

## Better off in the wild? Evaluating a captive breeding and release program for the recovery of an endangered rodent



Robert McCleery<sup>a,\*</sup>, Jeffrey A. Hostetler<sup>b</sup>, Madan K. Oli<sup>a</sup>

<sup>a</sup>Department of Wildlife Ecology and Conservation, University of Florida, Newins Zeigler Hall, Gainesville, FL 32611, USA

<sup>b</sup>Smithsonian Migratory Bird Center, National Zoological Park, P.O. Box 37012-MRC 5503, Washington, DC 20013, USA

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### ABSTRACT

The critical question for the success of all captive breeding and release programs (CBRPs) is the same: will the benefit of augmenting or reestablishing a population with captive animals outweigh the loss of taking individuals from the wild? Yet, few studies have simultaneously evaluated the impact of removal of animals for captive breeding on the source population and the potential contribution of the released animals to the augmented populations. We used the endangered Key Largo woodrat (*Neotoma floridana smalli*, KLWR) as a model system to simultaneously examine the effect of animal removal, captive breeding, and reintroduction on the dynamics and persistence of a wild population. We used mark-recapture and telemetry data, as well as zoo records from a recent CBRP for the endangered KLWR to parameterize a matrix population model and to simulate the response of the KLWR population to alternative captive breeding and release strategies. Our results suggest that a CBRP as practiced previously would not contribute to KLWR recovery; instead, removal of wild KLWR for captive breeding could harm the population. Captive breeding programs will not contribute to the recovery of KLWR unless survival of released animals and breeding success of captive individuals are improved. Our study provides a framework for simultaneous consideration of animal removal from the wild, breeding success in captivity and survival of released animals for a comprehensive evaluation of captive breeding programs.

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### 1. Introduction

Over the last four decades humans have directly threatened at least one fifth of the planet's vertebrate species with extinction (Hoffmann et al., 2010). One management strategy that has been used to help prevent the extinction of rare or threatened species is captive breeding and release programs (CBRPs; Snyder et al., 2002). Under these programs, animals are removed from the wild and placed in a controlled captive environment where they are bred and their offspring are reared. Eventually, some or all of this captive population is released into its habitats to augment struggling populations or reestablish expatriated ones. CBRPs have yielded some high profile successes (e.g., California condor [*Gymnogyps californianus*] and the black-footed ferret [*Mustela nigripes*]), but such programs often fail to achieve the desired outcome (Fischer and Lindenmayer, 2000; Mathews et al., 2005; Snyder et al., 2002).

The critical question for the success of all CBRPs is the same: will the benefit of augmenting or reestablishing a population with

captive animals outweigh the loss of taking individuals from the wild? One way to address this question is to use population models. Specifically, matrix population models provide a flexible framework for evaluating dynamics and persistence of biological populations, and for evaluating effects of alternative management strategies on population dynamics; these models can be used for evaluating the efficacy of expensive CBRPs before they are initiated or modified (Caswell, 2001; Ezard et al., 2010; Morris and Doak, 2002; Hostetler et al., 2013; Seddon et al., 2007). However, most modeling studies of reintroduction programs have focused on either evaluating the impacts to the source population of animal removal for captive breeding, or predicting the influence of the released individuals on the dynamics of augmented populations (Armstrong and Reynolds, 2012). Rarely have studies evaluated the potential costs (removal of wild animals) and benefits (increased population size or viability) of a CBRP simultaneously within a single modeling framework (Bustamante, 1996). Yet, it is only by weighing these costs and benefits that we can critically determine the overall benefit of starting or continuing a CBRP.

Concerned by the threat of extinction, in 2002 the U.S. Fish and Wildlife Service established captive breeding colonies and a release program for Key Largo woodrat (*Neotoma floridana smalli* [KLWR], McCleery et al., 2005, 2006; McCleery et al., 2013; Winchester

\* Corresponding author. Tel.: +1 352 846 0566; fax: +1 352 846 6984.

E-mail address: [ramccleery@ufl.edu](mailto:ramccleery@ufl.edu) (R. McCleery).

et al., 2009). This cryptic, nocturnal subspecies of the eastern woodrat (*Neotoma floridana*) has been isolated in the approximately 972 ha of remaining hardwood hammock forests on the northern 1/3 of Key Largo, Florida where its population is believed to have steadily declined since the 1970s (McCleery et al., 2005; U.S. Department of the Interior, 1973, 1984). In fact, a population viability analysis (PVA) suggested a 70% probability of extinction by 2012 (McCleery et al., 2005). The causes for the KLWR's decline remain unknown but has been attributed to altered habitats (McCleery et al., 2007), predation (Winchester et al., 2009) and reduced recruitment during drier years (McCleery et al., 2013).

Captive breeding facilities were established at Lowry Park Zoo (Tampa, Florida, USA) and later at Disney's Animal Kingdom (Orlando, Florida, USA) in 2002 (Alligood et al., 2011). Subsequently, a release program was designed to put captive-bred KLWRs into their native hammock habitats. In an effort to augment the population, 41 KLWRs were released into the wild over a period of two years (McCleery et al., 2013). The survival rates of released KLWRs during the first 3 months were exceedingly low, with only a few released KLWRs surviving long enough to contribute to the growth of the wild population through reproduction. In fact, most of the released animals were lost to predation shortly after their release (McCleery et al., 2013). Low survival rates of released KLWRs have been attributed to inadequate anti-predator and vigilance behaviors of released individuals (McCleery et al., 2013). These results effectively halted the KLWR CBRP until the program could be thoroughly evaluated. However, it may be possible to address the behavioral shortcoming, and improve survival of released animals through prerelease conditioning programs and/or *in situ* captive-breeding program (Kock et al., 2007; Seddon et al., 2007).

