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Demographics of Reintroduction Special Section

Optimal Allocation of Captive-Reared Puerto Rican Parrots: Decisions When Divergent Dynamics Characterize Managed Populations

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ABSTRACT Reintroduction programs often face the challenge of sustaining multiple populations, each with unique demographic rates. Decision makers must determine how to allocate a finite number of captive-reared animals among these populations to achieve the fundamental objective of the program. We explored the optimal allocation of captive-reared Puerto Rican parrots (*Amazona vittata*) to 3 distinct populations: a struggling relict (population 1), a successfully reintroduced population (population 2), and a potential (new) population (population 3). We illustrate decision tradeoffs using 4 hypothetical scenarios of demographic performance created using the parrot literature and expert opinion and find the optimal decision by formulating the problem as a Markov decision process. Across all scenarios, our analysis favored releasing parrots into population 2 first when population sizes were small, followed by releases into population 3, and subsequently to population 1. The point in the decision space at which these transitions occurred was a function of location demographic rates. Releasing parrots in a location harboring an extant population versus a location that does not is advisable if differences in environmental conditions that promote population growth between locations are small. If management actions cannot ameliorate limiting factors in a location, decisions will favor translocations from such locations and allocations to locations where growth is more likely. When the cost of conducting a release is considered, managers should occasionally postpone releases to avoid these costs. This is optimal whenever the weighted contribution of the additional parrots to the sum of the discounted additional expected future population levels is less than the size of the fixed costs. This was most often the case for population 1 as costs increased. © 2013 The Wildlife Society.

KEY WORDS allocation, captive-reared birds, conservation, costs, optimization, population growth, Puerto Rican Parrot, recurrent decisions, reintroduction.

Once widespread throughout the island, the Puerto Rican parrot (*Amazona vittata*) was reduced to a relict population at El Yunque National Forest (EY), one of few forested areas left on the island by the late 1930s (Brash 1987, Snyder et al. 1987). The range contraction was followed by a marked decrease in population size. Estimated at 2,000 individuals in the 1940s, the parrot numbered under 20 individuals by the late 1960s when recovery efforts started in earnest (Rodríguez-Vidal 1959, Snyder et al. 1987, United States Fish and Wildlife Service [USFWS] 2009). Nearly every aspect of the species' life cycle, including most biotic interactions (e.g., predators, ectoparasites), have been managed to promote its persistence (USFWS 2009). Moreover, 55 captive-reared parrots were released at EY between 2000 and 2010 to foster population growth. Yet, after more than 40 years, the population size at EY remains at 15–20 individuals. Of the factors restricting population growth, rainfall and raptors are considered the most influential (White et al. 2005, Beissinger et al. 2008, USFWS 2009, Collazo et al. 2010). The former affects post-fledging survival and breeding productivity (e.g., respiratory diseases); the latter impinges upon juvenile and adult survival.

The reintroduction of the Puerto Rican parrot into historical habitat is central to the recovery and persistence of the species (Lacy et al. 1989, USFWS 2009) by providing a means to reduce the risk of extinction due to environmental and demographic stochasticity. This recovery strategy was implemented in 2006 when captive-reared parrots were released in the Rio Abajo Forest, a state reserve imbedded in the northern karst region of the island (USFWS 2009). The

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incipient population exhibits demographic attributes associated with successful reintroductions (White et al. 2012). These include a greater number of breeding pairs (10) than the maximum (6) recorded in El Yunque since 1973, similar breeding productivity (1.6 chicks/nesting attempt), a core population size (around the release area) of 40–50 individuals, and a floating population of >20 individuals with the potential of pioneering a separate location. Efforts to start a third population are in motion (White et al. 2010), triggered by the successful trajectory of the Rio Abajo Forest population but also by the negative trajectory of the population at El Yunque. The observed finite rate of increase ($\hat{\lambda}$) at El Yunque has averaged 0.94 since 1998 despite intensive management aimed at increasing breeding productivity and supplementing the population since 2000 (Collazo et al. 2010). Parrots released at a third site, scheduled to start in 2015, are expected to perform as well as those released at the Rio Abajo Forest based on similarities in habitat quality parameters (White et al. 2010).

The confluence of the aforementioned circumstances has ushered the recovery program into a phase of expanded and competing needs to sustain 2 extant populations and create a third one. The constraint is largely imposed by the production capacity of 2 captive breeding facilities (USFWS 2009), 1 located at El Yunque and the other at the Rio Abajo Forest. Together these facilities are projected to produce, on average, 8 birds for release annually. Managers must decide how to allocate captive-reared parrots within an emerging metapopulation (Armstrong and Seddon 2008). For example, should parrots be used to build up a single large population or to supplement multiple smaller ones? This challenge is underscored by mounting evidence indicating that El Yunque is a sink habitat for parrots (Muiznieks 2003, Beissinger et al. 2008). In this context, decisions to perpetuate this relict population could undermine efforts to foster growth of reintroduced populations, and thus, an assessment of tradeoffs among alternative release options is important.

We assessed a population on a downward trajectory (henceforth population 1), a successfully reintroduced population (henceforth population 2), and a third, potential population expected to perform much like population 2 (henceforth population 3). In this context, we explored how to allocate a finite number of captive-reared parrots among 3 populations with distinct vital rates. We also explored how these decisions would be affected if a cost was assessed on releases. This is a hypothetical scenario aimed at assessing tradeoffs, given the costs of releasing 8 parrots or none in a given year.

We present a recurrent decision framework aimed at assessing different allocation options to maximize population numbers of parrots. We consider 4 population scenarios, where scenarios depict distinct demographic rates for each population, and are based on expert opinion and available data. The scenarios represent different possible models of demographic performance for the 3 populations, and so capture uncertainty (Regan et al. 2002). Decisions are guided by the fundamental objective of the recovery program, that is, attain self-sustaining, viable populations (USFWS 2009). We focused on population numbers because endangered species face the possibility of extinction due to both demographic and environmental stochasticity. Risk of loss due to demographic stochasticity decreases as the population size increases, whereas risk of loss due to environmental stochasticity decreases as the geographic extent or the number of populations increases. Risks were minimized by establishing a second population at a location (Rio Abajo) with more favorable environmental conditions (e.g., less precipitation) and reduce risk of a direct hit by a hurricane compared to the El Yunque parrot population (Lacy et al. 1989, USFWS 2009). These 2 populations (El Yunque and Rio Abajo) are considered independent, allowing for an exploration of different allocation options to meet our fundamental objective. We used a population growth model that incorporated Allee effects (Wang et al. 1999, Armstrong and Wittmer 2011) because the individual population numbers at El Yunque can be very small thus raising the probability that these effects might undermine population growth (e.g., predator avoidance, inbreeding; Beissinger et al. 2008). Finally, we articulate ways in which the decision framework presented here could incorporate uncertainty and learning, and opportunities to adopt similar approaches to address other challenges in recovery programs. The decision context discussed here is not unique to the Puerto Rican parrot, and thus, we hope that insights derived from this assessment will be useful to other programs facing similar challenges.

