# ANATOMY OF A BOTTLENECK: DIAGNOSING FACTORS LIMITING POPULATION GROWTH IN THE PUERTO RICAN PARROT

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*Abstract.* The relative importance of genetic, demographic, environmental, and catastrophic processes that maintain population bottlenecks has received little consideration. We evaluate the role of these factors in maintaining the Puerto Rican Parrot (*Amazona vittata*) in a prolonged bottleneck from 1973 through 2000 despite intensive conservation efforts. We first conduct a risk analysis, then examine evidence for the importance of specific processes maintaining the bottleneck using the multiple competing hypotheses approach, and finally integrate these results through a sensitivity analysis of a demographic model using life-stage simulation analysis (LSA) to determine the relative importance of genetic, demographic, environmental, and catastrophic processes on population growth. Annual population growth has been slow and variable (1.0 ± 5.2 parrots per year, or an average λ = 1.05 ± 0.19) from 16 parrots (1973) to a high of 40–42 birds (1997–1998). A risk analysis based on population prediction intervals (PPI) indicates great risk and large uncertainty, with a range of 22–83 birds in the 90% PPI only five years into the future. Four primary factors (reduced hatching success due to inbreeding, failure of adults to nest, nest failure due to nongenetic causes, and reduced survival of adults and juveniles) were responsible for maintaining the bottleneck. Egg-hatchability rates were low (70.6% per egg and 76.8% per pair), and hatchability increased after mate changes, suggesting inbreeding effects. Only an average of 34% of the population nested annually, which was well below the percentage of adults that should have reached an age of first breeding (41–56%). This chronic failure to nest appears to have been caused primarily by environmental and/or behavioral factors, and not by nest-site scarcity or a skewed sex ratio. Nest failure rates from nongenetic causes (i.e., predation, parasitism, and wet cavities) were low (29%) due to active management (protecting nests and fostering captive young into wild nests), diminishing the importance of nest failure as a limiting factor. Annual survival has been periodically reduced by catastrophes (hurricanes), which have greatly constrained population growth, but survival rates were high under non-catastrophic conditions. Although the importance of factors maintaining the Puerto Rican Parrot bottleneck varied throughout the 30-year period of study, we determined their long-term influence using LSA simulations to correlate variation in demographic rates with variation in population growth (λ). The bottleneck appears to have been maintained primarily by periodic catastrophes (hurricanes) that reduced adult survival, and secondarily by environmental and/or behavioral factors that resulted in a failure of many adults to nest. The influence of inbreeding through reduced hatching success played a much less significant role, even when additional effects of inbreeding on the production and mortality of young were incorporated into the LSA. Management actions needed to speed recovery include (1) continued nest guarding to minimize the effects of nest failure due to nongenetic causes; (2) creating a second population at another location on the island—a process that was recently initiated—to reduce the chance that hurricane strikes will cause extinction; and (3) determining the causes of the low percentage of breeders in the population and ameliorating them, which would have a large impact on population growth.

*Key words: Amazona vittata; conservation; demographic model; demography; endangered species hatching failure; extinction; hurricane effects; Luquillo Experimental Forest; population bottleneck; Puerto Rican Parrot; sensitivity analysis.*

## INTRODUCTION

As a population declines toward extinction, it may remain in a population bottleneck of small size for short

or extended periods of time. Bottlenecks have long been of concern to conservation geneticists (Denniston 1978, Franklin 1980, Soulé 1980, Frankham et al. 2002) because they can result both in inbreeding, which is often expressed through reduced fertility or fitness of offspring, and in genetic drift, which results in the loss of both genetic variation and rare alleles in proportion to the severity and duration of the bottleneck (Frankel and Soulé 1981, Hedrick and Miller 1992, Crnokrak and Roff 1999, Keller and Waller 2002, Frankham 2005a). While the genetic consequences of population bottlenecks are well known, the processes that maintain populations in bottlenecks have received little consideration even though they must be diagnosed and ameliorated to promote recovery. Factors other than genetic processes, such as deterministically-reduced survival or reproduction, environmental stochasticity, and catastrophes, can cause populations to decline to or remain at bottleneck levels (Lande 1988, Caro and Laurenson 1994, Caughley 1994, Ringsby et al. 2006, Jamieson 2007a). These same factors, and potentially others, may limit population growth and produce slow recovery from the bottleneck. A clear understanding of the roles, interactions, and relative importance of genetic, demographic and environmental stochasticity, and catastrophes in maintaining bottlenecks is needed (Gilpin and Soulé 1986, Lande 1988, Brodie 2007, Jamieson 2007b).

A drastic population decline leading to a prolonged, severe bottleneck, from which it has yet to recover despite intensive conservation efforts, characterizes the Puerto Rican Parrot (Amazona vittata). The parrot was abundant and widespread on Puerto Rico and nearby islands until 1650, when the human population began to increase substantially (Snyder et al. 1987). By the early 1900s, Puerto Rican Parrots were confined to five sites on Puerto Rico and by the 1940s the parrot's range had contracted to the Luquillo Mountains. Population size continued to decline from an estimate of 2000 in 1937 to 200 in 1954, 24 in 1968, and finally to a low of 13 birds in 1975 (Wadsworth 1949, Rodriguez-Vidal 1959, Snyder et al. 1987). Massive deforestation, harvest for pets and food, shooting to protect crops, and mortality from hurricanes probably caused the historic decline (Rodriguez-Vidal 1959, Snyder et al. 1987). Intensive recovery efforts begun in 1973 included (1) monitoring, guarding, and modifying nest sites to reduce predation by Pearly-eyed Thrashers (Margarops fuscatus) and black rats (Rattus rattus), and parasitism by botflies (Philornis sp.); (2) increasing nest-site availability by rehabilitating deficient natural cavities and adding nest boxes; and (3) captive breeding to provide a source of nestlings for fostering into wild nests and, more recently, for direct release into the wild (Snyder et al. 1987, White et al. 2005b). These efforts stopped the decline and produced modest growth, but the population remains in a bottleneck of 25–40 birds after more than 30 years of intensive management and may be suffering from effects of inbreeding (Brock and White

1992). Recent conservation efforts have focused on bolstering the Luquillo birds through reintroductions and attempting to establish a second population (U.S. Fish and Wildlife Service [USFWS] 1999, White et al. 2005b).

The Puerto Rican Parrot's continued persistence in a population bottleneck provides an important example of the difficulties of distinguishing among various limiting factors, and their relative importance in constraining a small population's growth. Four processes, acting alone or in various combinations, are primary candidate factors responsible for maintaining the bottleneck based on three decades of field studies (Table 1): (1) inbreeding could reduce nesting success; (2) a large percentage of adult parrots could fail to nest because they lack nest sites, or because small population size or a skewed sex ratio could inhibit pair formation or social (flocking) structure (i.e., Allee effect); (3) nests could fail frequently due to predation, parasitism, hurricanes, or other nongenetic causes; or (4) survival of adults, subadults or juveniles could be reduced. These factors can be distinguished by their predicted effects on attributes of parrot demography, or by environmental conditions (Table 1). They also reflect various roles of genetic, demographic, environmental, and catastrophic processes.

Here we conduct a risk analysis for the Puerto Rican Parrot and then examine evidence for the importance of specific processes maintaining the bottleneck (Table 1) using the classical multiple competing hypotheses approach (Chamberlin 1890) and sensitivity analysis of demographic models of population growth (Caswell 2001). The multiple competing hypotheses approach is a framework of analysis that has been adapted to diagnose causes of population decline (Peery et al. 2004). It develops a suite of predictions for the effects of potential liming factors and evaluates them against multiple data sets to look for concordance of results. We developed predictions for the hypothesized causes of the current bottleneck discussed above based on their effects on long-term measures of demographic and behavioral performance that have been collected for this species and were made available for our use. Unfortunately no direct genetic or pedigree data are available for the wild population, but a variety of prevalent phenotypic indicators of inbreeding depression in birds have been well documented, most notably reduced hatchability of eggs (Briskie and Mackintosh 2004, Marr et al. 2006).

We constructed the following set of hypothesized effects of the factors constraining Puerto Rican Parrot population growth. If inbreeding prevented parrot population growth, we predicted that (1) hatchability of eggs should be low but may fluctuate over time as the level of inbreeding varies due to changes in pair composition or purging of deleterious alleles; (2) when pairs which previously had low hatchability change composition, hatchability should often increase because mates may no longer be nesting with a close relative, whereas pairs that previously had high hatching success

TABLE 1. Predicted effects of factors potentially maintaining the Puerto Rican Parrot (*Amazona vittata*) population bottleneck.

| Stochastic processes | Species or environmental attribute | Factors maintaining the bottleneck | | | |
|---|---|---|---|---|---|
| | | Inbreeding | Failure to nest | Nest failure | Survival |
| Genetic | hatchability | low | | | |
| | hatchability after mate change for members of pairs with previously low hatching success | increase | | | |
| | deformities of chicks | frequent | | | |
| Genetic, demographic | percentage of birds nesting | | low | | |
| | rate of mate replacement | | high | | |
| Demographic | sex ratio | | skewed | | |
| Environmental | cavity availability | | low | high | |
| | nest failure rate (nongenetic) | | low | high | |
| | annual survival of juveniles | | | | low |
| | annual survival of adults | | | | low |
| Environmental, catastrophe | rainfall | | | high | negative |
| Catastrophe | hurricanes | | | high | reduced |

might experience lower hatchability upon repairing because they could remate with a close relative; and (3) deformities of chicks should often occur. If a failure of adults to nest maintained the bottleneck, we predicted that (4) a low percentage of adults would breed annually due to (5) a skewed sex ratio, which could reduce mate availability, or (6) to a lack of nest cavities, in which case breeding pairs should rarely switch nest cavities and mortality of breeders should result in rapid mate replacement from a pool of nonnesting birds. If nest failure due to nongenetic causes limited population growth, we predicted that (7) rates of nest failure should be high; and (8) nest cavities should be highly available and would be frequently abandoned following nest failure, leading to a high rate of cavity switching. If catastrophes maintained the bottleneck, we predicted that (9) hurricanes and extremes in annual rainfall would increase nest failure and reduce adult survival immediately following these events due to food scarcity and flooding of cavities (Snyder et al. 1987). We recognize that other environmental factors will also influence the hypothesized relationships discussed above, so we examined a variety of alternative factors whenever possible.

