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RESEARCH ARTICLE

# The Puerto Rican Parrot Reintroduction Program: Sustainable Management of the Aviary Population

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The cornerstone of the recovery plan for the critically endangered Puerto Rican parrot (*Amazona vitatta*) is an actively managed, long-term reintroduction program. One captive population distributed across two aviaries in Puerto Rico is the sole source for release but its ability to persist as a managed resource has not been evaluated since 1989. We conducted an assessment for sustainable management of the aviary population while harvesting for release. To assess demographic rates such as population growth, vital rates, and age/sex structure, we compiled a studbook database on all living, dead, and released individuals in the aviary population. Using an individual-based risk assessment model we applied population specific data based on the management period from 1993 to 2012 to simulate future aviary population dynamics and evaluate future potential production. We modeled four potential management strategies to harvest parrots for proposed releases; these scenarios vary the number of parrots and the life stage. Our simulations revealed that the aviary population can be simultaneously managed for sustainability and harvesting of parrots for release. However, without cautious management, overharvesting can jeopardize sustainability of the aviary population. Our analysis of the aviary breeding program provides a rare opportunity to review progress relative to conservation program objectives after four decades of active management. The successful growth of the aviary population and its ability to serve as a sustainable source for reintroductions supports the 1973 decision to build a breeding program from a small population of 13 parrots. Zoo Biol. XX:XX–XX, 2014. 

**Keywords: *Amazona vitatta*; captive population management; PopLink; risk analysis; ZooRisk**

## INTRODUCTION

Reintroduction programs for any species are risky, complex conservation actions but these programs may be even more of a challenge when captive populations are the sole source of individuals for release [Kleiman, 1989; Seddon et al., 2007; Snyder et al., 1996; Wilson et al., 1994]. For captive populations, managers must consider changes in genetic structure, loss of behavioral competency, and sustainability of the captive population [Earnhardt, 2010; Leus and Lacy, 2009; McPhee, 2004]. Due to challenges inherent to reintroduction efforts and a need to manage wisely, scientists and managers have attempted to assess individual factors contributing to potential success or failure of a release program. Most of the species-specific case studies have focused on factors such as management of threats in the wild, methodology for releases, monitoring after releases, evaluation of release programs, and adaptive management of wild populations [Seddon et al., 2007]. Few published case studies exist evaluating sustainability for the source population (wild or captive) when individuals are harvested for release; this is true even when captive populations are the sole

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source for recovery [but see Coonan et al., 2010; Earnhardt et al., 2009]. The IUCN Reintroduction Guidelines [1998] and other publications caution managers against jeopardizing the sustainability of a source population [Earnhardt, 2010; Kleiman, 1989]. Sustainability, defined by Lacy [2012] as "management of the resource in a manner that does not deplete its value for the future" is a well-recognized demographic and genetic challenge for captive populations. In our study, we evaluate past progress as well as current status and generate a computer model to assess sustainability of the captive source population as it contributes to the reintroduction program of the Puerto Rican parrot (*Amazona vittata*), an iconic and high-profile conservation species.

Conservation actions taken on behalf of the Puerto Rican parrot have a four-decade history. At one time these parrots were abundant and widespread, estimated near 1 million birds, but due to diverse threats including habitat loss and fragmentation, the wild population declined to 13 parrots by 1975 [Snyder et al., 1987]. In 1973, managers made a decision to establish an aviary population with chicks and eggs taken from the small remaining wild population [U.S. Fish and Wildlife Service, 1982, 1999, 2009]. The long-term management objective was to breed these birds and harvest from a future (i.e., larger) captive population for a reintroduction program. For reintroductions based on captive breeding programs, concerns exist that captive programs can (1) be costly, (2) direct funds away from habitat restoration, (3) alter genetic structure of future wild populations, (4) compromise natural behavior of the species, and (5) have low likelihood of success [Earnhardt, 2010; Griffith et al., 1989; Leus and Lacy, 2009; McPhee, 2004; Snyder et al., 1996; Wilson et al., 1994]. Yet for some highly endangered species like the Puerto Rican parrot, managers have no alternate options as a reintroduction program based on captive breeding may be the only viable recovery solution, despite the risks.

Similar to the wild population, the new captive population faced a suite of diverse inherent threats. When conserving small wild or captive populations, scientists and managers must navigate through demographic, genetic, and environmental threats that can thwart population growth or lead to extinction [Ballou et al., 2010; Caughley, 1994; Gilpin and Soulé, 1986; Soulé et al., 1986]. The 1973 aviary population of Puerto Rican parrots was vulnerable to these threats: demographic stochasticity intrinsic to small size; genetic factors such as inbreeding depression; and environmental hazards including hurricanes and disease [Beissinger et al., 2008; Lacy et al., 1989; Leus and Lacy, 2009; Snyder et al., 1996; Wilson et al., 1994]. Throughout development of the program, managers of the Puerto Rican parrot recovery effort have attempted to reduce these potential environmental, genetic, and demographic threats to the aviary populations [U.S. Fish and Wildlife Service, 1982, 1999, 2009]. However, demographic challenges persist as the number of parrots is a limiting factor. Reintroduction managers want to harvest as many parrots as possible from the aviaries to release at reintroduction sites because greater release numbers can increase probability of successful establishment [Griffith et al., 1989]. Simultaneously, aviary managers want to retain as many parrots as possible to boost production of offspring in the aviary. Aviary production is considered a measure of management success. While the aviary population has supplied parrots for release to two reintroduction sites in the past, a third potential reintroduction site has been proposed for the future. Harvesting parrots for all three sites could create additional risk for the sustainability of the aviary population.