METHODS

We formulated the problem as a Markov decision process (MDP; Puterman 2005). We assumed stationarity in the transitions and rewards and solved for an infinite horizon stationary solution with stochastic dynamic programming using the MATLAB toolbox MDPSolve (Fackler 2011) to determine the optimal allocation of parrots. Following Puterman (2005), MDPs are models for sequential decision making when outcomes are uncertain. The MDPs consist of 4 essential elements: states, actions, transition probabilities to determine how each state evolves given the different actions (i.e., model of the system), and rewards (i.e., utility or objective function). Two additional pieces are necessary to solve MDPs as well, a time horizon and discount factor, which are necessary to ensure convergence of the algorithms. We were interested in exploring the consequences of choosing different actions in a state, which generates a reward (through our objective function), and determines the future state at the next period through our model. The goal of solving an MDP is to obtain an optimal policy or strategy (optimal in the sense it maximizes our utility) that provides a prescription of which action to choose given any possible state at a future time. It allows one to explore and understand the implications of choosing specific actions when one is uncertain about how the actions may influence the system. Therefore, MDPs provide a logical and transparent approach to making optimal decisions in the face of uncertainty.

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We considered a setting in which 3 independent populations exist with the current size of population i given by N_i where the N_i define a discrete set of states. Suppose further that X animals are available for release and that R_i are released into population i. Therefore, our set of available actions consist of the number of parrots to be released into population i (here capped at 8). The managers have the further option to refrain from releasing any animals in a given year, so the total number released is either X or 0.

Each subpopulation is governed by the same population dynamics function except with population-specific parameter values (see conservation scenarios below; Table 1). We used a population growth model whose functional form balanced structural simplicity with realism (Wang et al. 1999, Armstrong and Wittmer 2011). Under this model, population size grows annually as follows

$$N_i^+ = \left(N_i S + N_i b\left(1 - \frac{N_i}{K}\right)\left(\frac{N_i}{N_i + \theta}\right)\right)e$$

where N_i is the current population size, N_i^+ is the population size at the next time period, and e is a unit-mean noise term with standard deviation 0.15 (i.e., $e \sim$ LogNormal(1,0.15)). By including e, we were able to directly incorporate environmental uncertainty into the population dynamics of each of the populations. Although we had no specific biological information to inform our choice of the standard deviation of e (0.15), the value chosen provided us with a sufficient level of variation to influence the dynamics of each population. The parameters have the following interpretations: S is the annual survival probability of current individuals in the population, b is the number of recruits per current individual per year at low density without Allee effects, K is the maximum population size where recruitment occurs, and θ is the strength of the Allee effect (reproduction is halved when $N = \theta$). For simplicity, we assumed that the population consisted of only adult individuals and we ignored juveniles; therefore, every individual in the population is available for breeding at year 1, hence the definition of b. We set K at 500 individuals for each population (Lacy et al. 1989) and we set θ, the strength of the Allee effect, at 35 individuals. Although previous research has not clearly defined at what population level the Allee effect should be set (e.g., Armstrong and Wittmer 2011), we chose a value of 35 because it is the level at which the El Yunque population hovered in the aftermath of hurricane Hugo in 1989 and before its downward trend in 1998 (USFWS 2009). This model assumes that survival is density independent, whereas recruitment of individuals is subject to both compensation of a logistic form and depensation of a rectangular hyperbolic (RH) form (Armstrong and Wittmer 2011). In addition to the random noise affecting the population transition model (e from above), we incorporated the possibility of a catastrophic event as an additional source of environmental uncertainty. We incorporated this uncertainty as follows:

$$N_i^+ = \begin{cases} \left(N_i S + N_i b\left(1 - \frac{N_i}{K}\right)\frac{N_i}{N_i + \theta}\right)e & \text{with probability } 1 - \exp(-\lambda N_i) \\ 0 & \text{with probability } \exp(-\lambda N_i) \end{cases}$$

We obtained λ by solving for a logistic function such that the probability of a catastrophic event (e.g., category $\geq$3 hurricane) wiping out a small population (15 individuals going extinct) was equal to 0.03, which is roughly the frequency of a hurricane (category $\geq$3) hitting Puerto Rico (3 times out of 100 yr; Lacy et al. 1989). This gave us a value of $\lambda = 0.2317$. Overall, our population transition function now incorporated 2 different sources of environmental uncertainty (random noise, e, and a catastrophic event) that we believe were relevant for island populations.

To incorporate a form of model uncertainty, we created 4 population scenarios, each representing a distinct demographic scenario with unique parameter values for each population (Table 1). These are hypothetical models, motivated by known and expected performance of Puerto Rican parrots, but whose primary purpose was to illustrate and gain insights about how different settings might influence allocation decisions. We assumed that post-release survival of captive-reared parrots during the first year was equal across populations in those scenarios (sensu Armstrong and Wittmer 2011). We focused on recruitment rates (b) as the primary source of variation for 3 of the 4 scenarios; survival rates (S) were equal among these 3 scenarios. Recruitment of individuals is partly a function of breeding productivity and survival, and thus, germane to reintroduction efforts during the early stages of population growth. For the last and fourth scenario, we gave survival (S) and

Table 1. Individual survival (S) and recruitment (b) values for 3 hypothetical populations (pop.) of Puerto Rican parrots. We obtained parameter values from the literature and from expert opinion, and used them to characterize the growth of each population under 4 demographic scenarios. Scenario 1 (base) reflects current conditions (population 1) and expected conditions for populations 2 and 3 based on expert opinion. Scenario 2 (relocate within reserve) reflects gains in recruitment if population 1 occurred in a more benign environment (i.e., less rainfall, lesser predator density). Scenario 3 (improved population 3) reflects similarities in recruitment rates between populations 2 and 3. Scenario 4 (divergent rates) portrays population 1 with strong negative growth, and populations 2 and 3 with strong positive growth. In the population growth model, K is the maximum population size where recruitment occurs, and θ is the strength of the Allee effect (reproduction is halved when $N = \theta$). Parameters K and θ were equal across all scenarios and populations.