We used the endangered KLWR as a model system to develop a comprehensive modeling framework that allows simultaneous consideration of animal removal from the wild for captive breeding, captive breeding success, and the influence of released animals on the dynamics and persistence of the wild population. We then use this framework for evaluating the KLWR CBRP, and for identifying strategies that can ensure success of CBRP. Accordingly, our objectives were to: (1) determine if CBRP as practiced previously would benefit or harm KLWR recovery; (2) evaluate population-level effects of alternative removal, captive breeding and reintroduction strategies; and (3) determine if improved recruitment rates of captive KLWR and improved survival of released KLWRs can improve a CBRP through growth of the wild population.

## 2. Materials and methods

### 2.1. Study area

KLWRs are isolated in an approximately 972 ha, 14-km stretch of protected tropical hardwood hammocks on the northern third of the island of Key Largo, the first and largest in a chain of islands (keys) extending from the southeastern tip of peninsular Florida. The hardwood hammock habitats on the island of Key Largo are unique, with a high diversity of mast producing trees and shrubs of West Indian origin (Karim and Main, 2009; Strong and Bancroft, 1994). Common trees found in the hammocks of Key Largo include gumbo-limbo (*Bursera simaruba*), poisonwood (*Metopium toxiferum*), wild tamarind (*Lysiloma bahamensis*) and pigeon plum (*Coccoloba diversifolia*). The climate of Key Largo is sub-tropical, exhibiting marked wet and dry seasons. Rainfall amounts and patterns can be variable but the region averages 1179 mm of rainfall annually, most of which occurs from May through September (Bancroft et al., 2000).

### 2.2. Population model

#### 2.2.1. Parameter estimation

Estimates of KLWR abundance have been varied. In 2002, McCleery et al. (2006) estimated the wild KLWR population to be 30–182 individuals. A more recent study using data from 2008 to 2011 estimated annual abundance between 78 and 693 individuals; however, the confidence intervals of these estimates ranged from 0 to 1164 KLWRs, indicating poor precision of those estimates (Potts et al., 2012). Due to uncertainty in the estimates of population size and the disparity in the estimates, we repeated our analyses using a range of initial abundance of 150, 300 and 500 KLWRs.

We used estimates of apparent survival ( $\phi$ ) and recruitment ( $f$ ) rates for wild-born KLWRs reported by McCleery et al. (2013) based on Capture-Mark-Recapture (CMR) analyses. KLWR recruitment varies seasonally as well as annually, with peaks in the spring and fall and little reproduction over the winter (Sasso and Gaines, 2002; McCleery et al., 2013). To account for this variation, we used seasonal and annual estimates of  $f$  from McCleery et al. (2013; Table 1).

To estimate true survival ( $S$ ) of the wild, zoo and released populations we used radio-telemetry data and captive breeding records reported by McCleery et al. (2013). However, instead of utilizing the non-parametric estimates reported in that study, we used parametric estimates of survival, because parametric survival models allow projections of survival and its variance to desired time intervals (Lee and Wang, 2003). We used R version 2.12.2 (R Development Core Team 2011) statistical software (survival package; Therneau and Lumley, 2011) and evaluated the fit of four different parametric models for survival (exponential, lognormal, Weibull, and log logistic) based on Akaike Information Criterion (AIC; Table 2). For the zoo and wild populations, the exponential model was the best fitting model, and we used estimates based on this model to parameterize our population model. Alternatively, the best model for the released population was the lognormal model, which allows the hazard rate (the instantaneous rate of mortality) to vary over time. In this case, the hazard rate increased rapidly until approximately the 9th day after release, after which it declined slowly. To account for the varying hazard rate we estimated different survival probabilities from the lognormal model for the first two months and the next two months (Table 1). We set true survival rate for zoo population to an exponential log-hazard scale and true survival of released animals to a lognormal log-hazard scale.

To estimate recruitment in the KLWR zoo population we used specimen reports from Disney Animal Kingdom (Orlando, FL) and Lowry Park Zoo (Tampa, FL) that detailed any changes in the health or reproductive status of each woodrat (McCleery et al., 2013). We acquired records on 58 individuals at Disney (47 born at the facility) and 33 individuals at Lowry Park Zoo (24 born at facility) from April 2002 to December 2011. We calculated the mean number of offspring per individual for every two month interval (time step of the model) that they were in captivity and used this as an estimate of recruitment rate for the population model.

Finally, we assumed that the difference between true survival and apparent survival reflected emigration rate (i.e.,  $E = S_{wild} - \phi$ ), and that this rate was the same for released and wildborn individuals.