Finally, we evaluated the relative importance of these genetic, demographic, environmental, and catastrophic processes in maintaining the population bottleneck using life-stage simulation analysis (LSA), a sensitivity analysis technique that measures the potential effects of variation and uncertainty in vital rates on population growth (Wisdom and Mills 1997, Wisdom et al. 2000). LSA is a retrospective, simulation-based approach to sensitivity analysis that evaluates the impact on population growth rate ($\lambda$) of simultaneous changes in vital rates (Cross and Beissinger 2001). It has the particular advantage of being able to integrate the effects of a variety of ecological factors on population growth rates. By incorporating sources of time-based variation in vital rates, LSA bridges static matrix analysis (Caswell 2001) and stochastic risk assessment (population viability) approaches that project populations into the distant future (Beissinger and McCullough 2002, Morris and Doak 2002, Lande et al. 2003).

## STUDY SITE AND METHODS

The Puerto Rican Parrot in the wild is now confined largely to the 11 330-ha El Yunque National Forest or Luquillo Experimental Forest, which ranges in elevation from 120 to 1075 m in eastern Puerto Rico. Birds nest mostly at mid-elevation (600–750 m) in the subtropical, lower montane, wet forest zone (Ewel and Whitmore 1973). Hurricanes are the dominant natural disturbance affecting the Luquillo Experimental Forest, striking at an average interval of 50–60 years (Scatena and Larsen 1991). Two hurricanes directly struck the forest during the 27-year period of this study and four others have passed nearby.

The Puerto Rican Parrot recovery effort is led by the U.S. Fish and Wildlife Service (USFWS) in cooperation with the U.S. Forest Service (USFS) and Puerto Rican Department of Natural and Environmental Resources (PRDNER). The wild population is supplemented with parrots produced in two aviaries: Luquillo (established by USFWS in 1973) and Rio Abajo (established by PRDNER in 1989). Details of intensive field research methods and management are in Snyder et al. (1987), Lindsey (1992), Vilella and Garcia (1995), Wilson et al. (1995), USFWS (1999), and White and Vilella (2004).

Data from 1973 to 1985 were obtained from Snyder et al. (1987), and from 1985 to 2000 from the Rio Grande Field Office of the USFWS and the Puerto Rican Parrot Recovery Plan (USFWS 1987, 1999). In instances of discrepancies between official reports and individual field notes on file at USFWS office, we used the individual field notes. The maximum count from annual parrot surveys conducted throughout the Luquillo Experimental Forest just prior to nesting (USFWS 1999) was used to estimate population size. Histories of hatching success, fledging success, and causes of failure for all nesting attempts from 1973 to 2000 are

summarized in Wunderle et al. (2003), although several inconsistencies were discovered and corrected. Nestling parrots have been individually marked with metal leg bands since the 1980s, and since 1996 nestlings were given one colored steel band per leg that identified year of birth and nest site. Identities of breeding parrot pairs were based on appearance (variation in plumage coloration or other markings due to injuries) in combination with individually distinguishable vocalizations and leg bands (Snyder et al. 1987). Nevertheless, there has been at least one case of mistaken identity of a nesting pair that was later corrected. Analyses of mate change and adult survival based on histories of individually recognized birds should be viewed as preliminary.

We looked for potential effects of inbreeding by examining rates of hatchability of eggs, embryo mortality in the shell, and nestling death due to abnormal development. Hatchability is the percentage of eggs that successfully produced chicks excluding eggs lost to predation, accidental breakage, flooding, and abandonment (Koenig 1982). We used logistic regression and Akaike's Information Criterion corrected for small sample size ($AIC_c$) to analyze factors affecting hatchability following the methods of Burnham and Anderson (2002). $AIC_c$ evaluates how well each model in a set of a priori candidate models fits a particular set of data. Models were ranked using $\Delta AIC_c$ (the difference in $AIC_c$ between a model and the model with the lowest $AIC_c$ value, or best model) and AIC weights (the relative likelihood of a model given a set of models, normalized to sum to 1). Parameters were evaluated individually by their cumulative $AIC_c$ weights for all models in which they appeared (Burnham and Anderson 2002).

Estimates of adult survival were based on individually recognizable nesting birds. The resighting rate of breeding birds was extremely high (98.4%; only two birds were missed for two years each yielding 250 of 254 transitions detected), because nesting pairs have high nest site fidelity and nearly always remain together until one dies. Because extremely few internal zeros were present in capture histories and the resighting rate is close to unity, we used return rates as a proxy for adult survival (Sandercock et al. 2000, Budden and Beissinger 2004). We used logistic regression and $AIC_c$ to analyse the factors affecting adult survival as described above for hatchability.

Annual survival of first-year parrots was estimated from 1973–1979 by observing the return of yearlings to the vicinity of the cavity from which they fledged in the early part of the following breeding season. Because returning yearlings are difficult to detect late in the following breeding season, we estimated yearling mortality on the basis of the percentage of individuals observed through March or April, which coincides with the timing of censuses in our population model (Appendix B). These estimates were combined with those from Lindsey et al. (1994) from a limited sample in 1985–1987 using radiotelemetry (see Appendix B for details).

We counted the number of times pairs switched nest cavities as an indication of the availability of cavities for nesting parrots. The position of the nest cavities relative to a breeding pair's territory are unknown and it is possible that the vacant cavities in a territory were unavailable to neighboring pairs. However, given that pairs are known to simultaneously occupy nearby cavities (i.e., 4 m minimum; Snyder et al. 1987), we believe most of the suitable cavities were dispersed sufficiently widely to be available for use by nonbreeding parrots.

Statistical analyses were conducted in SYSTAT (SYSTAT 2004). Variables were examined for normality before determining whether to conduct parametric or nonparametric tests. Type I error rate of $\leq 0.05$ was accepted as significant. Standard deviations (SD), standard error (SE), or 95% confidence intervals (CI) provide information on variation.

We conducted a risk analysis using the population prediction interval (PPI) approach with 28 years of annual estimates of parrot population size $N_t$ (Sæther et al. 1998, 2007, Engen et al. 2001, Sæther and Engen 2002). Uncertainty in model parameter estimates can create large problems for making population projections from population viability analysis models (Beissinger and Westphal 1998, Fieberg and Ellner 2000). A PPI is a stochastic interval that includes the unknown future population size with a probability of $(1 - \alpha;$ Dennis et al. 1991, Engen et al. 2001). Interpretation of a prediction interval is similar to a confidence interval (Sæther et al. 2002), except that inference is for a stochastic quantity rather than a parameter. Width of the PPI increases with increasing stochasticity (Hyede and Cohen 1985) and with increasing uncertainty in parameter estimates. Appendix A details methods for calculating PPI.

We also developed a stage-structured, prebreeding, deterministic population model (Appendix B) to estimate the proportion of the population expected to nest annually and to evaluate the efficacy of different management options. The model used an annual time step and events matched timing of field measurements. It was structured around three nodes: breeding pairs, nonbreeders, and 1-year-olds. Only a small portion of the wild parrot population nests each year and breeders have been the subject of most demographic measures. The nonbreeding portion of the population is sizable (see Results) and characteristic of psittacids (Beissinger and Snyder 1992, Sandercock et al. 2000). A transfer rate ($G$) from nonbreeder to breeder node permitted evaluation of the impact of this rate on population growth. A node for first-year birds allowed survival ($P_1$) to increase with age and age of first breeding to be no less than 3 years; breeding at this age occurs in captivity, although it may be later in the wild (Snyder et al. 1987). Appendix B details parameterization of the model.
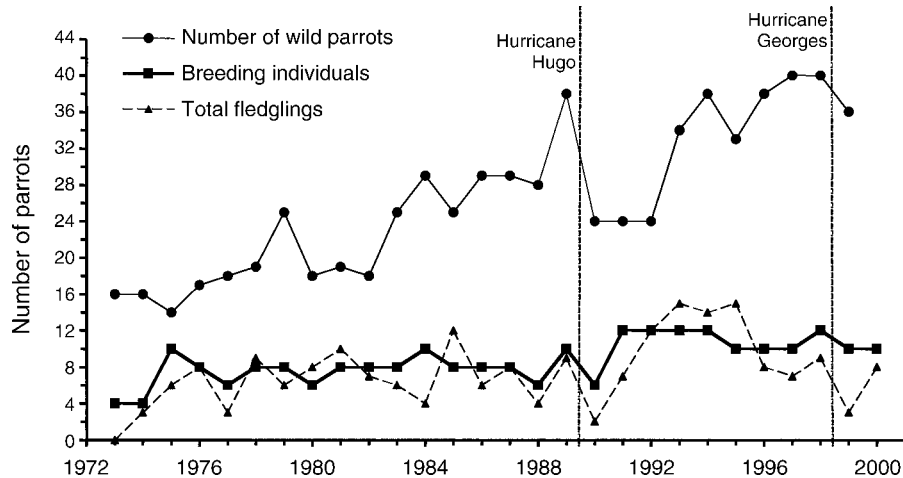
FIG. 1. Annual change in the number of Puerto Rican Parrots (*Amazona vittata*) in the Luquillo Experimental Forest, Puerto Rico, from 1973 to 2000. Shown are the number of parrots in pre-breeding counts each year, fledglings produced per year, and breeding individuals per year. Annual production of fledglings includes fledglings of both wild and aviary origin. Dates of Hurricanes Hugo and Georges are indicated by vertical dashed lines. Data are from the U.S. Fish and Wildlife Service, Rio Grande, Puerto Rico, USA.

The model was also used to evaluate the relative importance of each rate on the annual rate of population growth ($\lambda$) using life-stage simulation analysis (LSA). One thousand matrices were constructed by randomly drawing vital rates from specified distributions and $\lambda$ was calculated for each matrix (Wisdom and Mills 1997, Wisdom et al. 2000). The coefficient of determination ($r^2$) between the value of each vital rate and $\lambda$ indicates the amount of variation in population growth attributable to the range of variation observed in each vital rate. Vital rates that account for the greatest variation in population growth rate have the greatest impacts on population dynamics (Cross and Beissinger 2001). Details of the model and estimation of parameters are in Appendix C.