Scenario	Population	S	b
1	Pop1	0.88	0.18
	Pop2	0.88	0.33
	Pop3	0.88	0.27
2	Pop1	0.88	0.22
	Pop2	0.88	0.33
	Pop3	0.88	0.27
3	Pop1	0.88	0.18
	Pop2	0.88	0.33
	Pop3	0.88	0.33
4	Pop1	0.78	0.08
	Pop2	0.90	0.60
	Pop3	0.90	0.58

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recruitment of individuals (b) different values as described below.

We obtained parameter values for each scenario from published literature and expert opinion. We acknowledge the uncertainty associated with all parameters, including post-release survival, but we did not explore this form of parametric uncertainty in this manuscript. However, we do discuss its implications later in the context of decision making. We parameterized the first (base) scenario using the most recent estimates of vital rates for parrots reported in the literature and used in population viability analyses for population 1 (Beissinger et al. 2008, Collazo et al. 2010), and expert opinion for populations 2 and 3. The second scenario (improved habitat at EY) reflected hypothesized gains in recruitment if population 1 occurred in slightly more suitable habitat, simulating a supplementation within El Yunque National Forest in an area where rainfall and avian predation pressure would be lesser (USFWS 2009). The third scenario (improved population 3) reflected similar recruitment rates between population 3 (potential population) and population 2, also reintroduced and deemed successful. The last scenario (divergent rates) portrayed a setting where populations 2 and 3 exhibit high but plausible survival and recruitment rates (sensu Snyder et al. 1987, Lacy et al. 1989), whereas rates for population 1 represent a set of plausible values of a severely struggling and down-spiraling population. We obtained parameter values from simulations aimed at tracking the El Yunque population trajectory since 1998 using program Vortex (Lacy et al. 2009) and insights from recent analyses of post-fledging survival (Collazo et al. 2010).

In addition to the available actions and the transition functions described above, we also defined a reward function (objective function), time horizon, and discount rate to complete a full specification of an MDP. The reward function used to determine an optimal strategy for the 4 scenarios is to maximize the total population size summed over all 3 populations with the constraint that all 3 populations have to exist (i.e., if 1 of the populations goes extinct, the reward is 0), which is a stated requirement of the recovery program. We used an infinite time horizon (i.e., we plan to make decisions indefinitely vs. a finite time frame wherein a terminal decision period would exist) and, therefore, needed a discount rate to ensure convergence of an optimal action. To reflect the sense that success in the near term is more valuable than success in the distant future, we used a discount rate of 2%, which means that future rewards (sum of population sizes for all 3 populations) are discounted relative to current rewards. This discount rate follows the current Office of Management and Budget (OMB) recommendations on evaluating the cost effectiveness of federal programs (OMB 1993, 2011).

We also examined how consideration of program costs would affect the optimal strategies. In other words, managers may want to have the ability to forgo releases in a given year to avoid costs. The optimal strategy depends strongly on the assessment of the monetary value of an additional bird in the population. Multi-criteria objective functions are difficult to specify, but a common way to do this simply places weights on metrics for different objectives (alternative performance indicators) such that a linear tradeoff exists among competing objectives. In our study, the performance indicators were the number of animals and the dollar costs. To illustrate the effect of the weighting factor, we depicted the effect of alternative weighting factors on the 100-year expected population sizes, based on scenario 1. We started populations at the estimated current population sizes in the wild for Puerto Rican parrots. These were 25 (population 1, El Yunque), 45 (population 2, Rio Abajo), and 0 individuals in population 3 (new reintroduction). The utility function to illustrate this effect was wN-C, where N is the total number of birds in the 3 subpopulations, C is the release cost, and w is a weight measuring the monetary value of an additional bird. We expressed weight as units of \$1,000 (i.e., a weight of 0.4 results in a value of \$400 put on each additional bird in N). We explored the sensitivity of the optimal strategy to this weighting factor. We considered the alternative actions of placing 8 parrots in the wild or placing none. Therefore, the relevant cost in this example is the money saved in a given year from forgoing the release of 8 birds in a given year, which was estimated to be C = \$88,000. This cost is based on the average cost of producing a parrot per year (approx. \$11,000) by the aviaries supporting the release program (Engeman et al. 2003).

RESULTS

In all scenarios, without incorporating environmental stochasticity, populations 2 and 3 always exhibited growth over a range of population sizes (Fig. 1, above horizontal dotted line), whereas population 1 always followed a negative growth trajectory (below horizontal dotted line). Populations 2 and 3 exhibited positive growth up to about 250–300 individuals.

Allocation decisions for scenario 1 suggested that population 2 should be supplemented and grown up to 70 individuals (Fig. 2, top panel). When population 2 is between 70 and 100, but population 3 is less than 70, parrots should be released into population 3 (Fig. 2, bottom panel). When populations 2 and 3 exceed 100 parrots, no more birds should be released to either population, but should be released into population 1 (i.e., shared black decision space for population 2 and 3; Supplemental 1.1, available online at www.onlinelibrary.wiley.com). Under optimal management, the expected population sizes for all 3 populations suggest that populations 2 and 3 grow, but at slightly different rates, leveling off around 40–50 years from the initiation of the supplementation effort at 280 and 230 individuals, respectively (Fig. 3, top panel). Population 1 starts growing around year 20, leveling off around year 60 at about 150 individuals in scenario 1.

Hypothetical gains in recruitment rates by reintroducing population 1 into more suitable habitat within the same reserve (scenario 2) did not change allocation decisions appreciably as compared to the base scenario (Fig. 4, top panel; Supplemental 1.2, available online at www.onlinelibrary.wiley.com). The benefit of this recovery action for

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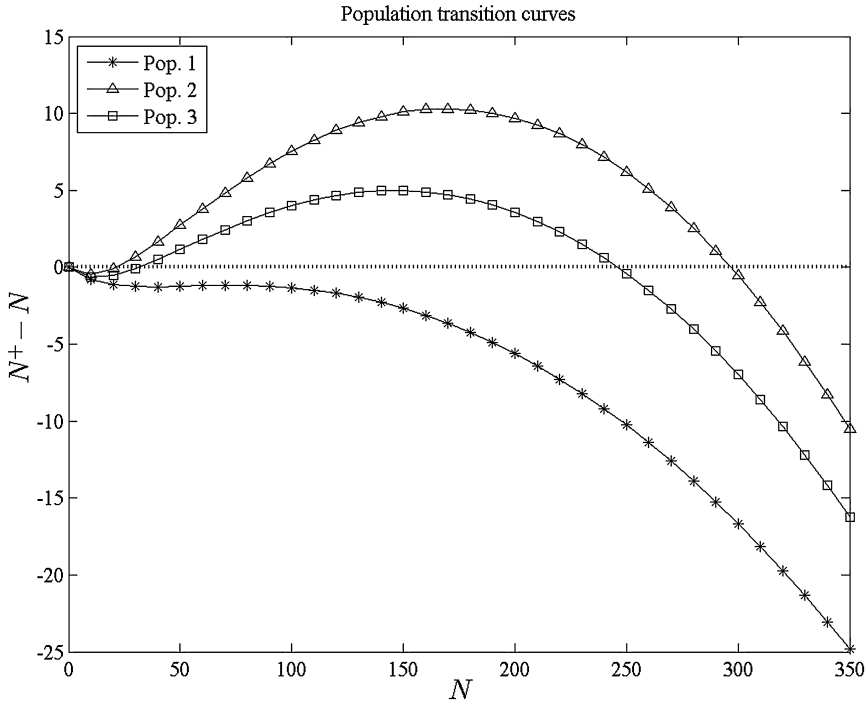

