become more dependent on food provisioning the longer they remain in captivity (Goetz *et al.*, 2018), (2) become diseased in captivity (e.g. *Cryptosporidium*; M. Hoffman, pers. obs.), and/or (3) experience persistent acclimation effects for multiple years after release into the wild (Cayuela *et al.*, 2019). However, head-started juvenile and subadult releases with acclimation effects up to 0.60 had less extinction risk than hatchling releases modeled with no acclimation effect (Fig. 5), a threshold we consider to be well above what true acclimation effects for head-started snakes are likely to be. In general, we suggest that a multi-objective optimization analysis (e.g. Robinson, McGowan & Apodaca, 2016) could use the principles of structured decision-making to incorporate additional objectives (e.g. minimizing cost of captive breeding, increasing genetic diversity) and tradeoff analyses to identify the optimal strategy that meets multiple objectives (Converse *et al.*, 2013; Canessa *et al.*, 2014).

The accuracy of model predictions of repatriation success in Alabama and Florida are largely dependent on whether demographic rates estimated from populations in southeastern Georgia (Stevenson *et al.*, 2009; Hyslop *et al.*, 2012) are relevant to habitats and climates at release sites. While habitat structure and climatic environment at release sites are comparable to southeastern Georgia, unknown factors could drive differences in snake demography and alter prospects of repatriation success at recipient sites. To incorporate this parametric uncertainty and potential site-specific variation in our analyses, we applied a modeling structure with parametric uncertainty that allows for large variability in simulated survival parameters (McGowan *et al.*, 2011). Preliminary demographic rates estimated from released individuals in CNF suggested that survival of released individuals is comparable to that of wild individuals in Georgia (Stiles, 2013), which supports assumptions and inferences made here. Future

efforts to model demography of *D. couperi* will benefit from additional data describing demographics in the field. For example, there are few data describing nest survival and hatching rates (Hyslop *et al.*, 2012). Future models might also consider additional density-dependent effects on reproduction, particularly when recipient site populations are at low density. Captive-bred individuals released into the wild will have limited experience interacting with conspecifics in reproductive contexts, and observations from releases to date have suggested that young males may be more likely to permanently disperse away from release sites. For these reasons, females may be sperm limited and egg productivity may be reduced during early stages of repatriations. To accommodate for this potential, we modeled density dependence as an effect in which subadult survival decreased at high densities, potentially because subadults may be incentivized to disperse away from high-density areas due to competition. However, to our knowledge, density dependence has never been documented for snake populations. Future modeling exercises might relax this assumption or expand the framework to model how younger life stages may disperse from release sites to form new populations at the regional level that are linked by dispersal in a metapopulation context. This will be particularly important for the species to recolonize the western portion of its range and to achieve conservation objectives in the context of the federal Species Recovery Plan (US Fish & Wildlife Service, 1982).

While our model generates useful guidelines and predictions for *D. couperi* repatriations, some questions remain unresolved. For example, is the threefold reduction in quasi-extinction probability from 0.33 to 0.11 when an additional 113 subadult females are released over five additional years of management (Table 2) worth the additional cost of breeding and raising four times more snakes in captivity to the subadult stage? Formal trade-off analysis in a structured decision-making context could organize and reduce such complexity among release scenarios. Weighting competing objectives and developing, in advance, a multi-attribute value or utility function can quantify the differences between management alternatives on the same scale and clarify the optimal management choice (Gregory & Keeney, 2002; McGowan, Lyons & Smith, 2015). Here, we articulated management objectives and developed a consequences model to assess management alternatives which constitutes components of a structured decision-making process (Gregory & Long, 2009). A full decision analysis process and potentially an optimization analysis could help resolve the remaining limitations to decision-making in this complex and uncertain system. Specifically, wildlife managers may want to release younger snakes during future repatriations, because of decreased costs of captive husbandry and/or decreased acclimation effects. Our results suggest that this strategy would require larger number of individuals for repatriation to generate comparable extinction risk with strategies releasing subadults; however, to better evaluate the costs and benefits of such approaches, we suggest that future decision-making processes expand the model here to evaluate costs of breeding and head-starting in captivity, costs of monitoring individuals

at recipient sites and the value of information gained by monitoring processes in a more formal decision analysis.