We conducted further analysis that explored additional impacts of inbreeding on population growth ($\lambda$) relative to other forms of stochasticity by specifically incorporating its effects on the rate of production and survival of young in the LSA analysis. For each iteration of the LSA, we reduced the rate of production and survival of young by $1 - \delta$, the coefficient of inbreeding depression, which is the average percent reduction in a trait of inbred relative to outbred individuals (Lande and Schemske 1985, Crnokrak and Roff 1999). The coefficient of inbreeding was calculated from the equation $\delta = b_{X_0}F$, where $b_{X_0}$ is the change in a trait due to inbreeding and $F$ is the average level of inbreeding (Crnokrak and Roff 1999). We used the mean value for $b_{X_0}$ of 0.818 for homeotherms from the meta-analysis of Crnokrak and Roff (1999). We calculated the average level of inbreeding as the mean of $F$ values randomly assigned to each of four breeding pairs, which is the long-term average number for the Puerto Rican Parrot, under two inbreeding scenarios: (1) a moderate level of inbreeding simulated using a beta distribution with mean $F = 0.142$, the average for House Sparrows (*Passer domesticus*) in an inbreed population (Jensen et al. 2007); and (2) for a highly inbred population with mean $F = 0.5$ using a uniform distribution.

## RESULTS

### Population growth, catastrophes and risk analysis

The Puerto Rican Parrot population has grown extremely slowly over the past three decades, despite bolstering by releases of captive-reared birds and intensive management efforts (Fig. 1). Annual population growth averaged 1.0 ± 5.2 parrots per year (mean ± SD), resulting in an average $\lambda = 1.05 \pm 0.19$. Despite growing from 12 to 40 individuals, the number of parrots nesting annually has remained between three and five breeding pairs. Population growth was slowed by the catastrophic effects of two hurricanes, which resulted in population declines of 49% (Hugo) and 10% (Georges). Recovery to pre-hurricane levels occurred in only four years after the passage of Hurricane Hugo. Nevertheless, even in the absence of hurricanes, the wild population grew slowly at an average rate of 1.6 ± 4.2 parrots per year ($\lambda = 1.07 \pm 0.17$).

Population prediction intervals indicate there is great risk and uncertainty in the future of this population (Fig. 2). The stochastic population growth rate was positive but small ($\hat{s} = 0.031$). The estimate of the environmental variance was moderate ($\hat{\sigma}_e^2 = 0.0343 \pm 0.0094$), but uncertainty in this estimate was large (SD = 0.0369). Thus, predictions of the future trajectories of this population quickly become very uncertain. Predicting only five years into the future from 2001 to 2006, the 90% PPI ranged from 22 to 83 birds (Fig. 2). Five years is slightly less than 20% of the length of the time series,
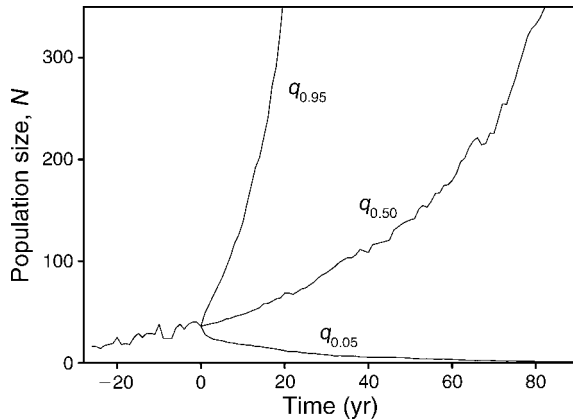
FIG. 2. The lower bound of different prediction intervals $q_\alpha$, where $\alpha = 0.05$, $0.5$, and $0.95$, for the future size of the Puerto Rican Parrot population in the Luquillo Experimental Forest based on the population prediction interval (Appendix A). Count data from 1973 (year −27) to 2000 (year 0) are followed by the projection interval to 85 years into the future.

which may represent a threshold for the accurate estimation of extinction risk (Fieberg and Ellner 2000). The 2006 population estimate of 30 parrots is slightly below the midpoint of this prediction interval. Thus, despite a slow upward trajectory from a low of 16 birds in the wild in 1973, the future of the Puerto Rican Parrot population in the Luquillo Experimental Forest is extremely uncertain.

### Evidence of apparent inbreeding effects

Few parrots were banded to facilitate the direct construction of pedigrees, so our analysis of the role of inbreeding depends primarily on indirect evidence. Direct evidence is limited to a mother–son breeding pair in North Fork (Snyder et al. 1987). In 1975 the North Fork female produced two eggs, which both

hatched but one chick was deformed and died soon after. The pair nested again in 1976 and produced three eggs of unknown hatchability.

Several forms of indirect evidence suggest inbreeding may have played a role in maintaining the bottleneck. Hatchability of 389 eggs (Fig. 3) from 34 wild parrot pairs averaged 70.6% ± 0.1% (mean ± SE) per egg and 76.8% ± 4.2% per pair. These values are well below the mean of 90.6% hatchability for eggs of 155 populations of 113 bird species (Koenig 1982), 88.7% for eggs of other cavity nesting birds (Koenig 1982), and 84.3% for Pearly-eyed Thrasher eggs laid in nest boxes in the same Puerto Rican forests as parrots (Beissinger et al. 2005). One parrot pair (West Fork 1) produced 43 eggs from 1975 to 1984 of which 75% failed to hatch primarily because the eggshells were thin or malformed (Snyder et al. 1987, Wunderle et al. 2003). Thin-shelled eggs can be produced by DDE, but levels of this contaminant were negligible in these eggs (Snyder et al. 1987). Even excluding this pair, hatchability was still low (76.3% per egg and 78.4% per pair). About 40% of unhatched eggs were either infertile or died in very early stages of development (see Birkhead et al. 1995 and Cook et al. 2003 for these distinctions), while 60% died after signs of visible development. The timing of mortality was nearly equally split among infertile/early and late developmental stages when the eggs of the West Fork 1 pair were excluded, which all died after visible development.

Pair composition was by far the most important single factor affecting variation in hatchability and logistic regression models that included it had an $AIC_c$ weight of 1.0 (Table 2). Hatching success varied greatly among pairs (0–100%); of 15 pairs where the hatchability of ≥10 eggs was known, four pairs had very low (<60%) hatching success, five pairs had low success (60–80%), and six had high (>80%) hatching success. Thus, eggs from 9 of 15 pairs (60%) exhibited seriously reduced
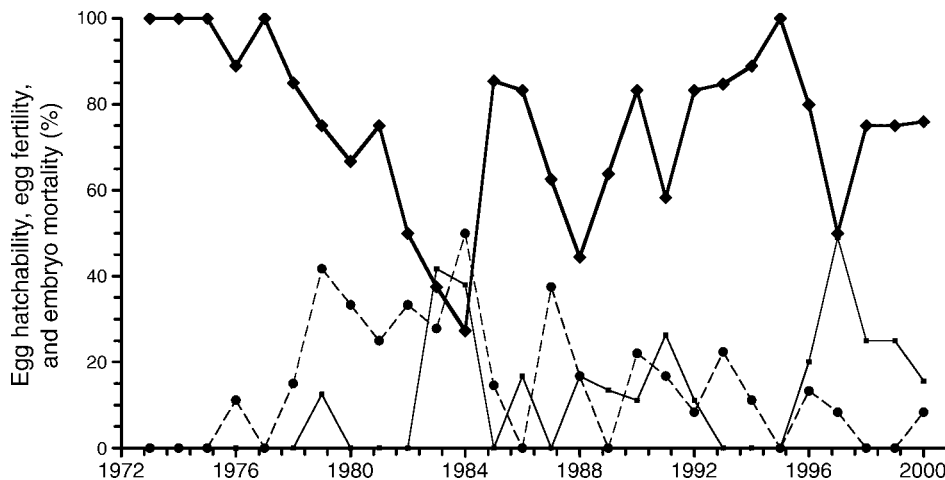


FIG. 3. Mean percentage of egg hatchability (heavy solid line), egg fertility (light solid line), and embryo mortality (dashed line) per Puerto Rican Parrot pair by year, from 1973 to 2000, in the Luquillo Experimental Forest. Data are from the U.S. Fish and Wildlife Service, Rio Grande, Puerto Rico, USA.

TABLE 2. Models of hatchability for Puerto Rican Parrot eggs in nests in the Luquillo Experimental Forest during 1973–2000.

| Model set and models | $K$ | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weight |
|---|---|---|---|---|
| Single factor | | | | |
| Pair identity (ID) | 34 | 413.62 | 0.00 | 1.000 |
| Nest site | 24 | 434.33 | 20.71 | 0.000 |
| Year, Year$^2$ | 3 | 454.88 | 41.26 | 0.000 |
| Area | 2 | 459.21 | 45.59 | 0.000 |
| Years paired | 2 | 463.64 | 50.02 | 0.000 |
| Rain | 2 | 464.40 | 50.78 | 0.000 |
| Year | 2 | 473.26 | 59.64 | 0.000 |
| Composite | | | | |
| Pair ID, Year, Year$^2$, Rain | 37 | 371.02 | 0.00 | 0.487 |
| Pair ID, Year, Year$^2$, Rain, Years paired | 38 | 372.49 | 1.48 | 0.233 |
| Pair ID, Year, Year$^2$, Rain, Area | 38 | 373.49 | 2.48 | 0.141 |
| Pair ID, Year, Year$^2$, Rain, Years paired, Area | 39 | 374.99 | 3.97 | 0.067 |
| Pair ID, Year, Year$^2$ | 36 | 375.89 | 4.87 | 0.043 |
| Pair ID, Year, Year$^2$, Years paired | 37 | 376.61 | 5.59 | 0.030 |
| Pair ID, Rain | 35 | 410.44 | 39.42 | 0.000 |
| Pair ID, Years paired | 35 | 413.89 | 42.87 | 0.000 |
| Year, Year$^2$, Rain, Area, Years paired | 6 | 433.27 | 62.26 | 0.000 |
| Year, Year$^2$, Rain, Area | 5 | 440.90 | 69.88 | 0.000 |
| Year, Year$^2$, Years paired | 4 | 443.95 | 72.94 | 0.000 |
| Year, Year$^2$, Area | 4 | 447.55 | 76.53 | 0.000 |
| Year, Year$^2$, Rain | 4 | 449.37 | 78.35 | 0.000 |
| Area, Rain | 3 | 449.75 | 78.73 | 0.000 |
| Years paired, Rain | 3 | 456.58 | 85.56 | 0.000 |