Figure 1. Growth curves for 3 hypothetical Puerto Rican parrot populations using a deterministic logistic growth model that incorporates Allee effects. We estimated growth under our base scenario (scenario 1). The *x*-axis corresponds to the population size (N); the *y*-axis corresponds to population growth ($N^+ - N$). One population (pop.) is on a downward trajectory (population 1), whereas a successfully reintroduced population (population 2), and a third, potential population (population 3) are expected to perform similarly. The black horizontal (dotted) line indicates population stability, the space above this line indicates population growth, and the space below this line indicates population decline.

population 1 is captured by more rapid growth between years 10 and 20, leveling off at 200 individuals (Fig. 3, second panel).

In a setting where population 3 was expected to perform like population 2 (scenario 3), birds should be released into population 2 first and releases should continue until the population reaches about 55 individuals (Fig. 5, top panel) to reduce the risk associated with the Allee effect. Parrots should be released into population 3 afterwards, and no parrots should be released to either population if they exceed 90 individuals. At those levels, parrots should be released into population 1 (i.e., shared black decision space for population 2 and 3, Supplemental 1.3, available online at www.onlinelibrary.wiley.com). Populations 2 and 3 leveled off at around 280 individuals (Fig. 3, third panel).

Situations where population 1 exhibits strong negative growth (scenario 4) and the others strong positive growth indicated that population 2 should be supplemented first, up to about 35 individuals, followed by releases into population 3 (Fig. 6, top panel). Subsequent decisions depend on the trajectory of each population up to about 175 individuals at which level birds should be released into population 1 (i.e., shared black decision space for population 2 and 3, Supplemental 1.4, available online at www.onlinelibrary.wiley.com). The response by populations 2 and 3 to supplementation is strong, leveling off at around 390 parrots by year 20–25 (Fig. 3, bottom panel). Although populations 2 and 3 are supplemented, population 1 exhibits a reduction in the expected number of parrots. Growth in population 1 is apparent between years 10 and 20, leveling off at about 40 individuals (Fig. 3, bottom panel).

We explored the effect of alternative weights for the value of an additional bird in the population (measured in units of \$1,000) on the 100-year expected population sizes and expected number of years of releases (Fig. 7). When no value is put on the population size ($w = 0$), releasing birds is not optimal. In this case population 3 is never established, population 2 is expected to grow to about 231 birds in 100 years, and population 1 is expected to go extinct. At low values of w (between 0.2 and 0.4, corresponding to values of \$200 and \$400 for each additional bird), releasing some birds into populations 2 and 3 is optimal, resulting in expected population sizes of 264 and 206 for populations 2 and 3, respectively, or a total population of 470 animals. This can be done with relatively few releases (about 18 in 100 years). When even greater value is placed on population size, releasing some birds into population 1 becomes optimal. With $w = 0.6$ (i.e., value of additional bird = \$600), a population of 594 animals is possible, but the expected number of releases in 100 years needed to accomplish this rises to 55. Further gains in population numbers are possible if a greater number of releases are undertaken. Using a weighting factor of $w = 2$, achieving an expected population size of 672 is possible, but it requires about 98 releases in 100 years. However, we found little gain in expected population sizes at 100 years with weights greater than approximately 1.3.

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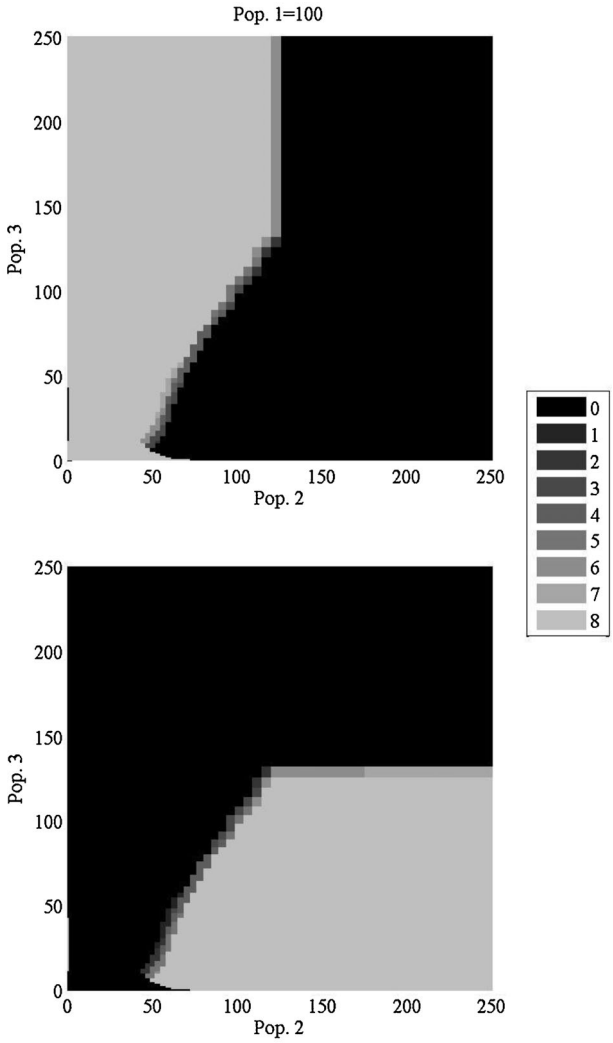

Figure 2. Decision space for allocations of a finite number of captive-reared parrots (8/yr) among 3 hypothetical populations (pop.) of Puerto Rican parrots under scenario 1 (base scenario). The *x*-axis corresponds to the size of population 2, the *y*-axis corresponds to the size of population 3, and population 1 is fixed at 100 in both subplots. Subplot 1 (on top) indicates the number of birds that are released to population 2 where black represents 0 and light gray represents 8 given the sizes of populations 1, 2, and 3 from above. Subplot 2 (on bottom) indicates releases to population 3 with the same conditions. We obtained optimal decisions by solving the problem as a Markov decision process. We parameterized scenario 1 using the most recent estimates of vital rates for Puerto Rican parrots reported in the literature and used in population viability analyses for population 1, and based on expert opinion for populations 2 and 3.