Given this combination of small population threats as well as aviary and reintroduction needs, managers recognized that planning focused on number of parrots produced by the aviary and available to harvest for release was essential. They proposed a schedule to harvest parrots from the aviaries over 7 years, a short-term management time frame; the schedule was based on interactive discussions and expert opinion of aviary and reintroduction managers. As an additional approach, we use a quantitative model (i.e., risk analysis) to assess tradeoffs between different harvest management strategies. These various strategies, which use different release numbers, frequency of events, and ages, have been proposed by managers as they seek a sound method to harvest parrots from the captive population. Our model addresses two specific management questions: (1) over the next 7 years, can the aviaries harvest the number of parrots necessary for the proposed releases while remaining self-sustaining and (2) what are the consequences of different strategies? Through comparisons of model outcomes, our study generates insights into alternate management strategies which can assist with the development of a conservation management plan.

## METHODS

### Study Site

The Puerto Rican parrot resides solely on the island of Puerto Rico in four populations (two aviaries and two release sites—one relic and one recently established). The Recovery Plan for the Puerto Rican parrot outlines background information on habitat, ecology, life history, and population threats as well as actions for the reintroduction and the aviary breeding program [U.S. Fish and Wildlife Service, 1982, 1999, 2009]. Daily management of the wild population and the aviary breeding population are separate with managers working together for the common goal of species recovery. Our study focuses on the aviary breeding population.

On the eastern side of the island, the Iguaca Aviary, formerly Luquillo Aviary, managed by U.S. Fish and Wildlife Service, was established in the mid-1970s with eggs and chicks collected from the wild [Snyder et al., 1987]. The exact genetic relationship among these founding parrots was unknown, and not all individuals produced offspring. On the western side, the J. L. Vivaldi Aviary managed by Puerto Rican Department of Natural and Environmental Resources received a series of transfers of parrots from the Luquillo Aviary to establish a second captive population in 1993. One objective for establishing the second aviary was to minimize environmental risk (such as hurricanes, disease, or fire) by maintaining two separate populations [U.S. Fish and Wildlife Service, 1999, 2009]. In addition to the physical transfer of parrots from Luquillo Aviary to Vivaldi Aviary, aviary protocols were synthesized to develop consistent husbandry and management approaches. Each aviary maintains detailed records on their parrots including parentage and hatch and death dates. All birds in the aviary are individually identified shortly after hatching with leg bands and unique identification numbers.

Aviary practices have evolved over the history of the program. Early challenges to management, record keeping, husbandry, and health practices were recognized, surmounted, and improved to today's standards. Aviary managers adopted recommended procedures to address potential limitations of captive breeding programs, including disease prevention and administrative continuity [Snyder et al., 1996; U.S. Fish and Wildlife Service, 2004; Wilson et al., 1994]. The aviaries are single-species facilities (although Hispaniolan parrots, *Amazona ventralis*, are used for fostering practices) that are closed to the public. Routine health monitoring and disease management are standard operations. The aviary staffs are dedicated to the highest quality care and success of the breeding population with a commitment to science-based management and best practices for maintaining the health and reproductive success of birds. Management staff has been consistent since 2000.

The aviary and wild parrot subpopulations function as an integrated population. Throughout the program, managers have transferred parrots from the wild to the aviary breeding facilities and from the aviaries to the wild. Transfers to the aviaries occurred primarily for health and welfare concerns and transfers to the wild occurred for recovery purposes. Despite these releases, the wild population remains small with about 80–95 parrots across the 2 reintroduction sites as of 2011 (Vélez, U.S. Fish and Wildlife Service, personal communication) and the majority of these parrots are recently released aviary parrots. The regular exchange of birds has likely produced aviary and wild populations with similar genetic composition but no molecular level comparison has been completed. Genetic management of the aviary population focused on inbreeding avoidance until 2006; after 2006, that genetic strategy continued along with prioritizing birds for breeding pairs based on their genetic representation in the aviary population [i.e., mean kinship, Lacy, 1995] and for the quality (i.e., completeness) of their pedigree. While the whole genome was recently sequenced [Olyeksyk et al., 2012], molecular analyses have not yet been able to establish a full detailed genetic structure (i.e., pedigree relationships) of the aviary population [Miller et al., 2011].