*Notes:* Model parameters are Area (geographical grouping of nesting regions East Fork, West Fork, and North Fork vs. South Fork); Rain (annual rain in mm), Pair ID (each unique nesting pair), Years paired (number of years a pair had nested together), and Year (continuous variable for study year). $K$ is the number of parameters in the model.

hatchability. None of the six other environmental factors in the single-factor model set received strong support. Nest site was the second most important factor affecting hatchability, but this factor fit the data poorly compared to pair composition (Table 2); the difference in $AIC_c$ between models was very large (20.71), and the evidence ratio (the relative likelihood of the model with pair composition fitting the data compared to the model with nest site) was 31 340:1 (Burnham and Anderson 2002:78). Nine of the 24 nest sites (37.5%) were used by more than one pair, which permitted some discrimination between the effects of nest site and pair identity, but nest site could not be used simultaneously in composite models with pair identity because 28 of 36 (78%) pairs nested in only one cavity.

The models that best accounted for variation in hatchability based on a combination of factors all included pair identity, which had a cumulative AIC weight of 1.0, but they also included temporal trends and some environmental factors (Table 2). Hatchability per pair declined greatly during the 1970s to a low of 28% in 1984 (Fig. 3), when two pairs produced eggs that failed to hatch and three others produced eggs with low hatchability. Thereafter, hatchability steadily improved, which accounted for the better fit of a quadric, rather than a linear, term for time. This trend might be expected if inbreeding effects had been purged, or were associated with particular pairs comprised of close relatives that dissolved and then one member remated

with an unrelated or less closely related individual. However, as recently as 1996–1998, a new pair in the Acostao cavity had low hatching success (33%), suggesting potential for continued problems. Composite models with temporal trend had a cumulative $AIC_c$ weight of 1.0. Hatchability was also negatively related to rainfall, potentially because moisture on eggshells facilitates invasion of the egg by microbes and can cause embryo mortality (Cook et al. 2003, 2005). Hatchability declined by 2.3–2.7% per meter of annual total rainfall and models with this term had a cumulative $AIC_c$ weight of 92.7. Hatchability also declined slightly (2–3%) with each year that pairs bred together and hatchability was greater for nests in the South Fork area (79%) than in other regions (61%). Models with the number of times pairs bred and nesting area were much less well supported, and together had cumulative $AIC_c$ weights of 0.33 and 0.21, respectively. The most highly supported model contained pair composition, a quadratic term for time, and rainfall, and had a rate of correctly predicting hatching success of 81.7%.

Changes in hatching success accompanying changes in pair composition support the hypothesis that inbreeding is likely to be an important cause of poor hatchability (Fig. 4). Members from six pairs with low or very low hatchability (26–80%) remated upon the death of a mate and the hatchability of their eggs greatly increased to 90–100%, except for one pair for which hatchability declined slightly by 8%. In contrast, when members from
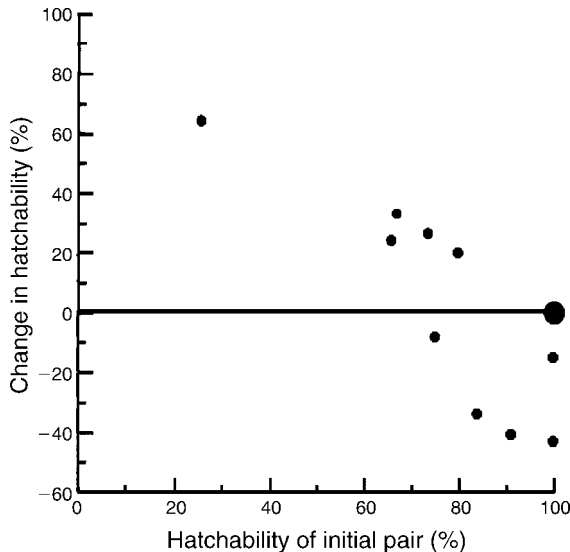
FIG. 4. Change in hatching success with a new mate, based on hatchability of the original pair, for 13 pairs where one member died and the other remated and nested. The large dot indicates overlapping values for three pairs.

composition on hatchability. Upon remating after his female died, hatchability of this male's eggs increased from 26% ($n = 43$) to 90% ($n = 11$), even though all eggs were laid in the same nest cavity. Like West Fork 1, most new pairs nested in the same cavity as the initial pair (58%) or used it in combination with another nest site (25%), whereas only 17% nested exclusively in a new site. Changes in hatching success with changes in pair composition were unrelated to whether the new pair nested in the same cavity or moved to a new one (Kruskal-Wallis = 1.50, df = 2, $P = 0.473$), but were negatively related to hatchability of the eggs of the initial pair (Fig. 4; $r = -0.77$, $P = 0.002$).

Developmental anomalies leading to chick mortality after hatching also occurred, but much less commonly than prehatching mortality. Chick mortality attributed to poor development occurred at nests in which at least one nestmate developed normally in 10 nesting attempts of six pairs. One such chick was the result of a documented mother–son pair in North Fork.

Hatching failure from infertile eggs and embryo mortality was by far the most important factor constraining reproductive success of Puerto Rican Parrots (Fig. 5). Eggs were 3–14 times more likely to fail from this cause than any other cause of either egg or chick mortality, such as predation and parasitism. Overall, eggs were significantly (Fisher's exact test, $P < 0.001$) more likely to die in the nest (0.35, CI = 0.30–0.41) than were chicks (0.233, CI = 0.18–0.30).

eight pairs with high hatchability (>80%) remated after the death of a mate, results were mixed; hatching success declined strongly (>25%) for three pairs, declined slightly (8–15%) for two pairs, and remained unchanged for three pairs (Fig. 4). The West Fork 1 pair provides an interesting example of the effect of changes in pair
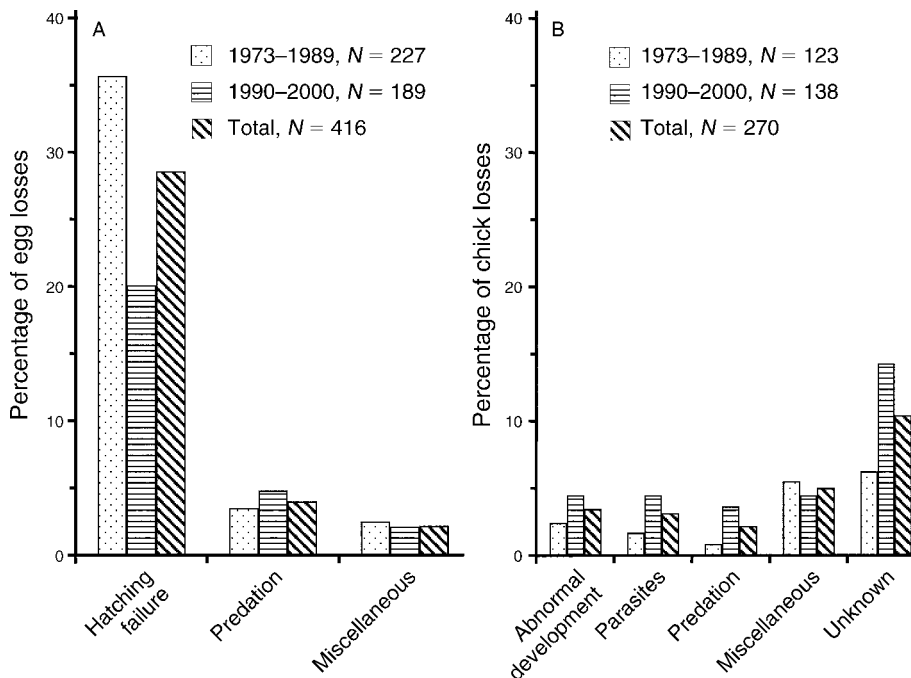


FIG. 5. Percentage loss of Puerto Rican Parrot (A) eggs and (B) chicks to various factors in the periods 1973–1989 and 1990–2000 in the Luquillo Experimental Forest. Details of the various factors are shown in Appendix B. Data are from the U.S. Fish and Wildlife Service, Rio Grande, Puerto Rico, USA; $N$ = sample size.

### Evidence for failure to nest

The Puerto Rican Parrot population has been characterized by relatively few breeding individuals (Fig. 6). Only three to six pairs attempted to nest per year and the mean number of breeding individuals constituted only 34% ± 11% (mean ± SD) of the population (range 21–71%). Although the number of breeding parrots increased during the recovery period (Fig. 1), the annual rate of increase of breeding parrots (mean = 0.22 ± 2.4 breeders per year) lagged well behind that of annual population increase. The percentage of breeding individuals decreased significantly (Spearman $r$ = −0.61, $P$ = 0.002) with increased population growth (Fig. 6), which might be expected if a large percentage of birds were younger than the age of first breeding. To estimate bounds for the percentage of the population expected to nest annually, we used a stage-structured, prebreeding deterministic population model (Appendix B) to calculate stable age distributions and determine the proportion of individuals old enough to nest. Model outcomes suggest 41% to 56% of the Puerto Rican Parrot population should have reached an age of first breeding of 3–5 years and be available to reproduce (Fig. 6), a level that is well above the 34% long-term average.