#### 2.2.2. Model structure

For modeling purposes, we created a population composed of four interacting subpopulations: (1) wildborn (*wild*) population on Key Largo, (2) captive (*zoo*) population for captive breeding, (3) released, 0–2 months post release ( $rel_1$ ), and (4) released, 2–4 months post release ( $rel_2$ ) (Fig. 1). We split the released rats

**Table 1**  
Parameter estimates of apparent survival ( $\phi$ ), true survival ( $S$ ), recruitment ( $f$ , seasonal and annual), and emigration  $E$  for wild born (wild), captive (zoo) and release ( $rel$ ) Key Largo woodrat populations adapted from McCleery et al. (2013) and used in the population matrix model. Recruitment was estimated for spring peak (March–April), fall peak (September–October), and non-peak (all other months) time periods. The time step of all demographic parameters is two months.

Parameter	Symbol	Mean	SE
Wildborn apparent survival probability	$\phi$	0.676 (study period 1) 0.770 (study period 2) 0.735 (study period 3)	0.057 0.062 0.101
Wildborn true survival probability	$S_{wild}$	0.893	0.038
Wildborn recruitment rate	$f_{wild}$	0.216 (non-peak, study period 1) 0.695 (spring peak, study period 1) 1.450 (fall peak, study period 1) 0.104 (annual average, study period 2) 0.503 (annual average, study period 3)	0.084 0.259 0.547 0.054 0.123
Zoo survival probability	$S_{zoo}$	0.974	0.004
Zoo recruitment rate	$f_{zoo}$	0.039	0.006
Released survival probability1	$S_{rel1}$	0.307	0.064
Released survival probability2	$S_{rel2}$	0.481	0.075
Average emigration rate	$E$	0.168	0.089

**Table 2**  
Comparison of fit for exponential, lognormal, Weibull and log logistic survival models to known fate data for wild born (Wild), captive (Zoo) and released (Released) Key Largo woodrats. Number of parameters ( $K$ ), Akaike’s Information Criteria (AIC), change in AIC from the top model ( $\Delta AIC$ ) and model weights (Weight) are presented.

Population	Model	$K$	AIC	$\Delta AIC$	Weight
Wild	Exponential	1	104.052	0	0.467
	Lognormal	2	105.852	1.8	0.19
	Weibull	2	106.016	1.964	0.175
	Log logistic	2	106.093	2.041	0.168
Zoo	Exponential	1	613.975	0	0.61
	Weibull	2	614.936	0.961	0.377
	Log logistic	2	621.68	7.705	0.013
	Lognormal	2	635.089	21.114	0
Released	Lognormal	2	333.974	0	0.626
	Log logistic	2	335.492	1.518	0.293
	Exponential	1	339.318	5.344	0.043
	Weibull	2	339.623	5.65	0.037

into two subpopulations because survival rates varied over time post-release (McCleery et al., 2013). For each time step the population was projected as

$$N_{t+1} = A_t N_t + \begin{bmatrix} -c_t \\ c_t - r_t \\ r_t \\ 0 \end{bmatrix}$$

where  $N_t$  and  $N_{t+1}$  are population vectors at time  $t$  and  $t + 1$ , respectively,  $A_t$  is the population projection matrix at time  $t$ ,  $c_t$  is the number of individuals transferred from the wild to the zoo population in time step  $t$ , and  $r_t$  is the number of individuals released from the zoo to the wild population in time step  $t$ . The population projection matrix was of the form:

$$A_t = \begin{bmatrix} \phi_t + f_{wild,t} & 0 & f_{zoo} & S_{rel_2} - E_t + f_{wild,t} \\ 0 & S_{zoo} + f_{zoo} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & S_{rel_1} - E_t & 0 \end{bmatrix}$$

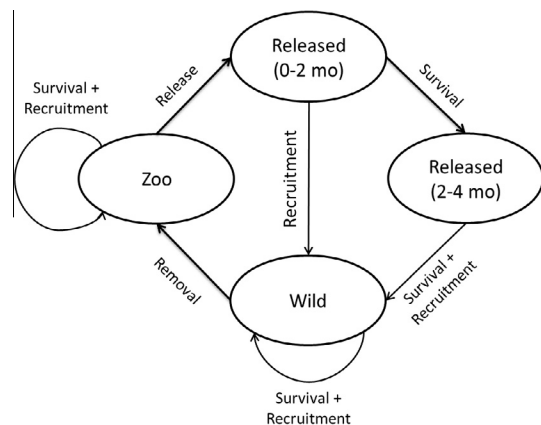
Released individuals transferred from the zoo population to  $rel_1$  and then  $rel_2$  before they joined the wild population and could produce wildborn individuals, if they successfully reproduced (we assumed that the  $rel_1$  population had the same recruitment rate as the zoo population but that the  $rel_2$  population had the same recruitment rate as the wild population). Individuals in the wild

subpopulation in time step  $t$  produce wildborn individuals in time step  $t + 1$  if they survive and reproduce. Transitions from the wild to the zoo and from the zoo to the  $rel_1$  populations only occurred when specified under model scenarios.

2.2.3. Parameter uncertainty, stochasticity and density-dependence

We explicitly incorporated parametric uncertainty, environmental stochasticity and demographic stochasticity into our population model because these factors can strongly influence dynamics and persistence of small populations (Bakker et al., 2009; Ellner and Fieberg, 2003; Hostetler et al., 2012, 2013; McGowan et al., 2011). We incorporated parameter uncertainty via a parametric bootstrap method (Efron and Tibshirani, 1993). First, we estimated a variance–covariance matrix for each set of parameters. Then, we sampled values by running 1000 parametric bootstraps. For each run we selected mean slope and intercept parameter values from a multivariate normal distribution and converted the results to the real scale. In this way, we sampled values of parameters from the empirically estimated distributions and parameter values.