## Data Collection

In preparation for analysis of the Puerto Rican parrot population dynamics, we created a studbook database using PopLink (version 2.1) which tracks demographic and genetic data of uniquely identified individuals [Faust et al., 2009a,b]. This software developed specifically for management of small captive (or wild) populations is the recognized standard approach used by the Association of Zoos and Aquariums (AZA). When we initiated the database in 2007, we obtained data from aviary records and documents as well as publications [Snyder et al., 1987; Wunderle et al., 2003]. We compiled and entered data on all living and past individuals including dam, sire, and sex, as well as life history events such as hatches, deaths, and transfers for the time period 1973–2007. After 2007, aviary staff regularly entered data on events directly into the studbook; thus, the studbook after 2007 represented primary data rather than data interpreted from other sources.

As of January 1, 2012, demographic and genetic data on 846 individual parrots existed in the studbook. While 771 parrots had known parentage (i.e., identified dams and sires), key pieces of their pedigrees beyond immediate parentage were missing for some parrots. The original 18 parrots (eggs and chicks) collected in the wild were traced back to 11 parrots that occupied wild nests in El Yunque based on information in published sources that described the inhabitants and reproduction in wild nests during 1969–1974 [Snyder et al., 1987; Wunderle et al., 2003]. However, the exact genetic relationships among these founding parrots were unknown. Because genetic changes through generations can impact vital rates, we wanted to use pedigree analysis to assess changes in inbreeding and relatedness levels over the four decades. To improve data analysis, we made a standard assumption used in genetic analysis of small, managed populations [Ballou, 1983; Ballou et al., 2010; Rudnick and Lacy, 2008]. We assigned founder status (wild, unrelated parents) to the 11 reproductive parrots; with this assumption, the pedigree of the living population was 66% known. However, clearly every bird living today is related to these founders; even today's wild populations may be similarly related due to releases from captive stock.

A second source of uncertainty arose because we could not identify parentage of eggs and chicks captured in the wild and brought to the aviary, a practice which has occurred throughout the program for management and welfare reasons. While location of nests was known, the breeding parents for those nests were difficult to identify. Many of these eggs and chicks from wild nests were likely the offspring or further descendants of parrots previously released in the forests and related to the aviary populations but we could not establish specific relationships. We made no assumptions for these cases; parentage was left as unknown during analysis.

## Demographic and Genetic Analyses

Our analysis began with January 1, 1993, the year that the second aviary initiated their breeding program and extended to January 1, 2012. Management practices for this 19-year time span were relatively consistent. We used PopLink to analyze annual population size, growth, fecundity and mortality rates, as well as age and sex structure [see

Poplink manual, Faust et al., 2009a,b]. We used PM2000 software [Pollak et al., 2005] to conduct pedigree and genetic analysis based on studbook data [see PM2000 manual, Lacy and Ballou, 2002]. We reported PM2000 output for mean inbreeding coefficient (F) and population mean kinship (MK) [a measure of genetic relatedness among the living population: Lacy, 1995].

## Risk Analysis Simulations

A Puerto Rican Parrot team of reintroduction and aviary managers met in 2009 to develop a plan that would quantify the number of birds that could be harvested for release across the two and potentially three sites over a period of 7 years. The 7-year time frame can be viewed as an initial management strategy with the intent to re-evaluate the program and adapt based on the outcomes. The final proposed numbers were a compromise between the desire of reintroduction managers to release as many parrots as possible and the need of the aviary managers to retain parrots for population growth and future production. The proposed annual numbers were: Year 1 = 14, Year 2 = 16, Year 3 = 12, Year 4 = 18, Year 5 = 16, Year 6 = 28, and Year 7 = 18 for a total of 122 to be selected for release. Armed with information on the proposed harvest numbers, the release team and the aviary managers could make decisions based on numbers for each year and each site.

To assess the demographic impact on the aviary population following harvest of parrots for the reintroduction program, we used the numbers proposed by the management team and modeled future changes in the population with ZooRisk software (version 3.8), a population viability tool designed for analysis of small, managed populations [Earnhardt et al., 2008]; this individual based model applies stochasticity to simulation events such as hatches, deaths, number of annual offspring, and sex ratio [see manual, Faust et al., 2008]. For the simulations, we used data on the age and sex structure of the population ($N = 297$) as of January 1, 2012 and the age and sex specific fecundity and mortality rates generated by ZooRisk from the studbook data (Appendix A). We excluded 10 individuals from the breeding population due to known medical and behavioral issues which prevent them from breeding. The breeding strategy was set for monogamous, the birth sex ratio for 0.5267 (as observed), and no target population size was implemented. We generated 1,000 iterations for each of our scenarios.