Could a lack of nest sites be responsible for the low percentage of breeding parrots? Cavity nesting birds are often limited by the availability of nest sites (e.g., Snyder 1978, White et al. 2005a), so managers created new cavities constructed of various materials, enhanced natural cavities, and actively managed cavities to prevent use by competitors (Snyder et al. 1987). Enhanced natural cavities in parrot nesting areas increased from 13 in 1990 to 82 by 2000, despite natural attrition from hurricanes (E. Garcia, *personal communication*). Pairs regularly nested in enhanced cavities, although a count is unavailable. Furthermore, breeding parrot pairs regularly used new nest cavities or switched between nest cavities, which suggests that appropriate, potential nest cavities were available for nesting. From 1986–2000, breeding pairs used 12 new nest cavities, six established breeding pairs switched cavities between breeding seasons, and one pair shifted cavities between clutches within a season. Switching nest cavities by established breeding pairs also occurred in earlier years (Snyder et al. 1987). Furthermore, traditional nest cavities abandoned by established pairs have either been recolonized by new breeding pairs (three pairs) after 2–8 years or in one case was recolonized by the original pair 8 years later. Thus, there is little evidence to support a scarcity of nest cavities as an important factor limiting nesting effort.

The rapid occurrence of mate replacements by both sexes suggests a pool of potential breeders was available in the Puerto Rican Parrot population throughout the recovery period. Mate replacements occurred quickly, sometimes within a few days, during the breeding season following the loss of one female and four male breeders. Mate replacements between breeding seasons occurred
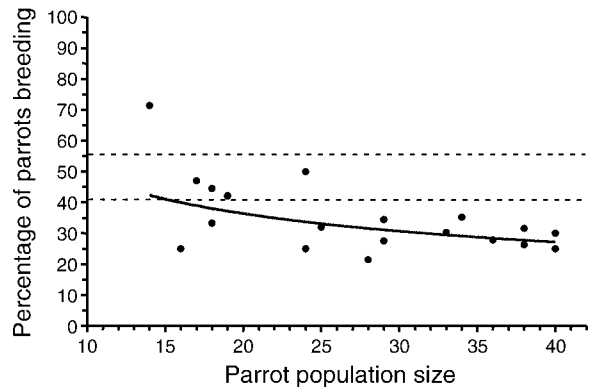


FIG. 6. Percentage of Puerto Rican Parrots breeding in relation to population size at the beginning of the breeding season in the Luquillo Experimental Forest from 1973 to 2000. Dashed horizontal lines represent the predicted range for the percentage of breeders for age-of-first-breeding ranging from three to five years, based on the stable age distribution from a stage-structured, pre-breeding, deterministic population model (Appendix B). The solid line is the nonlinear regression fit between population size and the percentage of parrots breeding. Data are from the U.S. Fish and Wildlife Service, Rio Grande, Puerto Rico, USA.

in 10 cases (five females and five males). Instances in which a breeder remains unmated for more than a year following mate loss are unknown.

There is little evidence that a skewed sex ratio is likely to be responsible for the chronic failure of many adults to breed, although few data are available. Wild nestlings sexed between 1992 and 2000 included 31 males and 26 females, a result not significantly different from unity ($\chi^2$ = 0.44, df = 1, $P$ = 0.508). At the Rio Abajo aviary between 1994 and 1999, there were 21 male and 20 female nestlings documented, indicating a nearly even sex distribution. Similarly, a historical sample of Puerto Rican Parrot skins in museums examined by Snyder et al. (1987), which presumably mainly represented older birds, included seven males and five females, a ratio close to 1:1.

### Evidence for nest failure

Rates of nest failure were low under intensive management compared to the preceding period (Snyder et al. 1987). The average percent of nests that were successful per year was 71% ± 23% (mean ± SD), which although variable among years, has remained relatively high. Management activities have successfully prevented most losses to predation, parasitism, and miscellaneous causes (Fig. 5). Few changes in the incidence of various egg or chick mortality factors occurred over time (Fig. 5), with the exception of the trends in egg hatchability presented earlier (Figs. 3 and 5) and a significant increase ($G$ = 8.09, df = 1, $P$ = 0.004) in the percentage of chick mortalities from 15.9% of hatched eggs in 1973–1989 to 30.4% of hatched in 1990–2000. Increased chick mortality was primarily due to a significant increase ($G$ = 6.85, df = 1, $P$ = 0.009) in mortality from unknown
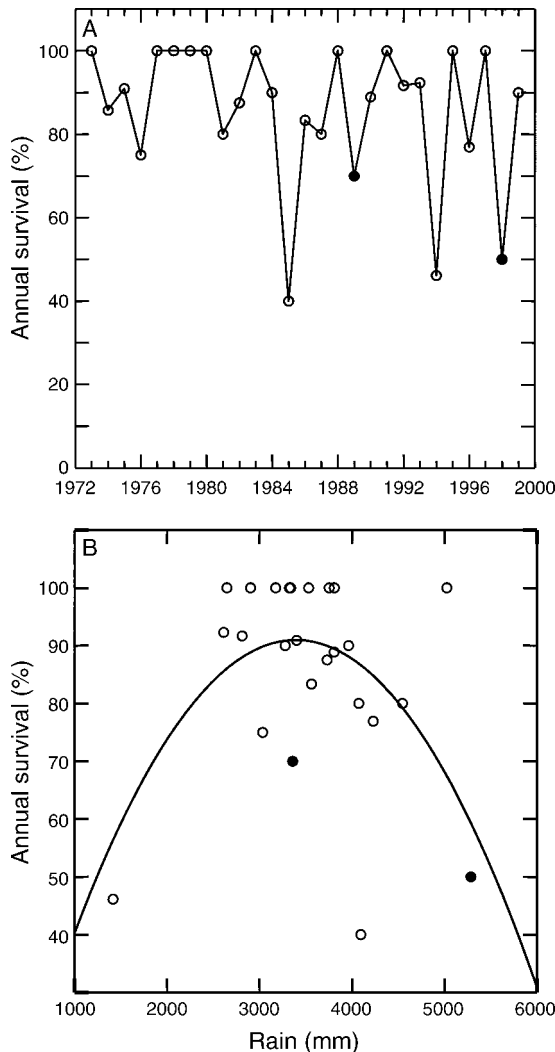
FIG. 7. (A) Percentage annual survival of breeding Puerto Rican Parrots by year from 1973 to 2000 in the Luquillo Experimental Forest. Solid circles are hurricane years. (B) The relationship of percentage annual survival of breeding Puerto Rican Parrots with average annual rainfall (mm) from 1975 to 2000 in El Verde, Luquillo Experimental Forest. Data are from the U.S. Fish and Wildlife Service. Solid circles are for hurricane years.

causes that resulted from less intensive effort to monitor and guard nests. Aided by fostering and nest guarding, breeding pairs have fledged an average of $1.7 \pm 0.7$ young into the wild ($1.4 \pm 0.7$ young per pair without fostering) or $2.3 \pm 0.8$ young per successful nest ($2.1 \pm 0.8$ young per pair without fostering). However, fledging success per pair was greatly reduced in the years immediately following two hurricanes (0.60 and 0.67 young per pair; Fig. 1), due in part to the absence of young fostered to the wild from the aviary.

### Evidence for reduced annual survival

Annual survival of breeding adult parrots averaged 86.3% (CI = 79–93%), but varied greatly among years

(Fig. 7). Logistic regression models that included the occurrence of hurricanes, total annual rainfall, and annual variation in survival best fit the data (Table 3). Hurricanes resulted in a 30% loss of breeders ($N = 10$) after Hurricane Hugo and 50% after Hurricane Georges ($N = 14$). Mean annual survival during non-hurricane years was $88.4\% \pm 0.03\%$ (mean $\pm$ SE) compared to survival during hurricane years of $60.0\% \pm 0.10\%$. Models with hurricane effects were strongly supported with cumulative $AIC_c$ weights of 97.5. The best model contained hurricane and rainfall terms (Table 3), and had a rate of correctly predicting survivorship of 74.6%.

Sex differences in mortality of breeding parrots were not found (20 females:22 males). The sexes in breeding pairs appeared to have similar vulnerabilities to hurricanes (six females:four males lost after Hurricanes Hugo and Georges), and all losses occurred during the nonbreeding season (10 parrots lost) following hurricane strikes. In the non-hurricane years (1973–2000), 10 breeders were lost during the breeding season and 22 breeders were lost in the non-breeding season. Although differences between hurricane and non-hurricane years in period of loss (breeding vs. non-breeding season) were suggestive, the differences were not significant (Fisher's exact test, $P = 0.080$).

Annual survival of first year (juvenile) parrots is not well known. Snyder et al. (1987) resighted 75% of 32 fledged young the following year with their parents at the onset of nesting. Based on data in Lindsey et al. (1994) for 15 radio-tagged juveniles, Collazo et al. (2000) derived an annual estimate of survival of 32.5%, which results in 91.1% monthly survival or a 52% survival to census (7 months). The mean of the two values weighted by the number of birds studied yielded 68%. Values are well within expected estimates for juvenile survival (Sæther 1989).

### The relative importance of factors maintaining the bottleneck

We used life-stage simulation analysis (LSA) to evaluate the relative roles of demographic factors on population growth rates (see Appendix C). After calculating the population growth rate ($\lambda$) for 1000 matrices constructed from potential combinations of vital rates, we regressed $\lambda$ against the value of each vital rate to yield a measure of importance ($r^2$).

Catastrophe (in the form of hurricane impacts on subadult and adult survival) and failure to nest (i.e., the probability of transitioning from a nonbreeder to a breeder) were the two most important demographic parameters affecting population growth of Puerto Rican Parrots (Fig. 8). Population growth was so strongly negatively correlated with the occurrence of hurricanes ($r^2 = 0.71$) that hereafter all LSA results are presented separately for years with and without hurricanes.