To account for the influence of environmental stochasticity we randomly selected recruitment and apparent survival estimates from one of three study periods (Table 1) from McCleery et al. (2013). For recruitment, we selected from one set of seasonal recruitment estimates (study period 1, non-peak, spring peak, and fall peak) or one of two annual estimates of recruitment (annual average, study periods 2 and 3). When we selected one of the annual estimates, we generated seasonal values for recruitment so that the proportional variation between seasons was the



**Fig. 1.** Conceptual representation of the population modeling framework used to evaluate the influence of a captive breeding and release program on the persistence of the endangered Key Largo woodrat. The time step of the model was 2 months.

same as estimated for study 1, but the average annual recruitment remained the same as the estimate we selected.

We accounted for demographic stochasticity when any of the four populations had a small number of individuals ( $>0$  and  $\leq 19$ ) at a particular time step by including stochasticity in projections to the next time step (Morris and Doak, 2002). We incorporated demographic stochasticity using a sampling approach (Caswell, 2001). The number of survivors was sampled from a binomial distribution, with parameters  $N$  and  $p$  (number of trials,  $N$  = number of individuals, and success probability,  $p$  = survival probability). Similarly, the number of recruits was sampled from the Poisson distribution (mean,  $\lambda$  = recruitment rate \* number of individuals). Finally, we sampled the number of emigrants (i.e., number of released individuals that permanently left the study area) from binomial distribution (number of trials,  $N$  = number of individuals that survived, and success probability,  $p$  = emigration probability). We assumed a ceiling population size of 4500 KLWR for the wildborn and released subpopulations such that projected population size never exceeded the ceiling, by setting the two released subpopulation sizes to 0 and the wildborn subpopulation size to 4500 (Aççakaya et al., 1997).

#### 2.2.4. Scenarios and evaluation

We used the population model to evaluate three alternative management scenarios for the KLWR CBRP: (1) no management, (2) a gradual captive breeding, and (3) rapid captive breeding. In the *no management* scenario, no individuals were removed from the wild to the zoo population, and we modeled the wild population only. Under the *gradual captive breeding* scenario 5 KLWRs were removed from the wild population every January for 5 years. For the *rapid captive breeding* scenario 20 KLWRs were moved from the wild to the zoo population at the beginning of the simulation period. During years 2–5, three KLWRs were taken from the wild each year and added to the zoo population. For both captive breeding scenarios, the zoo population size was limited to 20 KLWRs and surplus KLWRs were released to the wild. After 5 years (consistent with USFWS planning cycles) both captive breeding programs were terminated and all KLWRs in the zoo population were released to the wild at that time. Nonetheless, to determine if any of the management scenarios had a lasting impact on the KLWR population we simulated population growth for an addition 10 years (15 years total).

In addition to evaluating different removal and release scenarios, we also were interested in understanding how improved survival of released KLWRs and increased recruitment in the zoo population might alter the success of the CBRP. Improved survival of released KLWR could possibly be achieved through pre-release conditioning or *in situ* breeding. Enhanced or modified captive breeding protocols could potentially increase recruitment in the zoo population. Accordingly, we evaluated how increased survival of released KLWRs and increased recruitment in the zoo population would alter the relative success of the three management scenarios. We reran our scenarios with three values of zoo recruitment rates: 0.039 (estimated value for the zoo population), 0.503 (highest annual estimate for the wild population), and 0.271 (halfway between the zoo and highest estimate for the wild population). Similarly, we reran the sets of simulations with survival of released rats closer to those estimated for the wild population. For the first two months post-release we used monthly estimates of 0.307 (estimated survival for released KLWRs), 0.893 (estimated survival for the wild population), and 0.6 (halfway between the estimated released and wild populations). For the second two months (2–4 months post-release) we set survival probability of released rats to 0.481 (estimated survival for released rates during 2–4 months post-release), and 0.893 (estimated survival for the wild population), and 0.747 (halfway between .06 released and wild population

estimate). The three values of recruitment for the zoo population and three sets of survival of released rats produced nine combinations of parameter values for which we ran simulations for each of the three management scenarios (i.e., no management, gradual captive breeding, and rapid captive breeding).

For all scenarios, we estimated the probability of quasi-extinction (PQE), defined as the probability that the simulated population size falls below a critical threshold. We considered three critical thresholds (1 [extinct], 20 and 50). We compared the mean and 90th percentile PQE ranges among scenarios over the 15 year simulation period for the three different initial abundances (150, 300, 500 rats). Additionally, to determine if there were significant differences among scenarios (at  $\alpha = 0.1$ ) we directly compared the differences (mean and 90th percentile) in the PQE among the three scenarios (Ellner and Fieberg, 2003). We also compared the mean and 90th percentile of the projected size of the wild population by year 15 years for the three different initial abundances. Finally, to examine if increased survival of released KLWR and recruitment of the zoo population might enhance the viability of the CBRP and grow the wild populations, we modeled the populations with enhanced survival and recruitment estimates (see above) at the intermediate starting population size (300) and a PQE threshold of 20, for no management and the rapid captive breeding scenarios only.