The four model scenarios represented alternate management strategies which focused on the number of parrots selected for release as well as the life stage (i.e., age) of the parrots (Table 1). The Young scenario, which has been implemented by managers in the past, harvests only juveniles for release using the numbers proposed by the recovery team. The Combo Scenario, recently implemented by managers, differs because a combination of adults and juveniles in equal numbers are harvested using the numbers proposed by the recovery team. Reintroduction managers have thought that releases of breeding adults might be more successful than releases of only juveniles because pairs would be pre-established [Collazo et al., 2010]. The Threshold scenario harvested only juvenile parrots above the current 297 size. To date, this strategy has not been implemented because managers wanted to increase the size of the aviary population; in future simulations, managers could set a model threshold for whatever size captive breeding population is desired. The Dble scenario simulates a harvest doubling the number of juveniles and adults; managers would like to harvest more parrots than proposed by the recovery team. We simulated harvests for 7 years, ended the simulations after Year 7, and then ran the model simulations out to 14 years to observe resilience of the populations following different harvest strategies. We compared the projections from these scenarios to assess the trade-offs among alternate strategies that have been proposed for the number and life stage to be harvested for releases over the short-term 7 years. For current management needs, the basic questions about number and stage were priorities; however, for future assessments of this species or other species, the simulation approach that we used should be conducted for longer periods of time and with additional strategies.

# RESULTS

## Demographic and Genetic Analysis

The combined aviary population grew every year from 1993 ($N = 64$) to 2012 ($N = 297$) with a mean annual growth rate of 10% (calculations include aviary hatches and deaths, captures and releases from/to the wild) (Fig. 1). The pattern of population growth within the two aviaries differed from the combined population, primarily due to management decisions regarding harvest of parrots for release to the wild. From 2001 to 2007, the increase in the Vivaldi Aviary from 74 to

**TABLE 1. Model scenarios: based on proposed release strategies for the Puerto Rican parrot program**

| Code | Scenario name | Description |
|---|---|---|
| **Young** | Young | 122 parrots (age 1–2) were selected for release during years 1–7 based on proposed numbers cited in text. |
| **Combo** | Young and adult | 61 young (age 1–2) and 61 adult (age 3–6) parrots were selected for release during years 1–7 based on proposed numbers cited in text. |
| **Thres** | Threshold | The number of young parrots (age 1–2) selected for release is the surplus above the threshold aviary population size of 148 males and 148 females (296) during years 1–7. |
| Dble | Double | 244 parrots selected for release with equal numbers of juveniles and adults during years 1–7 (double the numbers in scenario P-AY). |

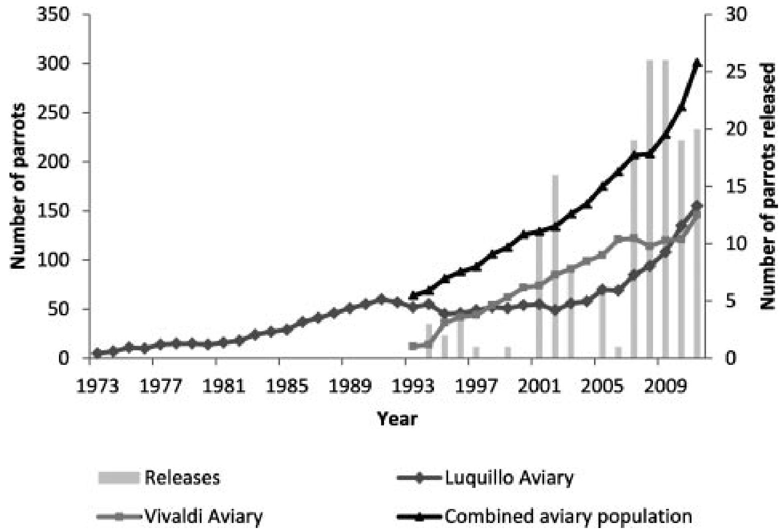


Fig. 1. Growth in the Puerto Rican parrot aviary populations from inception of the program in 1973–2012. A single aviary (Luquillo) bred parrots from 1973 to 1993; parrots from the Luquillo Aviary stocked the Vivaldi Aviary beginning in 1993. As of January 2012, Luquillo and Vivaldi Aviaries house 150 and 146 parrots respectively. Parrots have been harvested from the aviary population for release to the reintroduction sites.

122 parrots can be attributed to a facility quarantine protocol (due to perceived disease risk) that effectively prohibited releases/transfers of parrots from that quarantined aviary (Fig. 1). Concurrently, the smaller increase in size at the Luquillo Aviary from 55 to 85 parrots can be attributed to the need to harvest parrots for release solely from the Luquillo aviary population. After the Vivaldi Aviary quarantine was lifted, that population declined in size due to the harvest of 26 parrots for release in 2008. In 2011, both aviary populations continued to grow with an annual growth rate of 15% at the Luquillo Aviary and an annual growth rate of 17% at the Vivaldi Aviary.