In the absence of hurricanes (Fig. 8), the probability of transitioning from a nonbreeder to a breeder ($G$) was the dominant factor ($r^2 = 0.41$) affecting Puerto Rican

TABLE 3. Logistic regression models for survival of nesting Puerto Rican Parrots and their corresponding rank, number of parameters (*k*), and AIC calculations.

| Rank | Models | $k$ | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ weight |
|---|---|---|---|---|---|
| 1 | Hurricane, Rain | 3 | 208.66 | 0.00 | 0.575 |
| 2 | Hurricane, Rain, Year | 4 | 210.32 | 1.66 | 0.251 |
| 3 | Hurricane, Rain, Year, Sex | 5 | 212.41 | 3.74 | 0.089 |
| 4 | Hurricane | 2 | 214.77 | 6.10 | 0.027 |
| 5 | Year(cat) | 27 | 216.13 | 7.46 | 0.014 |
| 6 | Hurricane, Year | 3 | 216.19 | 7.53 | 0.013 |
| 7 | Hurricane, Sex | 3 | 216.79 | 8.12 | 0.010 |
| 8 | Hurricane $\times$ Sex | 4 | 217.85 | 9.19 | 0.006 |
| 9 | Rain | 2 | 218.04 | 9.38 | 0.005 |
| 10 | Hurricane, Sex, Year | 4 | 218.23 | 9.56 | 0.005 |
| 11 | Year(cat), Sex | 28 | 218.64 | 9.98 | 0.004 |
| 10 | Year | 2 | 222.06 | 13.40 | 0.001 |
| 13 | Sex | 2 | 225.25 | 16.59 | 0.000 |
| Post hoc models: | | | | | |
| 14 | Hurricane, Rain, $Rain^2$ | 3 | 199.06 | −9.61 | † |
| 15 | Rain, $Rain^2$ | 2 | 200.61 | −8.05 | † |

*Notes:* Models are based on 27 male and 25 female Puerto Rican Parrots (for a total of 258 transitions over 27 years). $\Delta AIC_c$ indicates the difference between each model and the best model, and $AIC_c$ weight is the relative likelihood of a model, given a set of candidate models, normalized to sum to 1. Two post hoc models were run once a quadratic relationship between rainfall and survival was identified.

† These two post hoc models were not part of the original candidate model set being evaluated.

Parrot population growth (Fig. 8). Fecundity (*m*) had the second highest correlation ($r^2 = 0.18$) with λ. The hatchability rate and the rate of nestling survival were nearly equally important components of fecundity, while the probability of renesting was an unimportant component (Fig. 8). Survival of adults and first-year birds ranked third ($r^2 = 0.14$), while variation in juvenile survival was much less important ($r^2 = 0.02$) to variation in the rates of population growth.

During hurricane years (Fig. 8), adult and subadult survival were most highly correlated ($r^2 = 0.45$) with λ. Fecundity ($r^2 = 0.30$) and the probability of transitioning to breeding status ($r^2 = 0.21$) were the next most important factors. Nestling survival and hatchability rates remained important components of fecundity. Variation in juvenile survival was again relatively unrelated ($r^2 = 0.02$) to λ as was the probability of renesting ($r^2 = 0.02$).

When additional influences of inbreeding were specifically incorporated into the LSA analysis through further reduction of the rate of production and survival of young (see *Methods*), they had little influence on population growth. Under moderate levels of inbreeding ($F = 0.142$), variation in the coefficient of inbreeding only accounted for a very small amount of the variation in population growth (λ) during hurricane and non-hurricane years ($r^2 = 0.024$ and $r^2 = 0.007$, respectfully). Even under severe inbreeding depression ($F = 0.5$), variation in the coefficient of inbreeding only produced $r^2 = 0.068$ and $r^2 = 0.08$ during hurricane and non-hurricane years, respectfully. Correlations of other demographic rates with λ changed only slightly from those shown in Fig. 8 when inbreeding was included in the LSA model.

## DISCUSSION

Risk analysis (Fig. 2) indicates the future of the Puerto Rican Parrot population is highly uncertain despite prolonged and intensive efforts to recover the species. Fluctuating in a bottleneck of 20–40 individuals for more than 30 years (Fig. 1), the rates of annual population growth have been low despite continued augmentation of the wild population with releases of captively reared individuals. Puerto Rican Parrot population dynamics are complex due to the interplay of a variety of natural and management processes and, as a result, confidence intervals of the projected population were wide (Fig. 2). Below we discuss evidence for or against specific causes maintaining the bottleneck (Table 1) and their relative importance (Fig. 8). We summarize by assessing the roles of genetic, demographic and environmental stochasticity and catastrophes in maintaining the bottleneck in the Puerto Rican Parrot, and conclude with recommendations for management.

### Primary factors maintaining the bottleneck

*Hurricanes.*—Hurricanes had large effects on parrot survival (Figs. 1 and 7, Table 3) and they occurred with sufficient frequency during our study to be among the most important factors contributing to the maintenance of the bottleneck (Fig. 8). Survival can be affected by hurricanes either directly or indirectly (Wiley and Wunderle 1993). Direct hurricane effects result in mortality from exposure to high winds and rain, are rarely documented in terrestrial birds, and have not been documented in the Puerto Rican Parrot. Parrots most likely died of food stress after hurricanes. Evidence for
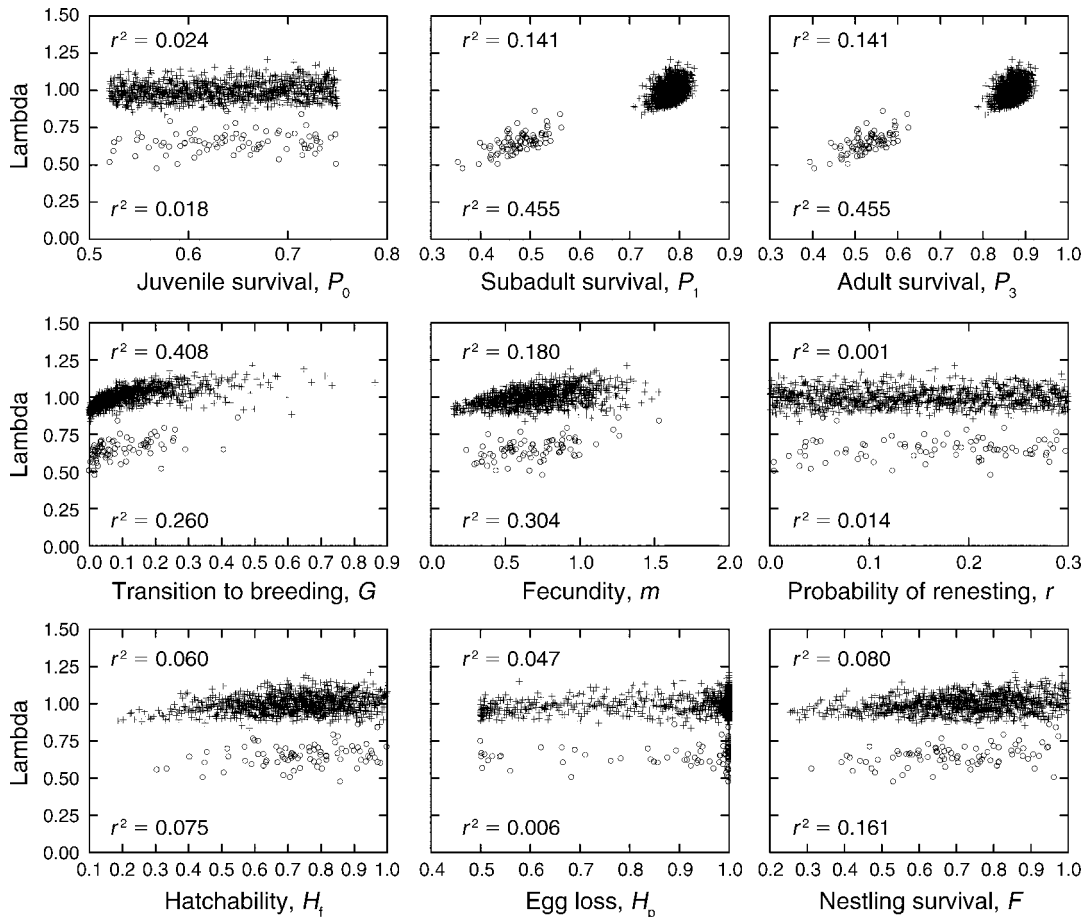
FIG. 8.  Results of the life-stage simulation analysis (LSA) based on creation of 1000 matrices drawn from parameters and distributions described in Appendix C. Hurricane years are depicted with open circles, and non-hurricane years with crosses. The coefficient of determination ($r^2$) between each vital rate and lambda was calculated separately for non-hurricane years (above) and hurricane years (below). Vital rates that account for the greatest variation in population growth rate have the greatest impacts on population dynamics. Key to variables: lambda ($\lambda$), geometric rate of annual population growth; $P_0$, probability of juvenile survival; $P_1$, probability of survival of one-year-olds; $P_3$, survival probability of breeders; $G$, probability of transitioning or ascendancy of nonbreeders to breeder status; $m$, annual fecundity or the number of female offspring produced per breeding female; $r$, probability of renesting within a breeding season if a nest fails; $H_f$, probability that an egg is fertile; $H_p$, probability that a fertile egg will survive to hatching; $F$, probability that a nestling will survive to fledge. See Appendices B and C for details of parameter estimation.

the indirect effects of hurricanes on mortality comes from studies showing that the magnitude of post-hurricane bird population declines is related to diet, indicating that a storm's greatest effect occurs in its aftermath rather than during its impact (Wiley and Wunderle 1993). Species relying on flowers, fruits, or seeds are especially vulnerable when hurricane winds strip these resources from plants, resulting in reduced food supplies, irregular fruiting periods, and increased patchiness of food (Wunderle 1995, 1999). At that time Puerto Rican Parrots may also be more vulnerable to predation from Red-tailed Hawks (*Buteo jamaicensis*) as they forage in storm-damaged canopies with limited cover. Confronted with these conditions, it is not surprising that after hurricanes parrots wandered widely and outside traditional areas (White et al. 2005b), and

that breeder mortality increased (Fig. 6) and population size declined (Fig. 1).