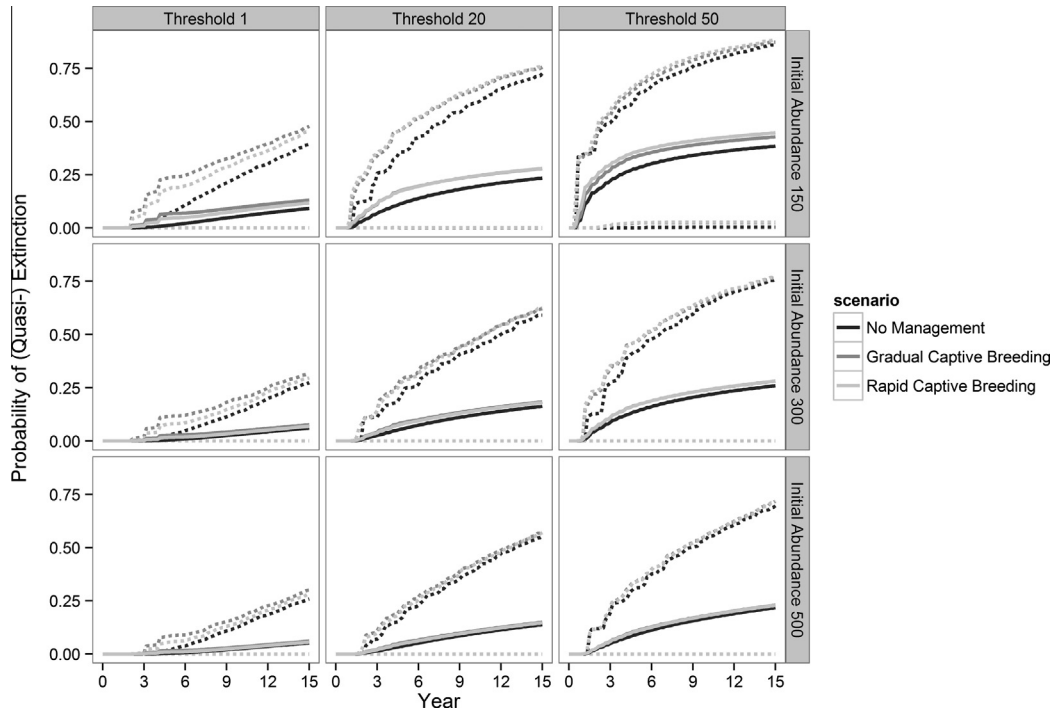
#### 2.2.5. Simulations

We simulated the KLWR population for 15 years on a two month time step; we chose a two month time step because it would allow us to account for seasonal variation in recruitment (McCleery et al., 2013). We ran a total of 3,000,000 simulations. To estimate PQEs and population sizes at each time step we ran 1000 simulations for each of the three management scenarios and each simulation utilized 1000 bootstrap runs to incorporate parametric uncertainty into the model. We specifically included parametric uncertainty, and environmental and demographic stochasticities by running simulations with the equivalent of four nested loops (see Hostetler et al., 2013).

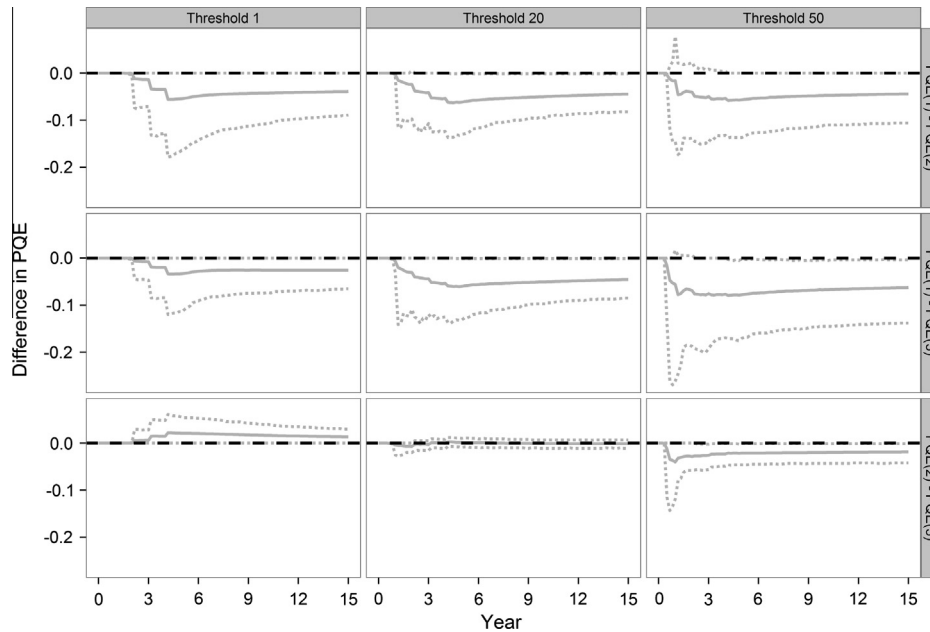
### 3. Results

The probabilities of quasi-extinction were similar among the three scenarios but were lower for the no management scenario across all values of critical population sizes and initial abundances (Fig. 2). Not surprisingly, PQE decreased as starting population size increased. At the end of year 15, the estimated probability of extinction with a starting population size of 300 were 0.060 (90th percentile range: 0–0.273), 0.076 (0–0.317), and 0.069 (0–0.296) for the no captive breeding, gradual captive breeding, and rapid captive breeding scenarios, respectively. For the critical population size of 20 KLWRs, estimated PQEs were 0.163 (0–0.591), 0.184 (0–0.623), and 0.180 (0–0.625) for the no captive breeding, gradual captive breeding, and rapid captive breeding scenarios, respectively (Fig. 2; same starting population size).