## Acknowledgments

Repatriation programs for *D. couperi* in Alabama and Florida were supported by a large and diverse partnership of academic, state, federal and private agencies/individuals (Supporting Information Appendix S1). We thank the participants of a structured decision-making workshop at Auburn University where the decision framework, management objectives, and model prototype were conceived. We thank P. Oxford and The Orianna Society for providing a photograph (Fig. 1). Last, we thank N. Angeli, K. Dunham, R. Stanton, A. Tucker and L. Smith for providing helpful comments on the manuscript. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## References

- Armstrong, D.P. & Reynolds, M.H. (2012). Modelling reintroduced populations: the state of the art and future directions. *Reintroduc. Biol. Integr. Sci. Manag.* **12**, 165–222.
- Bauder, J.M., Stevenson, D.J., Sutherland, C.S. & Jenkins, C.L. (2017). Occupancy of potential overwintering habitat on protected lands by two imperiled snake species in the Coastal Plain of the southeastern United States. *J. Herpetol.* **51**, 73–88.
- Canessa, S., Hunter, D., Mcfadden, M., Marantelli, G. & Mccarthy, M.A. (2014). Optimal release strategies for cost-effective reintroductions. *J. Appl. Ecol.* **51**, 1107–1115.
- Canessa, S., Guillera-Arroita, G., Lahoz-Monfort, J.J., Southwell, D.M., Armstrong, D.P., Chadès, I., Lacy, R.C. & Converse, S.J. (2015). When do we need more data? A primer on calculating the value of information for applied ecologists. *Methods Ecol. Evol.* **6**, 1219–1228.
- Canessa, S., Genta, P., Jesu, R., Lamagni, L., Oneto, F., Salvidio, S. & Ottonello, D. (2016). Challenges of monitoring reintroduction outcomes: Insights from the conservation breeding program of an endangered turtle in Italy. *Biol. Conserv.* **204**, 128–133.
- Cayueta, H., Gillet, L., Laudelout, A., Besnard, A., Bonnaire, E., Levionnois, P., Muths, E., Dufrene, M. & Kinet, T. (2019). Survival cost to relocation does not reduce population self-sustainability in an amphibian. *Ecol. Appl.* **29**, e01909.
- Converse, S. J. & Armstrong, D. P. (2016). Demographic modeling for reintroduction decision-making. In *Reintroduction of fish and wildlife populations*: 123–146. Jachowski, D.S., Millspaugh, J.J., Angermeier, P.A. & Slotow, R. (Eds). Oakland: University of California Press.
- Converse, S.J., Moore, C.T., Folk, M.J. & Runge, M.C. (2013). A matter of tradeoffs: reintroduction as a multiple objective decision. *J. Wildl. Mgmt.* **77**, 1145–1156.
- Dodd, C.K.J. & Seigel, R.A. (1991). Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? *Herpetologica* **47**, 336–350.
- Durso, A.M., Willson, J.D. & Winne, C.T. (2011). Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. *Biol. Conserv.* **144**, 1508–1515.
- Enge, K.M., Stevenson, D.J., Elliott, M.J. & Bauder, J.M. (2013). The historical and current distribution of the Eastern Indigo Snake (*Drymarchon couperi*). *Herpetol. Conserv. Biol.* **8**, 288–307.
- Ewen, J.G. & Armstrong, D.P. (2007). Strategic monitoring of reintroductions in ecological restoration programmes. *Strategic monitoring of reintroductions in ecological. Écoscience* **14**, 401–409.
- Folt, B., Bauder, J., Spear, S., Stevenson, D., Hoffman, M., Oaks, J., Jenkins, C., Steen, D. & Guyer, C. (2018). Phylogenetic, population genetic, and morphological analyses reveal evidence for one species of Eastern Indigo Snake (*Drymarchon couperi*). *bioRxiv*. <https://doi.org/10.1101/318766>.
- Folt, B., Bauder, J., Spear, S., Stevenson, D., Hoffman, M., Oaks, J.R., Wood, P.L., Jenkins, C., Steen, D.A. & Guyer, C. (2019). Taxonomic and conservation implications of population genetic admixture, mito-nuclear discordance, and male-biased dispersal of a large endangered snake, *Drymarchon couperi*. *PLoS ONE* **14**, 1–21.
- Gibbs, J.P. (2000). Monitoring populations. In *Research techniques in animal ecology: controversies and consequences*: 213–252. Boitani, L. & Fuller, T. (Eds). New York: Columbia University Press.
- Gitzen, R.A., Keller, B.J., Miller, M.A., Goetz, S.M., Steen, D.A., Jachowski, D.S., Godwin, J.C. & Millspaugh, J.J. (2016). Effective and purposeful monitoring of species reintroductions. In *Reintroduction of fish and wildlife populations*: 281–319. Jachowski, D., Millspaugh, J.J., Angermeier, P.L. & Slotow, R.H. (Eds.). Oakland: University of California Press.
- Godwin, J., Wines, M., Stiles, J., Stiles, S., Guyer, C., & Rush, E.M. (2011). *Reintroduction of the Eastern indigo snake (Drymarchon couperi)* into Conecuh National Forest. Unpublished report submitted to the Alabama Department of Conservation and Natural Resources, 93 pp.
- Goetz, S.M., Godwin, J.C., Hoffman, M., Antonio, F. & Steen, D.A. (2018). Eastern indigo snakes exhibit an innate response to pit viper scent and an ontogenetic shift in their response to mouse scent. *Herpetologica* **74**, 152–158.
- Gregory, R.S. & Keeney, R.L. (2002). Making smarter environmental management decisions. *J. Am. Water Resour. Assoc.* **38**, 1601–1612.