Hurricanes might provide long-term positive impacts on parrot population growth, despite the immediate mortality they cause that prolongs the bottleneck. Hurricanes create nesting cavities and in the long-term increase food availability (Meyers et al. 1993). In the years immediately following Hurricane Hugo, the number of parrot breeding pairs increased despite a decline in population size, and breeders laid larger clutch sizes and had greater fledging success. The highly frugivorous diet of the Puerto Rican Parrot may lead to frequent deficiencies in the proteins necessary for breeding (Morton 1973). Increased primary productivity in the storm's aftermath may also have provided a food supply of superior nutritional quality for several years (Scatena et al. 1996). Enhanced reproduction following

Hurricane Hugo was also documented in the omnivorous Pearly-eyed Thrasher in the Luquillo Experimental Forest (Arendt 2006).

These beneficial, but delayed, effects of hurricanes raise a fundamental question of whether in the long run hurricanes result in detrimental or positive effects on parrot populations. Hurricanes may kill enough individuals to drive a small population below a threshold for recovery, but they also increase nutrient cycling and create cavity nest sites. Thus, hurricanes promote the long-term functioning of forest ecosystems that support Puerto Rican Parrots. However, given the small size of the parrot population and its low growth rate, the increasing trend in North Atlantic hurricane activity since 1995, which has been attributed to both natural variability (Goldberg et al. 2001) and anthropogenically induced climate change (Emanuel 2005), suggests future challenges for sustaining Puerto Rican Parrots.

*Failure to nest.*—The failure of a large percentage of adult parrots to breed annually was the most important factor reducing population growth during non-hurricane years (Fig. 8). A significant demographic feature of the wild Puerto Rican Parrots has been the relative rarity of breeding pairs (Fig. 6), which was first recognized in the 1970s (Snyder et al. 1987). While the population has shown a slow, steady increase during non-hurricane years (Fig. 1), the number of egg-laying pairs has increased much more slowly, leading to a steadily declining percentage of the population engaged in reproduction (Fig. 6). Only about one-third of the total birds or one-half of the pairs holding and defending territories have laid eggs, a much lower fraction than seen in other large psittacines. For example, 77% of territorial pairs of Hispaniolan Parrots (*Amazona ventralis*), the closest relative of the Puerto Rican Parrot, produced eggs (Snyder et al. 1987). Relatively low breeding effort is also known for *Amazona oratrix* (Enkerlin-Hoeflich 1995) and for several species of large macaws of the Amazon basin (Munn 1992). For the latter species, low breeding effort appears related to nest site scarcity, but in the former, low breeding effort has been chronic despite an abundance of good nest sites.

A diverse set of factors could cause low breeding effort in the Puerto Rican Parrot, including nest-site scarcity, sex or age structure imbalances, social structure disruption, inbreeding avoidance, and nutritional constraints. Low nest-site availability is probably not a primary factor because managers have added many good nest sites and improved over 80 natural cavities in the Luquillo Experimental Forest, and several pairs have switched nest sites, or abandoned and reoccupied sites over the years. We found no evidence of skewed sex ratios, although our sample sizes were small. Moreover, the rapid occurrence of mate replacements by both sexes suggests a pool of potential breeders of both sexes exists and that sex ratio imbalances seem an unlikely cause of low rates of nest initiation. The rapid rate of mate replacement also suggests that it is unlikely that the population contains a large number of sexually immature birds, physiologically incapable of breeding. Our modeling outcomes support this conclusion (Fig. 6). The percentage of birds that should have reached the age of first breeding and were available to reproduce each year was usually well above the long-term average percentage of breeders (Fig. 6), unless the age of first breeding in the wild is substantially higher than 3–5 years. Parrots may have a complex social system based on flocking and interactions among breeding and nonbreeding individuals (Beissinger 2008) that may limit the number of nesting pairs. Little is known, however, about a higher order social structure in parrots or how it would change with a reduction in population size.

Inbreeding avoidance behavior may limit mate choice options in small populations, resulting in fewer acceptable mates and a higher percentage of nonbreeding birds. In many vertebrate species capable of individual recognition, there are inhibitions to breeding with close relatives or early close associates (Hoogland 1982, Blouin and Blouin 1988, Pusey and Wolf 1996). Psittacines are capable of individual recognition, especially on the basis of vocalizations (Saunders 1983, Bradbury 2003). Considering that the wild Puerto Rican Parrot population in recent decades has consisted largely of the progeny of about four wild pairs, at any one time a sizeable portion of birds of the opposite sex might be either perceived as close relatives or as unacceptable due to other behavioral characteristics. If low breeding effort is attributable to perceptions of close genetic relationships among birds in the remnant flock, the number of nesting pairs could be increased by introductions of free-flying captive-bred birds into the flock. Consistent with this prediction, one of three captive-bred parrots that were released to the wild as free-flying birds in 1985 became a member of a productive wild pair. More recently, two captive-bred males released into the Luquillo Experimental Forest bred with wild females at traditional nest sites (White et al. 2005*b*; USFWS, *unpublished data*).

Two patterns of breeding behavior contradict the evidence that inbreeding avoidance may be responsible for the low number of breeding pairs. First, the rate of mate replacement should be low in a small population where the probability of finding an unrelated mate is low. Nevertheless, breeders rapidly replaced lost mates, and it seems unlikely that all these replacements were unrelated or were perceived as unrelated by the remaining breeder. Second, a period of relatively high reproduction in the Puerto Rican Parrot followed Hurricane Hugo, which suggests that low breeding effort depends on environmental factors rather than inbreeding avoidance. More research is needed to determine the relative importance of environmental factors and inbreeding avoidance in limiting the number of breeding Puerto Rican Parrot pairs.

*Low hatching success due to apparent effects of inbreeding.*—Our analysis of the role of inbreeding

primarily depends on corollary evidence because few Puerto Rican Parrots were banded to facilitate the direct construction of pedigrees. Direct evidence is limited to a mother–son breeding pair in North Fork (Snyder et al. 1987). Nevertheless, there is indirect evidence to support the hypothesis that inbreeding occurs and may have reduced fecundity (Fig. 3).

The negative effects of inbreeding, often expressed through reduced fertility or fitness of offspring, may become more acute as the duration of the bottleneck increases and population size decreases (Frankel and Soulé 1981, Frankham et al. 2002, Briskie and Mackintosh 2004). The wild Puerto Rican Parrot population has consisted of fewer than 50 individuals and fluctuating between three and six breeding pairs for more than 30 years. Even with the inclusion of the aviary parrots, the total Puerto Rican Parrot population has remained below 150 birds. Relatively few breeders have contributed most offspring to the wild population, despite fostering into the wild of 35 young produced in captivity. Thus, we expected Puerto Rican Parrots to provide an example where inbreeding effects could be strongly expressed and could contribute to the maintenance of the bottleneck.

The apparent impact of inbreeding may be most evident on hatchability of eggs (70.6%), which was markedly lower than the mean value (89%) for other cavity nesting birds (Koenig 1982). The moderately high level of hatching failure (29.4%) observed for the Puerto Rican Parrot is similar to the mean hatching failure of New Zealand birds (25%) that experienced bottlenecks of <150 individuals (Briskie and Mackintosh 2004). Moreover, when Puerto Rican Parrot pairs with low hatchability changed composition, hatchability increased (Fig. 4) presumably because they were no longer mated to a close relative. Furthermore, hatchability varied markedly among parrot pairs and pair composition was the most important single factor accounting for variation in hatchability (Table 2). Nevertheless, both nest site and rainfall also affected hatching success (Table 2), although they explain much less of the variation in hatchability than pair composition. While we cannot rule out the potential influence of environmental factors on hatching success, hatchability of Puerto Rican Parrot eggs averaged almost 14% less than hatching success of the abundant Pearly-eyed Thrasher (84%) nesting in similar environmental conditions in the Luquillo Experimental Forest (Beissinger et al. 2005). Analyzing the data in Table 3 of Brock and White (1992), captive Puerto Rican Parrots also exhibited significantly lower hatching success ($U = 120.5$, $P = 0.019$) than outbreed congeneric Hispaniolan Parrots (*A. ventralis*) nesting in the same aviary, although we do not know if hatching success may have been influenced by differences in husbandry. Chick deformities were also expected as an indication of inbreeding depression but the incidence of chick deformities was low relative to the incidence of egg hatching failure, which constituted the overwhelming cause of offspring loss (Fig. 4).

A consistent temporal trend in egg hatchability per pair did not occur in the Puerto Rican Parrot (Fig. 4). Such a trend was observed in an apparently genetically stressed small population of Greater Prairie Chickens (*Tympanuchus cupido pinnatus*) in which hatchability declined from 91–100% to less than 80% over a 30-year period (Westemier et al. 1998). There was, however, a decline and a recovery in Puerto Rican Parrot egg hatchability, which suggests either inbreeding effects were purged (but see Crnokrak and Roff 1999, Briskie and Mackintosh 2004) or more likely were associated with particular pairs that disbanded. Nevertheless, a recent pair with low egg hatchability indicates that the negative effects of inbreeding may still persist. Brock and White (1992) also concluded that poor reproduction of both wild and captive Puerto Rican Parrots traced to inbreeding depression on the basis of band-sharing coefficients derived from DNA fingerprinting of captive birds. Analyzing the data in Table 3 of Brock and White (1992), hatchability of captive Puerto Rican Parrot eggs was significantly negatively related to the band-sharing coefficients ($r_S = -0.544$, $n = 12$, $P < 0.05$).

### Less important limiting factors: survival and nest failure

Despite the potential importance of changes in annual survival to Puerto Rican Parrot population dynamics (Thompson 2004), there is little evidence that low levels of survival kept the parrot in a bottleneck except through the catastrophic impacts of hurricanes (Figs. 7 and 8). Elasticity analysis of a matrix population model for this species (Thompson 2004) similar to the one used in this paper (Appendix B) indicate that adult survival is the most sensitive (elastic) element. Nevertheless, adult survivorship was relatively high during non-hurricane years (88%) from 1973 to 2000, although it may be lower in recent years (T. H. White, Jr., *personal communication*). Only extremes in annual rainfall associated with hurricanes or droughts increased parrot mortality (Fig. 5), perhaps through reduced food abundance as discussed above. Much less is known about juvenile and subadult survival, but estimates from previous work provide no evidence of extremely low rates (Snyder et al. 1987, Lindsey et al. 1994, Meyers et al. 1996; Appendix B). Annual survival of captively reared Puerto Rican Parrots during the first year after release into the wild was similar to fledgling survival (White et al. 2005b), although well below rates for birds released into predator-free habitat on Hispaniola (Collazo et al. 2003). While maintaining high levels of survival is critically important to recover the Puerto Rican Parrot, there is little evidence that survival during non-hurricane years was responsible for the population bottleneck (Fig. 8).