PQE generally increased from the no management strategy to both captive breeding strategies, and the magnitude of difference in PQE between the no management and captive breeding scenarios decreased as the initial abundance increased (Fig. 3, Supplemental Figs. S1 and S2). Additionally, for all three initial abundances PQE was generally lower for the rapid captive breeding scenario compared to the gradual captive breeding scenario at the PQE threshold of 1; however, the difference dissipated and once reversed as the thresholds increased (Fig. 3, Supplemental Figs. S1 and S2). There were clear trends in the results showing difference among the scenarios for all initial abundances; however, there were only very marginally statistically significant differences (at  $\alpha = 0.1$ , measured by overlap of 90th percentile ranges with zero).



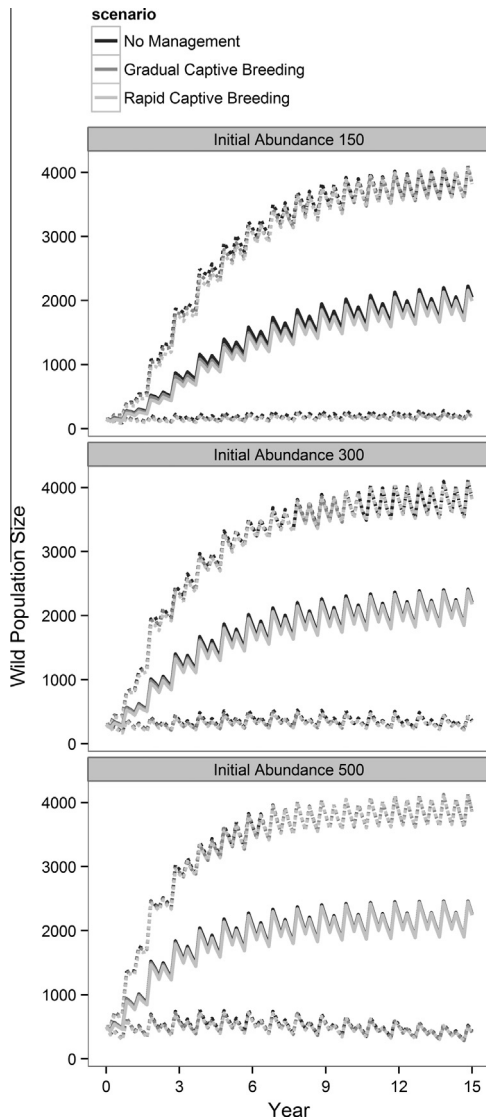
**Fig. 2.** Projected mean (solid lines) and 90th percentile ranges (dotted lines) for probability of quasi-extinction for the wild Key Largo woodrat population by year and management scenario, for three critical thresholds (1, 20, and 50 individuals) and starting wild population size of 150, 300 and 500 individuals.



**Fig. 3.** Projected mean (solid lines) and 90th percentile ranges (dotted lines) for differences in probability of quasi-extinction (PQE) for the wild Key Largo woodrat population by year, critical threshold (1, 20, 50), and management scenario combinations, for starting wild population size of 150 individuals. The top row of panels shows the differences in the probabilities of quasi-extinction between no captive breeding and gradual captive breeding scenarios (PQE(1) – PQE(2)); the second row shows the differences in the probabilities of quasi-extinction between no captive breeding and rapid captive breeding scenarios (PQE(1) – PQE(3)); the third row shows the differences in the probabilities of quasi-extinction between gradual and rapid captive breeding scenarios (PQE(2) – PQE(3)). The dashed line at 0 represents no difference between scenarios.

Projected average population sizes were almost identical among management scenarios, especially by year 15, with higher ending population size with increasing initial abundances (Fig. 4). Population sizes showed a distinct seasonal trend, with peaks corresponding with the two peaks of reproduction. Average population size generally increased until year 7 or 8 followed by a leveling off to year 15.

Using higher survival probabilities for released KLWR reduced PQE slightly (threshold of 20; end of year 15; starting population 300) for the captive breeding scenarios (Figs. 5 and 6), but at most to a level very similar to PQE for the no management scenario (gradual = 0.169 [0–0.613]; rapid = 0.162 [0–0.608]). Increasing zoo recruitment alone moderately decreased PQE, to a level less than the no management scenario (gradual = 0.097 [0–0.454],



**Fig. 4.** Projected mean (solid lines) and 90th percentile ranges (dotted lines) for wild population sizes for the Key Largo woodrat population by year and management scenario, for starting wildborn population size of 150, 300 and 500 individuals.

rapid = 0.095 [0–0.44]). Improving both vital rates further reduced PQE to as low as 0.077 (0–0.376); however, differences in PQE among the scenarios were not significant at  $\alpha = 0.1$  (measured by overlap of 90th percentile ranges with zero).

