ORNITOLOGIA NEOTROPICAL

Volume 15 | 2004 | No. 3

ORNITOLOGIA NEOTROPICAL 15: 289–297, 2004

AN AGE-STRUCTURED POPULATION MODEL OF THE PUERTO RICAN PARROT (*AMAZONA VITTATA*)

Jeffrey J. Thompson[1]

Department of Biology, University of Puerto Rico, P.O. Box 23360, San Juan, Puerto Rico 00931-3360, USA & Institute for Tropical Ecosystem Studies, University of Puerto Rico, P.O. Box 23341 San Juan, Puerto Rico 00931-3341, USA.

Resumen. – Un modelo poblacional estructurado por edad para la Cotorra Puertorriqueña (*Amazona vittata*). – Escribí el modelo de simulación por computadora PARPOP para investigar la dinámica poblacional de la Cotorra Puertorriqueña (*Amazona vittata*), una especie con < 50 individuos en la naturaleza. La matriz del modelo esta basada en clases de edad e incorpora los efectos de los huracanes en la mortalidad y reclutamiento. Tomando en cuenta el manejo intensivo actual, la probabilidad de extinción de la población es 4.7% en un período de cien años, con una población promedio de 206 pájaros después de 100 años. Usando datos reales de los juveniles del período 1985–2000, el modelo predijo las tendencias generales de la población de manera adecuada, pero sobreestimó el tamaño de la población en los 1990. Sin embargo, los estimados poblacionales son presentados sin valores de error, haciendo difícil la evaluación de la precisión del modelo. La población modelada fue más sensible a los cambios en mortalidad de los individuos reproductivos de mayor edad , seguidos por la proporción de hembras que intentaron anidar. El modelo resalta la importancia de continuar e incrementar, si es posible, el manejo intensivo de la especie para su supervivencia. Adicionalmente, el modelo demuestra la necesidad de un mayor rigor cuantitativo en la estimación de la población y de la supervivencia para clases de edad diferentes. Para lograr esto, se sugiere marcar individuos con transmisores ya que las técnicas para capturar y marcar las cotorras son bien conocidas, han sido aplicadas con éxito en la Cotorra Puertorriqueña y otras especies de *Amazona*, y el valor de los datos es mucho mayor que el riesgo mínimo asociado con la técnica .

Abstract. – I wrote the computer simulation model PARPOP to investigate the population dynamic of the Puerto Rican Parrot (*Amazona vittata*), a species with < 50 individuals in the wild. The matrix model is age-class based and incorporates the effects of hurricanes on mortality and recruitment. Under the present intensive management, the probability of extinction for the population over a one hundred year period is 4.7%, with an average population of 206 birds after 100 years. Using actual fledging data for 1985–2000, the model adequately predicted the overall trends in the population but over-predicted population size

---

[1]*Current address:* D. B. Warnell School of Forest Resources, University of Georgia, Athens, Georgia 30602-2152, USA. *E-mail:* perdiz@uga.edu

through the 1990's. Population estimates, however, are presented without error values, making an evaluation of the accuracy of the model difficult. The modeled population was most sensitive to changes in mortality of older breeding individuals followed, closely by the proportion of females that attempt to nest. The model highlights the importance of maintaining, and increasing if possible, the intensive management of this species for its survival. Moreover, the modeling highlights the necessity for greater quantitative rigor in population estimation and in the estimates of survival for different age classes. To accomplish this, it is suggested that radio tagging be used since the techniques for capturing and radio-tagging parrots are well researched, have been successfully applied to the Puerto Rican Parrot and other species of *Amazona*, and the value of the data out-weigh the minimal risk associated with the technique. *Accepted 12 January 2004*.

Key words: Puerto Rican Parrot, *Amazona vittata*, population modeling, age-structured, Puerto Rico, Luquillo Mountains, Caribbean, West Indies.

INTRODUCTION

The Puerto Rican Parrot (*Amazona vittata*) is one of the most endangered birds in the world with < 50 individuals in the wild, all located in the Luquillo Experimental Forest of northeastern Puerto Rico (United States Fish & Wildlife Service 1999). Because of the small size of the population, intensive management is essential for the species's recovery. However, the small population also makes collection of data necessary for successful management decisions difficult and, possibly, counter-productive to management efforts.

In a case such as this where data collection is difficult, the application of population modeling is not only useful, but also essential for prioritizing research as well as for investigating the potential effectiveness of management decisions (Starfield 1997). Population models allow managers to test assumptions and to predict the outcome of management decisions without the possible adverse impacts or costs associated with such actions. Moreover, simulation models allow for assessing the quality of data that are being collected, as well as indicating what data are needed (Starfield 1997).