DISCUSSION

We used a recurrent decision framework to illustrate how various demographic settings influence decisions to allocate a finite number of captive-reared individuals among 3 populations. We incorporated 3 relevant sources of uncertainty into our optimization: 2 sources of environmental uncertainty (random noise and catastrophic events), and a form of model uncertainty (exploring 4 relevant scenarios using different parameter values for each population). Although the parameter values are not known with certainty, we explored a range of possible values based on available data and expert knowledge about Puerto Rican parrots. Thus, insights and implications for the recovery program of the parrot are discussed in conjunction with results. In our scenarios, decisions favored releasing individuals in population 2 first when population sizes were low, followed by decisions to release into population 3, and subsequently, to population 1. Not surprisingly, the points (population sizes) at which changes in the release policy occurred were a function of site demographic rates. This overarching inference is in concert with current and expected performance of extant populations. At present, the Rio Abajo Forest parrot population exhibits attributes associated with successful reintroductions (White et al. 2012). These include similar fledging success as in El Yunque, but are produced with minimal management interventions. The breeding cohort is already made up of 10 pairs, 40% more than recorded at El Yunque since 1973, and its population is more than twice that of El Yunque (40–50 individuals). Reintroductions are frequently unsuccessful (Armstrong and Seddon 2008), but when they are successful, several factors are common denominators (White et al. 2012). Among the most fundamental of these is selecting reintroduction sites of high quality. In the specific case of the Puerto Rican parrot, these are characterized by lesser precipitation and density of avian predators, primary factors impinging upon vital rates (Lindsey et al. 1994; White et al. 2005, 2010; Beissinger et al. 2008; Collazo et al. 2010).

The Puerto Rican parrot population at El Yunque has exhibited negative growth since 1998 ($\hat{\lambda} = 0.94$; USFWS 2009, Collazo et al. 2010). Negative growth was common to all scenarios for population 1, most notably in scenario 4 (divergent rates). Accordingly, releasing parrots into a population under such conditions would not be favored until allocations were first directed towards populations where the prospect of achieving population growth was more attainable. Moreover, when the cost of conducting a release is considered, occasionally postponing releases to avoid these costs is optimal. In our scenarios, this consideration was shown to affect population 1 markedly because the potential for population growth was the smallest. These findings were in concert with Chauvenet et al. (2010) who showed that optimal allocations of funds among subpopulations of the threatened Sumatran tigers (*Panthera tigris sumatrae*) favored saving subpopulations with the greatest potential for growth that were more efficient to manage (higher-quality habitat). However, supplementing population 1 led to an increase in population size, even under scenario 4. This raises an important point for conservation, best illustrated by scenario 4. Expected population levels dipped during the first 10 years, increasing after supplementation was initiated, but leveling off at around 40 individuals. However, the expected population size of 40 can only be maintained if 8 parrots are released annually and indefinitely over the infinite time horizon. This inference is consistent with simulation results that indicate that the El Yunque parrot population responds positively to supplementation of $\geq$8–10 individuals annually, but increases in population numbers taper off and the population decreases soon after supplementation is stopped

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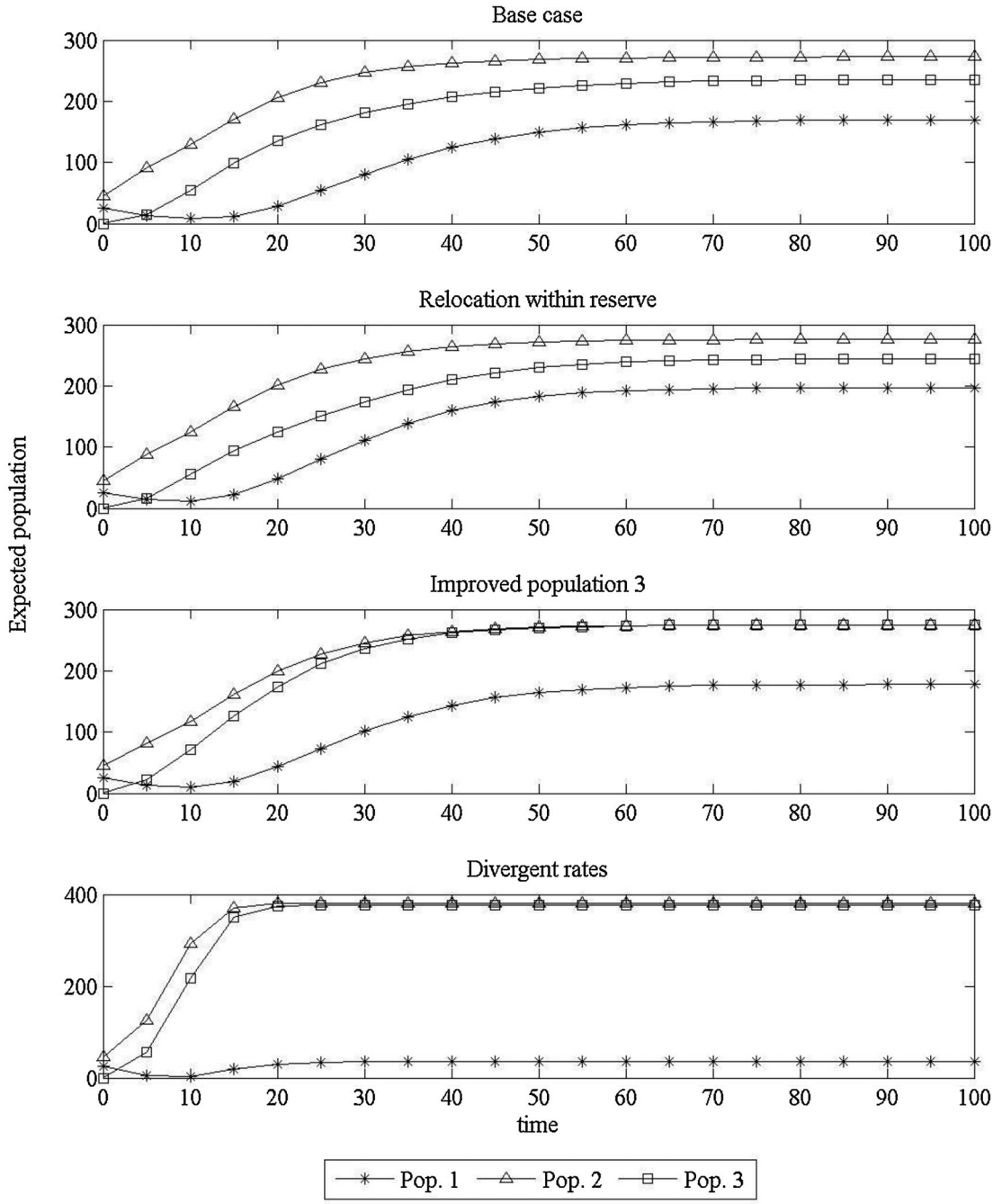

Figure 3. Expected population size of 3 hypothetical populations (pop.) of Puerto Rican parrots subject to releases of captive-reared birds over a 100-year time horizon. The top panel represents expected population size under scenario 1 (base), the second panel under scenario 2 (relocation within a reserve), the third panel under scenario 3 (improved population 3), and the bottom panel under scenario 4 (divergent rates).