#### 4. Discussion

We developed a straightforward and effective framework for linking all important facets of a captive breeding and release program (CBRP) to critically evaluate if augmenting a population with captive reared animals outweighed the loss of individuals from the wild. For our study, the answer was clearly no; KLWRs are better left in the wild. As currently practiced, there is no evidence that a CBRP would contribute to the recovery of KLWR. The mean sizes of the wild KLWR population under rapid and gradual CBRP protocols were marginally lower than that under no management scenarios (Fig. 4). Both captive breeding scenarios also increased (sometimes significantly) the probability of quasi-extinction (PQE) over a no management protocol.

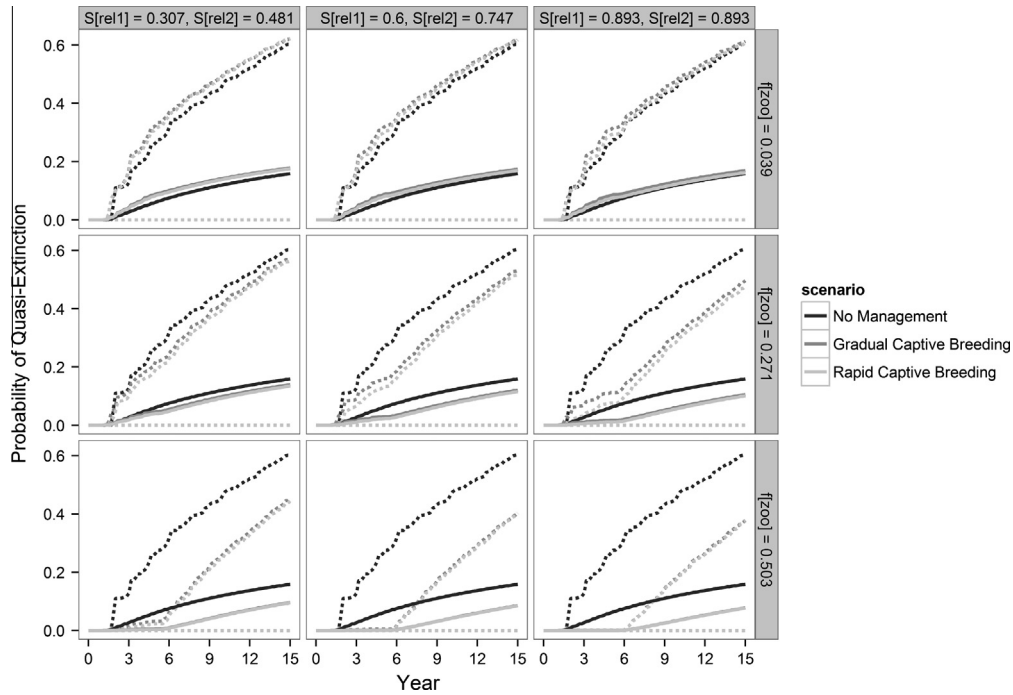
Previous modeling of CBRPs has advocated that every single wild animal of a small population (<20 females) be brought into captivity (Tenhumberg et al., 2004). However, this was predicated on the assumption that growth of captive population exceeds that of the wild population. Our modeling framework allowed us to test this assumption and for the KLWR CBRP it was violated; the rate of recruitment in captivity was substantially lower than that in the wild, and released individuals mostly died before they could reproduce. As with most vertebrates, it was clearly difficult to have a productive and consistent breeding program for KLWRs in captivity (Snyder et al., 2002). Less than 50% of female KLWR in captivity gave birth and it was reported that fewer than 15% of KLWR copulations in captivity resulted in pregnancy (Alligood et al., 2011). Thus, any rush to bring animals in from the wild highlights a critical point: if the captive population does not have a better growth rate than the wild population the CBRP will not be successful. Assuming captive breeding will increase growth rates may be a risky assumption and it may be impossible to test without first establishing a breeding program.

Our comprehensive modeling framework that simultaneously considered animal removal from the wild for captive breeding, captive breeding success, and the influence of released animals on the dynamics and persistence of the wild population allowed us to identify weak linkages in KLWR CBRP. The survival rates of released KLWR were notably lower than wild KLWR (Table 1), which clearly contributed to the apparent failure of KLWR CBRP. However, improvements in survival rates even to the levels of wild KLWRs were insufficient to improve KLWR population persistence (Figs. 5 and 6). Alternatively increased recruitment from the captive breeding programs, in the form of increased breeding success, can likely contribute to KLWR population growth and help with recovery. Still, the most effective approach to increasing the KLWR population in the wild appears to be to improving both recruitment in the captive setting and survival rates of released KLWRs. Alligood et al. (2011) reported improvements and modifications of Disney's Animal Kingdom captive breeding program over the period 2005–2009. However, it is likely that the captive breeding protocols would still need considerable improvements (i.e., environment, nutrition, enhancement, handling) before recruitment rates approach even half of what has been recorded in the wild.