Under intensive management, rates of parrot nest failure have been low (Fig. 5) yet still contribute to the maintenance of the bottleneck (Fig. 8). Nest failure rates

in the absence of management are believed to be high, as only 11–26% of parrot nests in the Luquillo Experimental Forest were estimated to be successful before initiation of intensive management in 1973 (Snyder et al. 1987). More recent estimates indicate that 38% of the nests might be successful in the absence of nest guarding (Lindsey 1992). Without management only 0.26–0.58 young were estimated to have fledged per active nest (Snyder et al. 1987). These estimates contrast sharply with the values for the managed population in which an average of 71% of the nests have been successful and an average of 1.7 young have fledged per active nest. These differences suggest that management has substantially diminished the effect of nest failure as a factor maintaining the bottleneck.

### Relative importance of factors maintaining the bottleneck

The paradigm for understanding population bottlenecks has concentrated on the effects of inbreeding, loss of genetic diversity, and genetic drift (Franklin 1980, Soulé 1980, Frankham et al. 2002). Such concerns are warranted as populations may require generations for genetic diversity to recover from losses during bottlenecks (Frankel and Soulé 1981, Hedrick and Miller 1992, Keller and Waller 2002, Frankham 2005a). While inbreeding and loss of genetic diversity may play important roles in reducing the growth of small populations, considerable controversy has ensued over whether these effects are primary causes of extinction or secondary contributors (Lande 1988, Caro and Laurenson 1994, Mills and Smouse 1994, Lande 1998, Elgar and Clode 2001, Frankham 2005a, Jamieson 2007a). Moreover, the causes of decline that created a bottleneck are not necessarily the same factors that maintain it.

Our results indicate that genetic, demographic, and environmental stochasticity and catastrophes all had roles in maintaining a bottleneck in the Puerto Rican Parrot for more than six generations, but they also suggest that some processes have played more important roles than others (Fig. 8). The persistence of a bottleneck was primarily attributable to three factors acting together to constrain parrot population growth in the Luquillo Experimental Forest. The most important limiting factor may be the failure of a large percentage of adult parrots to breed annually, because it constrains population growth in both non-hurricane and hurricane years (Fig. 8). Although the exact cause of this form of demographic stochasticity is unclear, a combination of genetic, demographic (e.g., social structure), and environmental factors may be involved (Table 1). Population growth was constrained further by periodic catastrophes in the form of hurricanes and extreme rainfall events which have reduced annual survival (Fig. 7). Finally, the apparent effects of inbreeding in the form of reduced egg hatching success appear to be moderately strong in the population but its influence on population dynamics was much weaker than the other two factors (Fig. 8), even when additional reduction in hatching

success and survival of young due to inbreeding was incorporated into the sensitivity model.

The relative importance of factors maintaining the Puerto Rican Parrot bottleneck varied throughout the 30-year period of study. Hurricanes emerged as important cause of adult mortality only during the last 15 years (Fig. 1), as no strikes occurred in earlier years. The percentage of parrots breeding annually varied from 25% to 71%, and declined from 39% during the first decade (1973–1982), to 33% from 1983–1992, to 29% from 1993–2000 (from Figs. 1 and 6). Low hatching success apparently due to inbreeding occurred in many years, but was a major cause of reproductive failure from 1978 to 1984 and again in the late 1980s (Figs. 3 and 5). Although average annual survival of breeders during non-hurricane years tended to be high, which made this factor appear less important, the two lowest values occurred during non-hurricane years (Fig. 7). Thus, any limiting factor could be important (or unimportant) in reducing population growth and maintaining a bottleneck for a particular year or period. Only by examining the patterns of candidate limiting factors over the course of three decades and integrating their impact through demographic modeling (Fig. 8) were we able to detect the relative importance of factors maintaining the bottleneck over the long-term.

We were unable to evaluate the role of interactions among stochastic processes. For example, mortality from hurricanes could occur differentially to individuals that were inbred relative to outbred survivors due to the interaction of inbreeding and stress (Keller et al. 2002, Armbruster and Reed 2005, Frankham 2005b, Marr et al. 2006), which would have resulted in an underestimate of the importance of genetic stochasticity in our study. However, the captive population of Puerto Rican Parrots, which is about twice as large as the wild population, is nearly devoid of genetic diversity (S. M. Haig, *personal communication*). This suggests that little genetic variation may remain in the wild population for selection against inbred individuals. Moreover, stresses may act to purge mutational load and increase long-term persistence (Robert 2006). Lastly, the magnitude of the interaction between inbreeding and mortality from hurricanes would have to be very large to change the rankings of the factors contributing to population growth (Fig. 8).

### Management recommendations

Active management of parrot nests has largely reduced the effects of nest failure due to nongenetic causes by guarding nests (Figs. 5 and 8) and has helped to ameliorate the high incidence of egg hatching failures by fostering aviary-produced offspring into wild nests. In the absence of nest guarding and fostering of young, Puerto Rican Parrot fecundity would likely decrease substantially due to a decline in nesting success (from 71% to 38%; Lindsey 1992) and in the number of young per successful nest (from 2.31 to 1.78). Casting these

rates into our population model (Appendices B and C), the Puerto Rican Parrot population during non-hurricane years would switch from slowly growing ($\lambda = 1.059$) under intensive management to slowly declining ($\lambda = 0.989$) in its absence. Combined with reduced survival associated with periodic catastrophes and the failure of some adult parrots to breed, increased levels of nest failure could result in extinction of the Puerto Rican Parrot. Nest guarding and fostering of young into the wild must continue to recover the Puerto Rican Parrot. Moreover, active management should also minimize inbreeding effects by capturing one member of pairs that show repeated evidence of low hatching success and moving them to captivity.

Hurricanes play a disproportionately important role in maintaining the bottleneck, but there may be little that management can do directly to reduce the impacts of hurricanes on parrot survival. The best solution may be to reduce the likelihood that hurricane strikes will cause extinction by creating a second population at another location on the island, a process that is now underway. Recent releases of aviary-produced parrots into the drier, lower elevation karst forests of north-central Puerto Rico and natural dispersal of parrots into the lower and relatively drier tabonuco forest of the Luquillo Experimental Forest may alleviate some of the stresses currently restraining recovery (see also White et al. 2005b). The mid-elevation Palo Colorado forest in the Luquillo Experimental Forest has been the final refuge of the Puerto Rican Parrot but may not represent the most optimal habitat for the species; it may simply be the habitat where parrots were able to persist the longest because of isolation from human disturbance (Snyder et al. 1987). Given the multitude and abundance of stresses faced by parrots in the Luquillo Experimental Forest including Red-tailed Hawks, bot flies, rats, Pearly-eyed Thrashers, bees, and the reduction of hatching success from heavy rainfall (Table 2), this habitat may be suboptimal for recovery. Recovery might be more rapid in drier habitats, as found in lower elevations, where thrasher and hawk densities are also lower (Snyder et al. 1987, Rivera-Milan 1995). However, other limiting factors may rise in importance to slow population growth in the lowlands.

While creating a second population should benefit recovery of any endangered species that survives in only a single population, such as the Puerto Rican Parrot, compromising the core population's chances of survival and recovery on the untested belief that healthier populations can be established elsewhere would be imprudent. This issue is especially crucial if the releases to a new wild parrot population involve translocations of wild birds from the Luquillo population, and as the limited financial and human resources devoted to the Puerto Rican Parrot recovery program become split between establishing a new population and managing the existing one. While there are concerns about achieving a faster growth rate for the Puerto Rican Parrot in the Luquillo Experimental Forest, intensive management has created a positive growth rate. Moreover, several of the factors that have maintained the bottleneck in the Luquillo Experimental Forest may also occur in a new population, such as hurricane strikes, reduced numbers of breeding pairs, and inbreeding. These factors, as well as others, are hypotheses that could be tested through properly conducted release efforts.

A primary factor constraining population growth that was identified from 27 years of intensive research has been low breeding effort of the Puerto Rican Parrot, but its causes remain unclear. The substantial, but temporary, increase in breeding following Hurricane Hugo suggests that the reluctance of adult Puerto Rican Parrots to breed may be attributed to environmental factors rather than inbreeding avoidance. Determining what these factors are and ameliorating them should be overriding research and management priorities. Special attention should be given to potential nutritional effects through food supplementation experiments and to the role of conspecifics and social structure in facilitation of breeding (Vernon 1995, Brooke et al. 2000, Waas et al. 2000, Thomas 2006). In addition, the role of inbreeding in reducing breeding effort can only be rigorously assessed by placing individually identifiable leg bands on every wild parrot and taking and analyzing blood samples to construct pedigrees. Techniques for capture and banding have been perfected with surrogate species for over a decade (Meyers 1994, 1995).

Increasing the proportion of breeders in the population would have a large impact on population growth. Increasing the proportion of breeders in our matrix population model (Appendix B) by 50% from the current mean value of 0.34 to 0.50 nearly triples the rate of population growth ($\lambda$ from 1.059 to 1.153), assuming current levels of nest guarding and fostering of chicks. These efforts, together with enhanced efforts to track the demographic characteristics of all populations are needed if full recovery of the species is to be achieved in an efficient manner. The rapid increase in population growth immediately following two hurricanes gives hope that the Puerto Rican Parrot population is not doomed to extinction. It could be recovered with effective field management and if efforts to establish a new wild population elsewhere on the island are successful.

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## APPENDIX A

Calculation of population prediction interval (PPI) (*Ecological Archives* M078-006-A1).

## APPENDIX B

Parameterization of the stage-based deterministic matrix model (*Ecological Archives* M078-006-A2).

## APPENDIX C

Life-stage simulation analysis (*Ecological Archives* M078-006-A3).

## APPENDIX D

Literature cited for Appendices A, B, and C (*Ecological Archives* M078-006-A4).