As of January 1, 2012, parrots occupy all age classes less than 20 years of age with the largest proportion of individuals in the youngest age classes indicating future population growth potential (Fig. 2). The 4-year age class (hatched in 2008) with 40 parrots is smaller than adjacent age classes due to the harvest of 19 parrots from that single age class for release to a reintroduction site. The number of males ($N = 150$) and females ($N = 145$) is nearly equivalent.

After 6 generations of reproduction, the aviary population of 297 parrots was assumed to descend from 11 parrots (collected as eggs or chicks). The gene diversity [expected heterozygosity: Lacy, 1995] retained in the living aviary population as of January 1, 2012 was estimated to be 86%. The population MK, or average relatedness among living birds [see Lacy, 1995], was 0.1347, indicating that the average relatedness of any two living birds is approximately equivalent to that of half-siblings. The average inbreeding level of the current generation of animals was 0.0852, indicating that parents of today's living birds were, on average, related at a level slightly higher than first cousins. The genetic calculations were based on our studbook database with assumptions (discussed previously); thus actual values such as gene diversity and inbreeding may be lower or higher than the calculated values because a portion of this population's pedigree is uncertain. Every living parrot whether known, partially known or unknown pedigree was related to other parrots in the combined population. Thus the individuals in the living population shared founder genes from the original lineages in complex relationships.

**TABLE 2. Differences in reproductive potential due to variations in release strategies**

| Model scenario | Mean number of simulated pairs in year 7 | Mean number of simulated hatches in Year 7 |
|---|---|---|
| Young | 41 | 93 |
| Combo | 36 | 81 |
| Dble | 18 | 41 |
| Thres | 30 | 67 |

## Risk Analysis Projections

Scenario results varied in the balance between aviary population size and number of parrots harvested for release (Fig. 3). Even with the simulated harvest of parrots for release, the Young and Combo scenarios projected an increase in the aviary population size above and beyond the number needed for release. While Scenario Young released only young parrots, Scenario Combo released a combination of young and breeding age parrots; thus, Combo grew at a slower rate than Young because fewer pairs were available to reproduce in the aviary in subsequent years (Table 2). The Threshold population, by design, did not grow; this scenario removed parrots in excess of that needed to maintain the

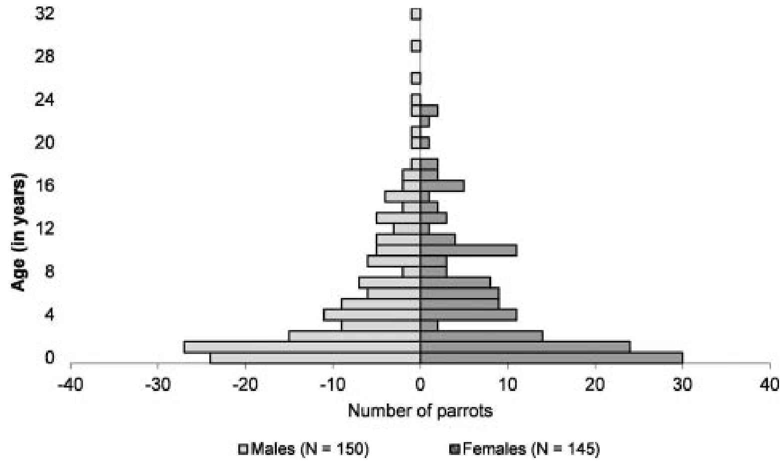


Fig. 2. The age and sex structure of the Puerto Rican parrot aviary population as of January 1, 2012. Males are on the left of center and females are on the right of center.

population at its current size ($N = 297$). However, this scenario produced the most parrots for release, ranging from an average of 22 at Year 1 to 49 at Year 6 (Table 3). In contrast, the population in the Dble scenario declined in size; too few breeding parrots were present to sustain the aviary population over 7 years. When we assessed the impact of the high harvest rate in the Dble scenario on the resilience of the population by halting harvests at Year 8 and projecting growth for another 7 years, we found that the population dynamics were resilient allowing the population to grow to a mean population size of 447 (±SD 76) by Year 14 (Fig. 4). The inherent potential for positive population growth appeared robust and able to overcome the depleted structure present at Year 7. Nonetheless, the Dble scenario population attained only 45% of the Young scenario population size by Year 14. None of the four scenarios produced a growing population and simultaneously the greatest number of parrots for release.

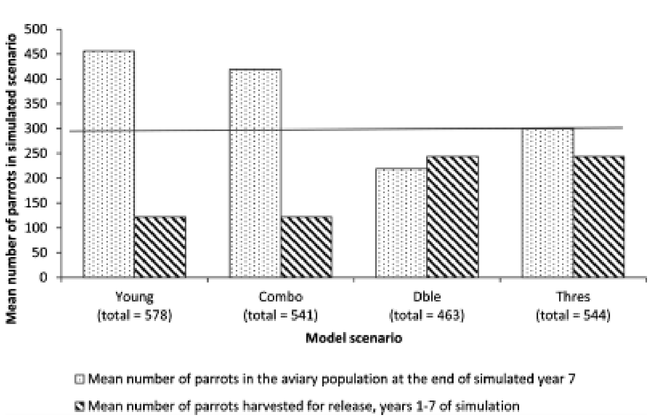


Fig. 3. Comparison of Puerto Rican parrot population sizes for the 4 model scenarios (as listed in Table 1). The dotted bars indicate mean aviary population size at Year 7 of the model and the hatched bars indicate mean cumulative number of parrots harvested for release during the 7 years of the model. The solid line is the initial population size of 297 (as of January 1, 2012).