- Gregory, R. & Long, G. (2009). Using structured decision making to help implement a precautionary approach to endangered species management. *Risk Anal.* **29**, 518–532.
- Hyslop, N.L., Meyers, J.M., Cooper, R.J. & Norton, T.M. (2009). Survival of radio-implanted *Drymarchon couperi* (Eastern indigo snake) in relation to body size and sex. *Herpetologica* **65**, 199–206.
- Hyslop, N.L., Stevenson, D.J., Macey, J.N., Carlile, L.D., Jenkins, C.L., Hostetler, J.A. & Oli, M.K. (2012). Survival and population growth of a long-lived threatened snake species, *Drymarchon couperi* (Eastern indigo snake). *Popul. Ecol.* **54**, 145–156.
- Hyslop, N.L., Meyers, J.M., Cooper, R.J. & Stevenson, D.J. (2014). Effects of body size and sex of *Drymarchon couperi* (Eastern indigo snake) on habitat use, movements, and home range size in Georgia. *J. Wildl. Mgmt.* **78**, 101–111.
- Keeney, R.L. (1996). *Value-focused thinking*. Cambridge: Harvard University Press.
- Mazerolle, M.J., Bailey, L.L., Kendall, W.L., Royle, J.A., Converse, S.J. & Nichols, J.D. (2007). Making great leaps forward: accounting for detectability in herpetological field studies. *J. Herpetol.* **41**, 672–689.
- McGowan, C.P., Runge, M.C. & Larson, M.A. (2011). Incorporating parametric uncertainty into population viability analysis models. *Biol. Conserv.* **144**, 1400–1408.
- McGowan, C.P., Lyons, J.E. & Smith, D.R. (2015). Developing objectives with multiple stakeholders: adaptive management of horseshoe crabs and red knots in the Delaware Bay. *Environ. Manage.* **55**, 972–982.
- Morris, W.F. & Doak, D.F. (2002). *Quantitative conservation biology: theory and practice of population viability analysis*. Sunderland: Sinauer Associates.
- Nichols, J.D. (2019). Confronting uncertainty: contributions of the wildlife profession to the broader scientific community. *J. Wildl. Mgmt.* **83**, 519–533.
- Nichols, J.D. & Armstrong, D.P. (2012). Monitoring for reintroductions. In *Reintroduction biology: integrating science and management*: 223–255. Ewen, J.G., Armstrong, D.P., Parker, K.A. & Seddon, P.J. (Eds). Oxford: Wiley Blackwell.
- R Core Team. (2018). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Robinson, O.J., McGowan, C.P. & Apodaca, J.J. (2016). Decision analysis for habitat conservation of an endangered, range-limited salamander. *Anim. Conserv.* **19**, 561–569.
- Rudolph, D.C., Burgdorf, S.J., Schaefer, R.R. & Conner, R.N. (1997). Snake mortality associated with late season radio-transmitter implantation. *Herpetol. Rev.* **29**, 155–156.
- Seddon, P.T., Armstrong, D.P. & Maloney, R.F. (2007). Developing the science of reintroduction biology. *Conserv. Biol.* **21**, 303–312.
- Seddon, P.J., Griffiths, C.J., Soorae, P.S. & Armstrong, D.P. (2014). Reversing defaunation: restoring species in a changing world. *Science* **345**, 406–412.
- Snyder, N.F.R., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, T.B., Toone, W.D. & Miller, B. (1996). Limitations of captive breeding in endangered species recovery. *Conserv. Biol.* **10**, 338–348.