(Muiznieks 2003, Collazo et al. 2010). Indeed, the numbers at the El Yunque population have been in a downward trend despite releasing 47 captive-reared parrots between 2000 and 2008 (Collazo et al. 2010), and another 8 between 2009 and 2010. The ecological basis for this predicament is rooted in the demographic vulnerability of the population (Beissinger et al. 2008), exemplified by the myriad of recovery actions targeting nearly every aspect of the species' annual cycle (USFWS 2009).

Continued recovery efforts and investment in the El Yunque Puerto Rican parrot population has its basis in preserving the biological culture of the species (USFWS 2009). That is, preserving the complex vocal repertoire and subtle behavioral nuances of the relict population. Otherwise, the contribution of this isolated population to an emerging metapopulation is limited to serving as a potential source of parrots for translocation to supplement other populations (Armstrong and Seddon 2008). The valuing of the biological culture has suggested the possibility of initiating a population elsewhere within El Yunque, where ostensibly less rainfall and fewer avian predation events could lead to improved vital rates (e.g., Nimitz 2005, USFWS 2009). Scenario 2 was aimed at capturing this possibility. From a practical point of view,

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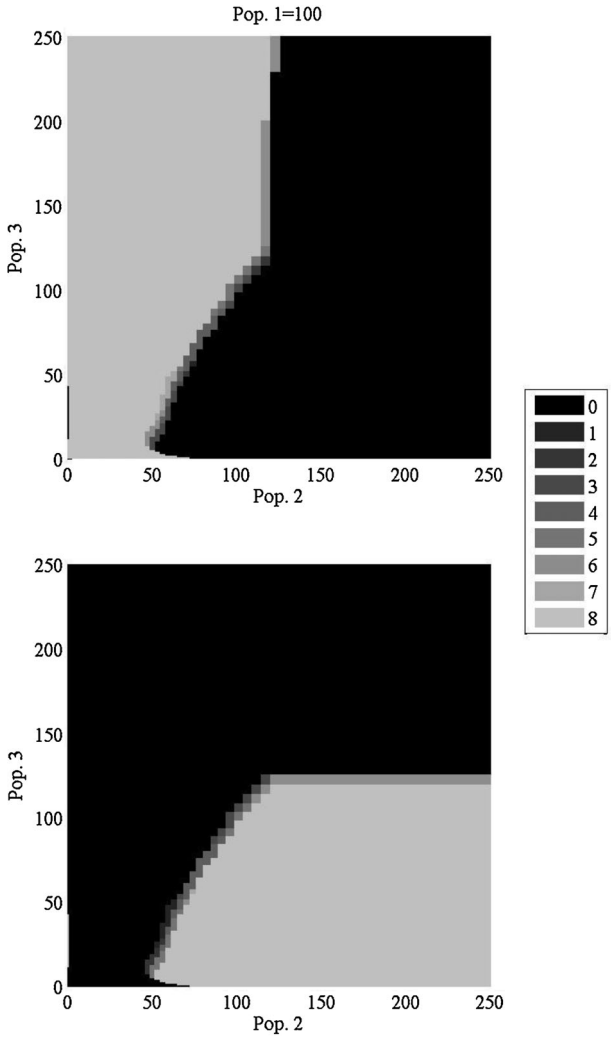

Figure 4. Decision space for allocations of a finite number of captive-reared parrots (8/yr) among 3 hypothetical populations (pop.) of Puerto Rican parrots under scenario 2 (relocation within a reserve). The *x*-axis corresponds to the size of population 2, the *y*-axis corresponds to the size of population 3, and population 1 is fixed at 100 in both subplots. Subplot 1 (on top) indicates the number of birds that are released to population 2 where black represents 0 and light gray represents 8 given the sizes of populations 1, 2, and 3 from above. Subplot 2 (on bottom) indicates releases to population 3 with the same conditions. We obtained optimal decisions by solving the problem as a Markov decision process. Scenario 2 represents hypothesized gains in recruitment if population 1 occurred in slightly more suitable habitat, simulating a reintroduction within El Yunque National Forest where rainfall and avian predation pressure would be less than in the currently occupied area of the reserve. Under this scenario, recruitment rates improved by 5%.