## DISCUSSION

The results of our study indicate that the aviary population can be sustainable at least in the short-term (7 years, under existing conditions) even while supplying birds for the release program at or above the numbers proposed by the recovery team. In addition to the two wild populations that have been supplemented with release parrots in the past, a third proposed population can be initiated which will enhance the recovery program's ability to meet plan objectives [U.S. Fish and Wildlife Service, 2009]. Recently Collazo et al. [2013] modeled an assessment of the optimal use of eight aviary-held parrots to be released and allocated across three populations with the objective to enhance species-level recovery. Our results suggest that a greater number of parrots than proposed would be available for release which can influence the optimal use model. Because Collazo et al. propose future routine re-evaluations as part of an adaptive management framework, we suggest integrating their modeling approach to optimal use and our modeling of aviary production through time. This synthesis will provide managers the basis for evidence-based decisions to enhance conservation management of the species.

**TABLE 3. Comparison of model results relative to growth rates, production, and release numbers for 4 strategies harvesting Puerto Rican parrots from the aviary population (strategies as listed in Table 1)**

| Strategy | Trade-offs |
|---|---|
| Young | Highest growth rate (7.2%)<br>Greatest overall production (*N*)<br>Smaller number for release than Dble or Thres |
| Combo | Lower growth rate (6%) than young<br>Smaller number for release than Dble or Thres |
| Dble | Lowest growth rate (0.0%)<br>Least overall production (*N*) |
| Thres | Low growth rate (2%)<br>Greatest number for release |

Our risk analysis also reveals that biological tradeoffs exist between aviary production and harvest for release. For example, any harvest of parrots for release results in less production by the aviary population and when reproductive rather than pre-reproductive age parrots are harvested for release, production in the aviary declines to a greater degree. If the only objective for the recovery program was optimal production of parrots for release, establishing a temporary moratorium on releases and growing the population to a larger size would be the most productive strategy. However, other divergent objectives are also considered in recovery planning: for example, managers deliberately release parrots to enhance program support and they need to refine release techniques using experimental approaches. Even if no program constraints are present, a management tradeoff is inevitable because the breeding program and the reintroduction program can both benefit from a greater number and from reproductive age parrots; their proximate objectives differ. If the size of the population that can be housed in aviary becomes a constraint, possibly due to facility resource limitations, the tradeoff values would change. Thus, managers need to weigh the costs and benefits of strategies that harvest different numbers and life stages of parrots as the program grows and objectives change.

During the history of the breeding and reintroduction program, managers faced expected and unexpected challenges from environmental, demographic, and genetic events and they addressed these challenges with careful proactive management. Managers initiated plans to reduce environmental risk from hurricanes with the addition of the western aviary (Vivaldi) in 1993 and construction of a new facility on the eastern side of the island (Luquillo Aviary) in 2007. During the first 20 program years while the aviary population size hovered around 50 parrots, demographic stochasticity was recognized as a major biological threat. However, over the last 19 years, as managers optimized opportunities for breeding and hatching success, hatches consistently outnumbered deaths in each year and the population grew to almost 300 parrots reducing immediate demographic risk. Success (such as population growth) can produce its own challenges. With each additional generation in captivity, the parrot population is more vulnerable to inbreeding depression and potential negative impacts of genetic load [Ballou et al., 2010; Frankham et al., 2002; Keller and Waller, 2002; Leus and Lacy, 2009]. While a population's genetic load can be detrimental and produce demographic consequences such as lower hatch rates and higher mortality, the impact varies from population to population [Lacy et al., 1996; Ralls et al., 1988]. As in any closed population, inbreeding levels in the aviary population have increased over the last four decades; yet demographic evidence from our study (i.e., the healthy rate of growth) indicates that the aviary population is either not genetically vulnerable at this time or inbreeding depression is being offset by high production.