- Soulé, M.E., Estes, J.A., Berger, J. & Martinez del Rio, C. (2003). Ecological effectiveness: conservation goals for interactive species. *Conserv. Biol.* **17**, 1238–1250.
- Steen, D.A. (2010). Snakes in the grass: secretive natural histories defy both conventional and progress statistics. *Herpetol. Conserv. Biol.* **5**, 183–188.
- Steen, D.A., Guyer, C. & Smith, L.L. (2012). Relative abundance in snakes: a case study. In *Reptile biodiversity: standard methods for inventory and monitoring*: 287–294. McDiarmid, R.W., Foster, M.S., Guyer, C., Gibbons, J.W., and Chernoff, N. (Eds). Washington: Smithsonian Institution Press.
- Steen, D.A., Stiles, J.A., Stiles, S.H., Godwin, J.C. & Guyer, C. (2016). Observations of feeding behavior by reintroduced indigo snakes in Southern Alabama. *Herpetol. Rev.* **47**, 11–13.
- Stevenson, D.J., Enge, K.M., Carlile, L.D., Dyer, K.J., Norton, T.M., Hyslop, N.L. & Kiltie, R.A. (2009). An Eastern Indigo Snake (*Drymarchon couperi*) mark-recapture study in southeastern Georgia. *Herpetol. Conserv. Biol.* **4**, 30–42.
- Stiles, J.A. (2013). *Evaluating the use of enclosures to reintroduce Eastern Indigo snakes*. Auburn: Auburn University.
- Stiles, S., Stiles, J., Godwin, J.C., Jenkins, C., Rush, E.M., Lock, B., Johnson, V.M., Wines, M., & Guyer, C. (2013). Repatriation of eastern indigo snakes to conservation lands in South Alabama, USA. In *Global re-introduction perspectives: 2013. Further case studies from around the globe*: 37–41. Soorae, P.S. (Ed.). Gland and Abu Dhabi: IUCN/SSC Re-introduction Specialist Group and Environment Agency-Abu Dhabi.
- Sutherland, W.J., Armstrong, D., Butchart, S.H.M., Earnhardt, J.M., Ewen, J., Jamieson, I., Jones, C.G., Lee, R., Newbery, P., Nichols, J.D., Parker, K.A., Sarrazin, F., Seddon, P.J., Shah, N. & Tatayah, V. (2010). Standards for documenting and monitoring bird reintroduction projects. *Conserv. Lett.* **3**, 229–235.
- Teixeira, C.P., Schetini de Azevedo, C., Mendl, M., Cipreste, C.F. & Young, R.J. (2007). Revisiting translocation and reintroduction programmes: the importance of considering stress. *Anim. Behav.* **73**, 1–13.
- US Fish and Wildlife Service. (1982). *Eastern indigo snake recovery plan*. Atlanta: US Fish and Wildlife Service.
- Weatherhead, P. & Blouin-Demers, G. (2004). Long-term effects of radiotelemetry on black ratsnakes. *Wildl. Soc. Bull.* **32**, 900–906.
- Wines, M.P., Johnson, V.M., Lock, B., Antonio, F., Godwin, J.C., Rush, E.M. & Guyer, C. (2015). Optimal husbandry of hatchling Eastern Indigo Snakes (*Drymarchon couperi*) during a captive head-start program. *Zoo Biol.* **34**, 230–238.

## Supporting information

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

**Appendix S1.** A detailed acknowledgment of the large and diverse partnership guiding and supporting repatriation of *Drymarchon couperi*.

**Appendix S2.** Analysis code.