I wrote an age-structured matrix model (PARPOP) in FORTRAN 77 ver. 4.0 to investigate the population dynamics of the Puerto Rican Parrot. The model is stochastic, simulating variations in adult mortality, reproductive success, and hurricane effects. I used the model to estimate the extinction probability for the remaining population of the Puerto Rican Parrot and population growth under continued intensive management. I then modeled the sensitivity of the population to changes in mortality and reproduction, to assess data needs, and to suggest directions for future research and management efforts.

METHODS

The age-structured population model PARPOP is a stochastic, matrix-based model that uses an annual time step (Fig. 1). The model determines the pre-breeding population and, based upon that, the number of nesting females and the fledging success of each nest. Following this, annual mortality is assessed for all birds. Birds are then all moved into the next age class and fledglings placed into the population and the process repeated.

The model uses annual mortality rates from the "best guess" life table from Snyder *et al.* (1987), which is based on data from the recovery effort and is best supported for first year and adult birds. Differential mortality rates were assigned to birds 0–1 (age class 1), 1–2 (age class 2), 2–3 (age class 3), and ≥ 3 (age class 4) years of age, with the maximum life span set at 45 years, and assuming that birds can breed up to their maximum age (Snyder *et al.* 1987) (Table 1). Subsequent sur-

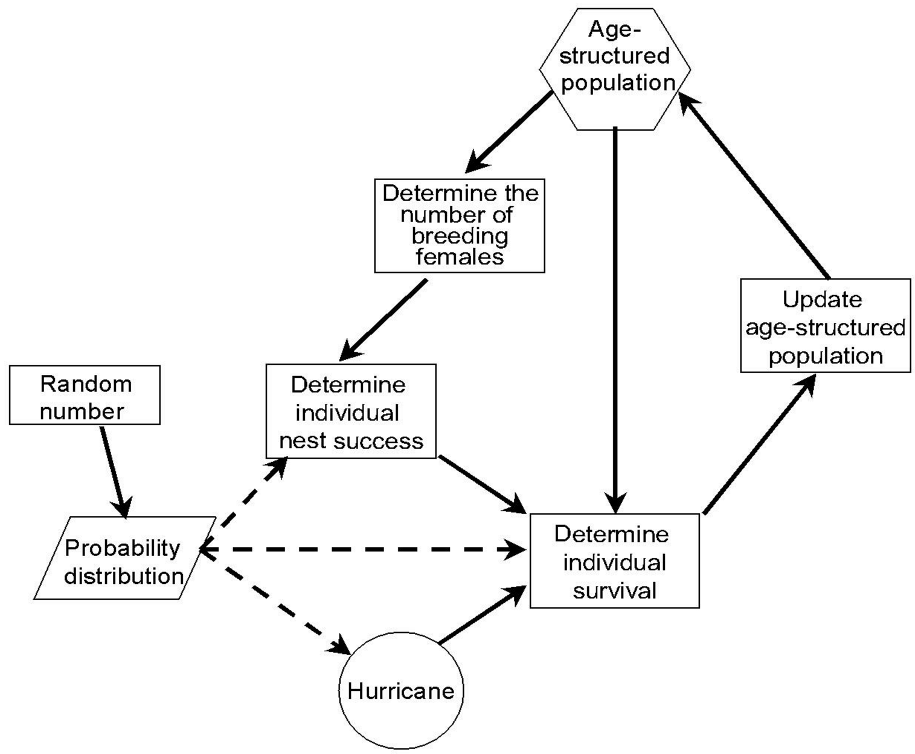

FIG. 1. Flow chart representing the model PARPOP.

vival data from radio-tagged birds are consistent with mortality rates given for subadults (Meyers *et al.* 1996).

Since Snyder *et al.* (1987) caution that their data were not long-term and may not represent variations in mortality, the model stochastically assigns mortality to individuals on an annual basis. Moreover, the model was run with annual mortality rates from the "optimistic" and "pessimistic" life tables for comparison (Snyder *et al.* 1987) (Table 1).

Reproductive success was expressed as the number of birds fledged per adult female breeding, which was stochastically assigned to individual nests based on data on fledging success. Since all breeding age females do not breed in a year (Snyder *et al.* 1987), it was assumed that 50% of the total female population nested within a year, and there is an even aged sex ratio (*sensu* Lacy *et al.* 1989). Data for annual fledgling success for the pre-recovery effort (pre-1973) come from Snyder *et al.* (1987), and for the recovery effort (1973–2000) from Wunderle *et al.* (2003) (Table 2).