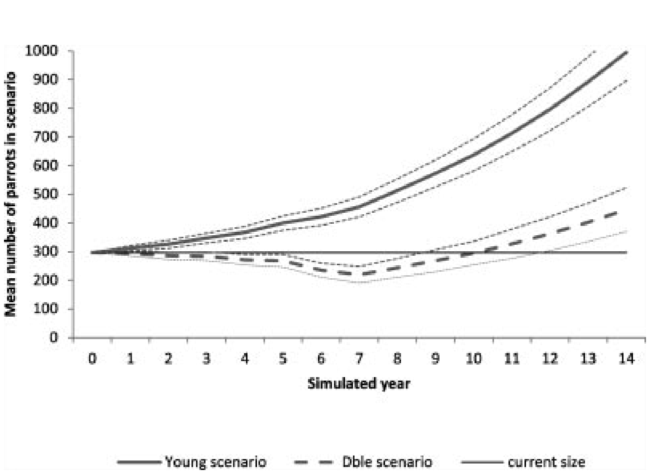


Fig. 4. Comparison of trajectories to evaluate resilience of the Puerto Rican parrot population growth for the Dble Scenario. In Dble and Young scenarios, parrots were harvested for 7 years, the harvest was halted beginning the 8th year and simulations continue to Year 14 using the same reproductive and mortality rates and age and sex structure simulated at Year 7. The means are shown with $\pm 1$ SD, dotted lines.

While growth of the aviary population is an important milestone in the reintroduction program, the ultimate goal is survival and reproduction in the wild by the aviary-bred parrots [White et al., 2012]. In the past, parrots released at El Yunque forest have not been able to establish a population; managers and scientists wondered about the suitability of the aviary-bred parrots. In an assessment of Puerto Rican parrot population growth at El Yunque, Beissinger et al. [2008] hypothesized that inbreeding of the parrot population was one potential limiting factor. Indeed, given the small size of the founding population, the potential for inbreeding depression was a concern in 1973 when the captive breeding program was initiated [Snyder et al., 1996; Wilson et al., 1994]; yet, the existing strong population growth suggests no apparent inbreeding depression for the aviary population. While the genetic structure of the wild and aviary populations are likely similar due to the continual exchange of parrots between the aviaries and the wild, inbreeding effects can be expressed differently in different environmental conditions [Araki et al., 2007; Armbruster and Reed, 2005; Frankham, 2008; McPhee, 2004; Miller, 1994]. Alternately, factors other than genetic characteristics may have prevented growth of the El Yunque population. In a heartening recent report, preliminary evidence from the Rio Abajo forest site indicates that release birds in that population are thriving. Rio Abajo, which is the newer of the two release sites, may have fewer stressors that challenge establishment of a release population. In 2012, 10 active nests (occupied by aviary-bred parrots) produced 15 chicks and 12 fledglings increasing that relatively new population to 49–80 parrots with flocks between 15 and 30 birds an almost daily sight from July to December (R. Valentin, Puerto Rico Department of Natural and Environmental Resources, personal communication).

Our analysis of the aviary breeding program provides a rare opportunity to review progress over four decades of active management in a conservation effort. When scientists and managers develop a recovery plan for an endangered and threatened species, they must weigh a diverse set of conservation alternatives including the option to capture some or all of the remaining individuals and initiate a captive breeding program. Success can be uncertain making a decision potentially controversial [Conway, 2011; Snyder et al., 1996]. In addition, for long-lived and slowly reproducing species, managers must expect long time frames before a recovery program can be declared a success. For the Puerto Rican parrot, the ability of the aviary population to grow and support the release program has not always been evident. While the population grew from 13 parrots in 1973 to 64 parrots in 1992, annual increases in numbers proceeded gradually due to the initial small population size. For program managers, progress seemed slow. During our study timeframe (1993–2011), the population continued to grow at an average annual rate of 10% but the increase in population size was more apparent going from 64 in 1992 to 297 parrots in 2011. Our analysis at this juncture reveals the strength of the growth pattern in the past and the potential for the future. With adaptive management practices and patience, the aviaries have reached the original objectives for the captive breeding program by growing to their current capacity. The successful growth of the Puerto Rican parrot aviary population supports the 1973 decision to build a breeding and reintroduction program.

## CONCLUSIONS

1. In conservation programs, resources (e.g., time, money, birds) are limiting factors. In the general daily management of the aviary populations, a wide range of tasks, which are essential for the survival and breeding of parrots, require skill and time. The collection of comprehensive demographic and genetic data also requires training, skill, and a substantial investment of time by the aviary staffs. While the tasks requiring immediate attention must be a priority for maintaining individuals in the aviary population, a standardized, long-term database benefits individual, population, and species level management objectives. By conducting quantitative analyses of the population studbook we were able to reveal patterns during the program's history and assist with planning for future management. With continuing standardized data collection, managers can monitor aviary population dynamics on a regular basis into the future, make necessary management adjustments to continue to meet their objectives, and evaluate program progress. This approach provides an opportunity to scientifically manage the aviary population, ultimately benefiting conservation of the species.
2. The risk analysis in our study demonstrates the value of modeling to provide quantitative evaluations that can be compared among alternate management strategies. This approach which uses a model specifically designed for risk analysis of small managed populations can be applied to management of many conservation species with breeding and reintroduction programs. While model scenarios did not reveal surprising results for the Puerto Rican parrot program, the analysis should reassure aviary managers and the recovery team regarding production and sustainability of the aviary population. For the future, we recommend that managers routinely continue to conduct these analyses, lengthen the time frame for release scenarios, and expand the number of scenarios that are considered based on management strategies; these expanded analyses will be valuable because the population size and structure will change, the vital rates and harvest rates will change, and management objectives may evolve. This information allows managers to make informed decisions and continue their conservation actions for this program.