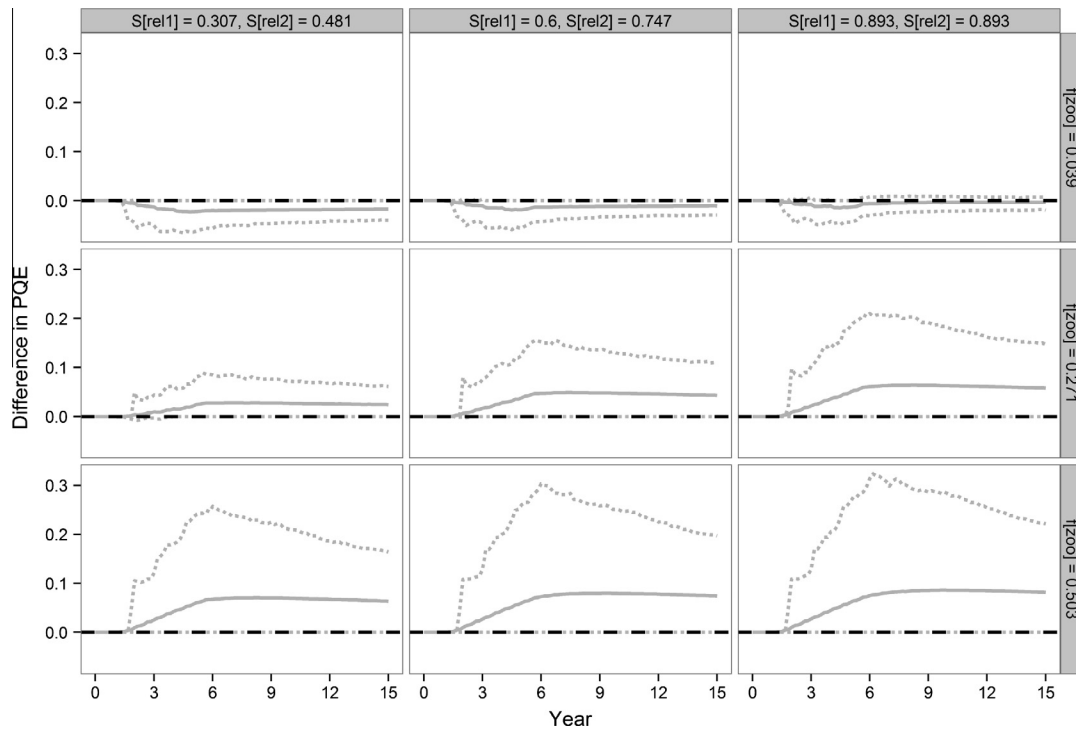
Given the small size of the wild KLWR population and apparent failure of the CBRP to improve persistence of the wild population, it would seem unwise to restart a CBRP. Nonetheless, a CBRP may be helpful for buffering the population against catastrophic events (i.e. hurricane, drought), maintaining genetic diversity, improving captive breeding success and developing pre-release conditioning protocols. Under these circumstances we would recommend the rapid CBRP that brings in a cohort of KLWRs at once and maintains the population around 20 individuals. Under most initial abundances and thresholds of quasi-extinction the rapid CBRP decreased or had comparable PQE to the gradual BRP (Fig. 3, Supplemental Figs. S1 and S2).

We caution readers when interpreting our results that although the estimates used to create this model were reasonably precise it is probable that the available data were biased. We estimated parameters for the wild population using data collected from 1995 to 2007, during periods of relatively high or growing KLWR populations when enough KLWRs could be captured to permit estimation of survival or recruitment rates (McCleery et al., 2013). Thus, our estimates of survival and/or recruitment likely led to an underestimation of PQE.

Our study provides a framework for simultaneous consideration of animal removal from the wild, breeding success in captivity, and survival of released animals for a comprehensive evaluation of captive breeding programs. This approach allowed us to identify weak links in the KLWR CBRP, and to make specific recommendations as



**Fig. 5.** Projected mean (solid lines) and 90th percentile ranges (dotted lines) for probability of quasi-extinction (critical threshold = 20 individuals) of the wild Key Largo woodrat population by year, management scenario, survival of released woodrats in the first two months ( $S[rel1]$ ), survival of released woodrats in the next two months ( $S[rel2]$ ), and zoo recruitment ( $f[zoo]$ ) for starting wildborn population size of 300 woodrats.



**Fig. 6.** Projected mean (solid lines) and 90th percentile ranges (dotted lines) for difference in probability of quasi-extinction (PQE, critical threshold = 20 individuals) of the wild Key Largo woodrat by year, released survival, and zoo recruitment for starting wild population size of 300 individuals. All panels show the probabilities of quasi-extinction for no captive breeding minus the probabilities of quasi-extinction for sudden captive breeding. All percentile ranges include 0 (dashed line, representing no difference between scenarios).

to how KLWR CBRP could be improved to aid in recovery of the wild population. Furthermore, our approach can be used at the planning stages of a CBRP to identified demographic targets that would make the program successful. Initially, we would recommend modeling a range of model parameters, like we did with

initial abundance in this study. As data from the CBRP becomes available, parameters can be continually modified to improve model performance. Our modeling framework was fairly simple with one wild population as a source and release site, (the only extant population of KLWR) but our framework can easily be extended

to account for more complex CBRPs with multiple source, release and captive populations, making it a robust tool for evaluating CBRPs, which remains a valuable tool in conservation biologists' toolbox.

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### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.11.026>.

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