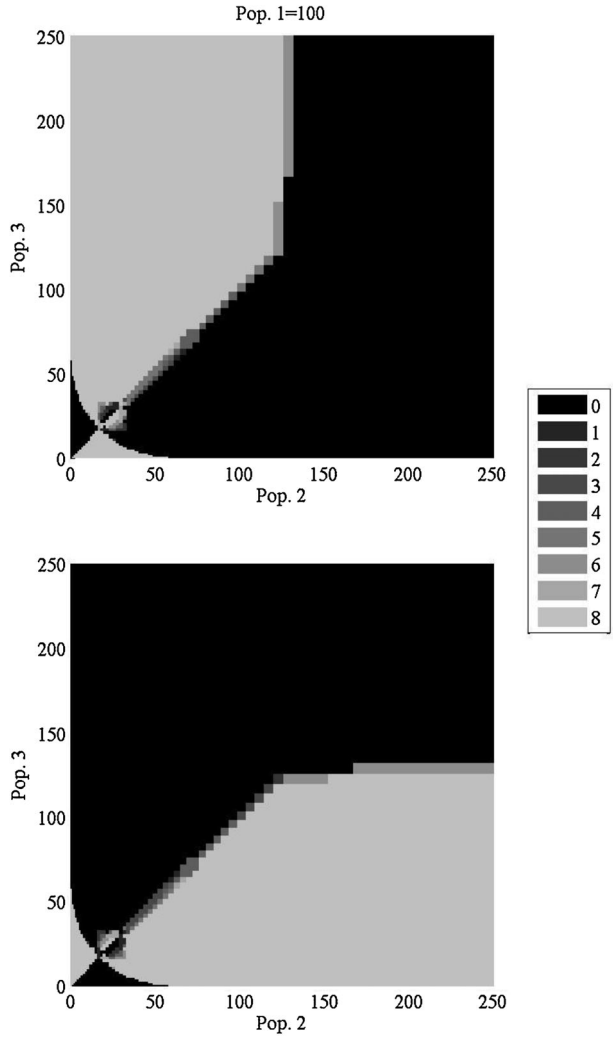

Figure 5. Decision space for allocations of a finite number of captive-reared parrots (8/yr) among 3 hypothetical populations (pop.) of Puerto Rican parrots under scenario 3 (improved population 3). The *x*-axis corresponds to the size of population 2, the *y*-axis corresponds to the size of population 3, and population 1 is fixed at 100 in both subplots. Subplot 1 (on top) indicates the number of birds that are released to population 2 where black represents 0 and light gray represents 8 given the sizes of populations 1, 2, and 3 from above. Subplot 2 (on bottom) indicates releases to population 3 with the same conditions. We obtained optimal decisions by solving the problem as a Markov decision process. Scenario 3 reflected converged (similar) recruitment rates between population 3 (newly reintroduced) and population 2, reintroduced and deemed successful.

advantages of releasing within the same reserve include shorter distances between the source and reintroduction sites, and tapping existing logistical support (e.g., aviary). More importantly, the uncertainty associated with expected gains might be smaller as the functional relationship between habitat and demographic rates would be better known. As illustrated by scenario 2, decisions would be influenced by the differential gains in vital rates between releasing within the reserve and sites elsewhere (e.g., McDonald-Madden et al. 2011). The reality is that options to substantially change the parrot population dynamics at El Yunque National Forest via changes in habitat quality are limited, if even existent. The primary factors impinging upon the population vital rates—rainfall and avian predation—are not expected to vary sufficiently across the reserve to produce marked changes in demographic rates.

Insights from this work are relevant to the growing field of reintroduction biology, mostly associated with endangered species conservation (Armstrong and Seddon 2008, Rout et al. 2009, Ewen et al. 2012). We focused on the influence of the availability of a finite number of parrots for release annually. Parrots would be used to reintroduce the species into suitable habitat and supplement existing populations, actions aimed at minimizing the extinction probability of a metapopulation (Possingham 1996). We also explored how decisions would be affected if a cost was associated with

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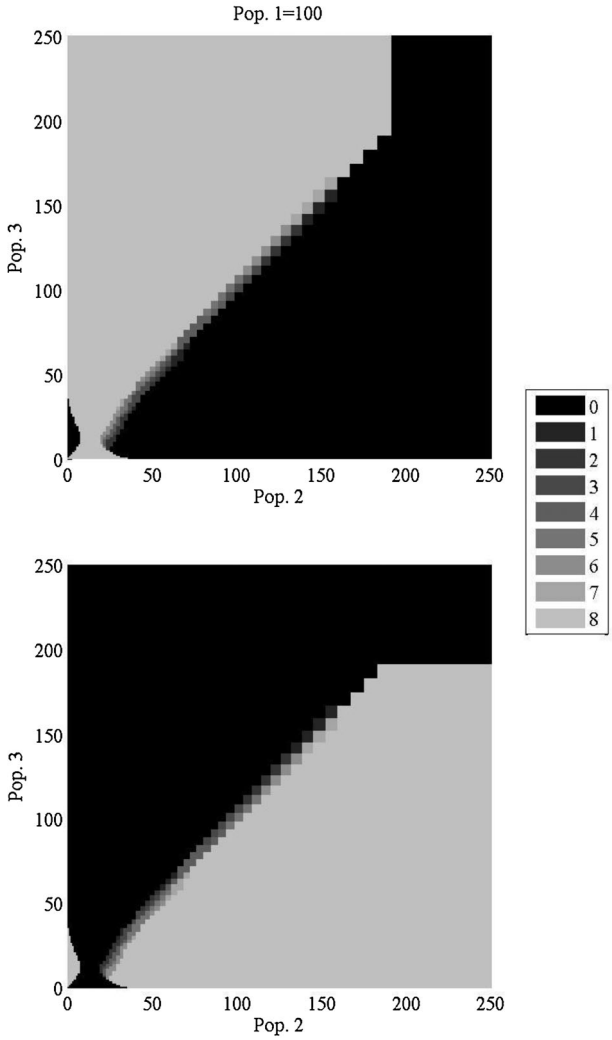

Figure 6. Decision space for allocations of a finite number of captive-reared parrots (8/yr) among 3 hypothetical populations (pop.) of Puerto Rican parrots under scenario 4 (divergent rates). The *x*-axis corresponds to the size of population 2, the *y*-axis corresponds to the size of population 3, and population 1 is fixed at 100 in both subplots. Subplot 1 (on top) indicates the number of birds that are released to population 2 where black represents 0 and light gray represents 8 given the sizes of populations 1, 2, and 3 from above. Subplot 2 (on bottom) indicates releases to population 3 with the same conditions. We obtained optimal decisions by solving the problem as a Markov decision process. Scenario 4 portrays a setting where populations 2 and 3 exhibit high but plausible survival and recruitment rates, whereas rates for population 1 represented a set of plausible values of a severely struggling and down-spiraling population.

releasing parrots in the context of differing population growth potential (sensu Chauvenet et al. 2010). Implicit in the hypothesized demographic rates of our scenarios was the influence of habitat quality on reintroductions and supplementations (Armstrong and Reynolds 2012, Chauvenet et al. 2010, McCarthy et al. 2012, White et al. 2012). Uncertainty about habitat quality at new release sites is an inherent component of any reintroduction program (Possingham 1996, McDonald-Madden et al. 2011). Acknowledging this uncertainty is important because it could also influence decisions regarding alternative but complementary actions to foster growth such as the age composition of released birds. For example, an evaluation of translocation strategies of griffon vultures (*Gyps fulvus*) showed that decisions were influenced by uncertainty with respect to the survival of individuals and the expected ability to learn (McCarthy et al. 2012). Finally, we adopted a growth model that acknowledged the potential influence of Allee effects in the context of supplementing small or incipient populations. Allee effects might exacerbate predation rates as low population numbers reduce the effectiveness of group defense (Deredec and Courchamp 2007) or contribute to decreased egg fertility by means of reduced optimal mating choices as suspected for Puerto Rican parrots in El Yunque (T. H. White, Jr., personal observation, USFWS). Although we did not formally explore Allee effects in this work, Armstrong and Wittmer (2011) did so and suggested that decision frameworks could be used to assess costs and benefits of alternative actions to avert these effects.