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## APPENDIX A

Age specific fecundity and mortality rates for Puerto Rican parrots housed in two aviaries

| | Fecundity (Mx) | | | | Mortality (Qx) | | | |
|---|---|---|---|---|---|---|---|---|
| Age class | Male Mx | *N* at risk | Female Mx | *N* at risk | Male Qx | *N* at risk | Female Qx | *N* at risk |
| 0–1 | 0 | 257 | 0 | 230 | 0.23 | 342 | 0.24 | 316 |
| 1–2 | 0 | 191 | 0.01 | 179 | 0.07 | 196 | 0.07 | 181 |
| 2–3 | 0.02 | 132 | 0.05 | 129 | 0.07 | 135 | 0.08 | 132 |
| 3–4 | 0.25 | 104 | 0.19 | 108 | 0.07 | 110 | 0.03 | 109 |
| 4–5 | 0.3 | 90 | 0.29 | 103 | 0.05 | 91 | 0.03 | 104 |
| 5–6 | 0.29 | 77 | 0.39 | 91 | 0.08 | 78 | 0.04 | 93 |
| 6–7 | 0.5 | 69 | 0.49 | 78 | 0 | 69 | 0.03 | 79 |
| 7–8 | 0.57 | 66 | 0.34 | 66 | 0.02 | 66 | 0.09 | 70 |
| 8–9 | 0.5 | 60 | 0.49 | 60 | 0.02 | 60 | 0 | 60 |
| 9–10 | 0.59 | 58 | 0.51 | 57 | 0 | 58 | 0.05 | 59 |
| 10–11 | 0.55 | 51 | 0.42 | 53 | 0.06 | 52 | 0.04 | 53 |
| 11–12 | 0.45 | 43 | 0.57 | 42 | 0.07 | 44 | 0.05 | 43 |
| 12–13 | 0.56 | 37 | 0.62 | 38 | 0.03 | 37 | 0.03 | 38 |
| 13–14 | 0.41 | 31 | 0.31 | 32 | 0.03 | 32 | 0.17 | 35 |
| 14–15 | 0.27 | 27 | 0.49 | 25 | 0 | 27 | 0.08 | 26 |
| 15–16 | 0.17 | 25 | 0.23 | 21 | 0 | 25 | 0.09 | 23 |
| 16–17 | 0.28 | 22 | 0.24 | 18 | 0 | 22 | 0.05 | 19 |
| 17–18 | 0.31 | 19 | 0.29 | 13 | 0.1 | 20 | 0.08 | 13 |
| 18–19 | 0.12 | 17 | 0.57 | 9 | 0 | 17 | 0.29 | 10 |
| 19–20 | 0.22 | 17 | 0.33 | 8 | 0.06 | 17 | 0 | 8 |
| 20–21 | 0.1 | 15 | 0.15 | 11 | 0.06 | 16 | 0 | 11 |
| 21–22 | 0.13 | 12 | 0.1 | 10 | 0.21 | 14 | 0 | 10 |
| 22–23 | 0.12 | 9 | 0.06 | 9 | 0.27 | 11 | 0.21 | 10 |
| 23–24 | 0.07 | 7 | 0 | 6 | 0.13 | 8 | 0.15 | 7 |
| 24–25 | 0 | 6 | 0 | 4 | 0 | 6 | 0 | 4 |
| 25–26 | 0 | 6 | 0 | 4 | 0.15 | 7 | 0.25 | 4 |
| 26–27 | 0 | 5 | 0 | 2 | 0 | 5 | 0.33 | 3 |
| 27–28 | 0.13 | 4 | 0 | 2 | 0 | 4 | 0 | 2 |
| 28–29 | 0 | 4 | 0 | 2 | 0 | 4 | 0 | 2 |
| 29–30 | 0 | 4 | 0 | 2 | 0 | 4 | 0 | 2 |
| 30–31 | 0 | 3 | 0 | 1 | 0 | 3 | 0.5 | 2 |
| 31–32 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 1 |
| 32–33 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 |
| 33–34 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 |
| 34–35 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 |
| 35–36 | 0 | 1 | 0 | 0 | 0.5 | 2 | 0 | 0 |
| 36–37 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 37–38 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 |
| 38–39 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Age-specific fecundity rate (Mx) = the number of same sex offspring an individual is expected to produce (=produced on average) during an age class.Number at risk for Mx or Qx = sample size that Mx rate was based on for a given age class.Age-specific mortality rate (Qx) = probability that an individual of age *x* dies during time period.