Decisions throughout the Puerto Rican parrot recovery program have been characterized by 1-time evaluations of alternative actions. Decisions on whether or not to supplement or reintroduce to a site were developed with the aid of population viability analyses (Lacy et al. 1989, Collazo et al. 2000, 2010). Reintroduction sites were selected using the strengths–weaknesses–opportunities–threats approach (SWOT; Trujillo 2005, White et al. 2010), and releases were preceded by studies aimed at maximizing post-release survival and genetic diversity (Daniels et al. 2001, Collazo et al. 2003, Haig et al. 2004, White et al. 2005). However, the recovery program has entered a new phase, 1 characterized by expanding and competing needs to maintain at least 3 populations. In this context, decisions will be recurrent and we suggest that decisions could be informed with a passive adaptive management framework (McCarthy et al. 2012). In our example, this would be accomplished by re-estimating model parameters each year based on targeted monitoring data obtained in the previous year (Nichols and Armstrong 2012), and the management model resolved using the new estimates.

Classifying the success of the program can be completed in a multitude of ways and this could be reflected in different reward functions. For example, the 3 populations may not be equally valued by managers; this would be captured by unequal weights placed on these populations in the objective function. In our scenarios, we treated all populations equally and were only interested in the total number of individuals summed across all 3 with the constraint that all 3 had to exist indefinitely. A different set of optimal actions may exist if, say, we could let 1 population go extinct, but still get a maximum number of birds. Thus, we recommend that the sensitivity of the optimal decisions to alternative reward functions be explored.

We have illustrated a decision framework that is germane to the recovery program of the Puerto Rican parrot, where circumstances (e.g., negative growth) place a high premium on informed decisions (Rout et al. 2010). We also considered alternative strategies that might include translocating wild birds from El Yunque to locations where the fundamental objective of the program—a self-sustaining, viable population—will more likely be attained.

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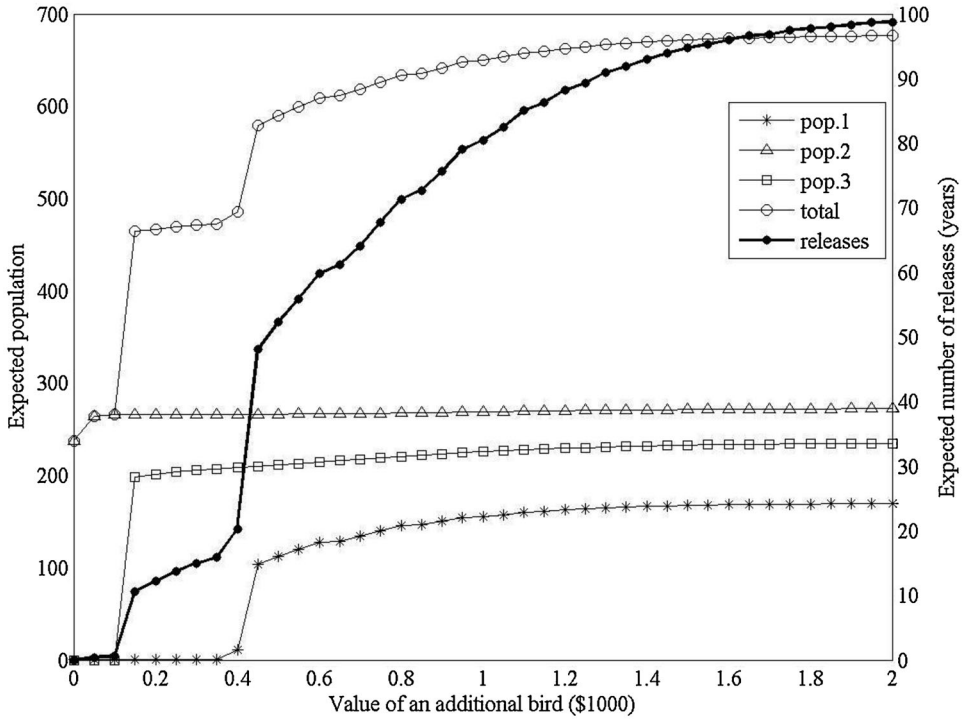

Figure 7. Exploration of alternative weights on population size relative to the cost of releasing parrots displayed as the 100-year expected population levels of 3 hypothetical populations (pop.) of Puerto Rican parrots. The left *y*-axis corresponds to the expected population; the right *y*-axis corresponds to expected number of years of releases (8 birds released per year). The value of an additional bird is measured in units of $1,000. Decisions involve the allocation of a finite number of captive-reared parrots (8/yr) under scenario 1 (base scenario). We obtained optimal decisions by solving the problem as a Markov decision process. We parameterized scenario 1 using the most recent estimates of vital rates for Puerto Rican parrots reported in the literature and used in population viability analyses for population 1, and based on expert opinion for populations 2 and 3. Populations were initialized at 25 individuals (population 1), 45 (population 2), and 0 (population 3).

MANAGEMENT IMPLICATIONS

The results of our optimizations suggest that if the fundamental objective of a reintroduction project is to attain self-sustaining, viable populations of a species, captive-reared birds should be allocated first where potential for growth is greatest. One should supplement such sub-populations until they are firmly established, before attempting to establish new ones. Exceptions to this generalization could come from other considerations (e.g., social values). Habitat quality is a paramount consideration in reintroduction and supplementation strategies and one should avoid costs and risks of releases in less than suitable habitat by formally evaluating competing sites and keying on factors germane to vital rates and carrying capacity. Given that all managers face budgetary limitations, they must also consider the effect of alternative costs on the long-term population level. Finally, one should account explicitly for the inherent level of uncertainty in alternative strategies. Reintroduction programs are best characterized as a process of recurrent decisions to prevent extinction. Uncertainty has a non-trivial influence over decisions such as determining the optimal group size for release and its age composition. We explored 2 major sources of uncertainty (environmental and model) in our analyses, but suggest that additional sources be incorporated. Specifically, other forms of parametric uncertainty (e.g., sampling error) and model uncertainty (e.g., different functional forms of the population growth model) would be valuable to explore. Ultimately an adaptive management framework could provide an opportunity to explicitly incorporate the aforementioned considerations into the decision process, to learn about model parameters and ecological systems under management, and to, thereby, improve the basis upon which subsequent decisions are made. Our 4 scenarios could be used as alternative models in adaptive management and a form of model uncertainty could be resolved by learning which scenario corresponds most closely to reality. In addition, alternative functional forms of the population dynamics could be suggested and evaluated. A management plan could be envisioned wherein release efforts are only undertaken if the existing subpopulations have reached a specific size sufficient to ensure viability and the cost of undertaking releases is warranted. We provided an optimization framework that allows exploring those competing objectives.

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