Hurricanes strike the Luquillo Experimental Forest on average at 60-year intervals (Scatena & Larsen 1991) and can cause higher than normal mortality (United States Fish & Wildlife Service 1999). To simulate hurricane related mortality, annual mortality rate was increased to 50% for all age classes in a year with a hurricane. Little data is available for

TABLE 1. Life table data for the best guess, optimistic, and pessimistic scenarios used in simulations with PARPOP (Snyder *et al.* 1987).

Age classes	Probability of mortality		
	Best guess	Optimistic	Pessimistic
0-1 year	0.35	0.3	0.4
1-2 years	0.22	0.15	0.33
2-3 years	0.15	0.9	0.25
3-4 years	0.1	0.9	0.18
>4 years	0.1	0.9	0.1
Maximum age (years)	45	52	41

TABLE 2. Mean probability of fledging success per nest for the pre-recovery effort period (< 1973) and for the recovery effort (1973-2000) (Snyder *et al.* 1987, Wunderle *et al.* 2003).

Number of fledglings/nest	Pre-recovery effort	Recovery effort (1973–2000)
0	0.7	0.39
1	0.04	0.09
2	0.15	0.27
3	0.11	0.23
4	0.0	0.02

this parameter and it is based upon the maximum hurricane related mortality of 50%, which followed hurricane Hugo in 1986 (United States Fish & Wildlife Service 1999).

In the model, hurricanes occur randomly using the mean of 1 in every 60 years. Although in the long-term hurricanes occur non-randomly (Scatena & Larsen 1991), this was not incorporated into the model because no more than 100 years were simulated. Moreover, the stochastic nature of the model does not preclude hurricanes from occurring at shorter return intervals. Also, the possibility does exist that more than one hurricane can strike the Luquillo Experimental Forest in a year, however, there is no record of this occurring and subsequently this was not included in the model.

For comparison with the real population, the model was initialized with the 1985 population of 35 individuals and, using the actual fledging values from 1985 through 2000, run for 1000 simulations. Additionally, the model was run using optimistic and pessimistic age-related mortality and maximum life span values.

To determine the probability of extinction for the species, I ran the model for 1000 simulations of 100 years, with a starting population of 48 birds (2000 population) (United States Fish & Wildlife Service 1999). Here too the model was run with the optimistic and pessimistic age-related mortality and maximum life span values, as well as the pre-recovery nest success data from Snyder *et al.* (1987). The population was considered to be extinct if < 2 birds remained after 100 years.

I tested the sensitivity of the modeled population to changes in mortality rates by altering each mortality rate, while all other parameters remained constant, and then running the model for 1000 simulations of 100 years with a starting population of 48 birds. The final populations for each run with a par-

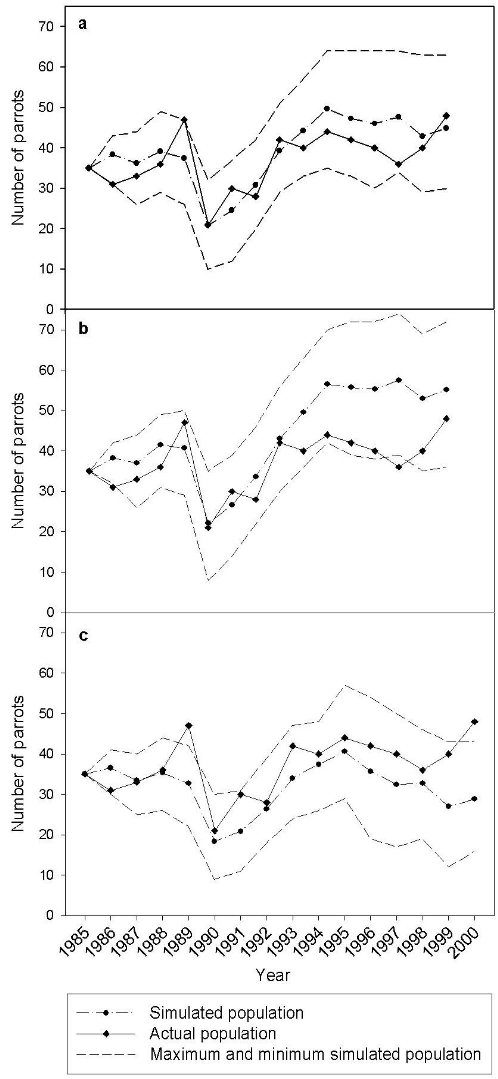

FIG. 2. Simulated mean annual population of the Puerto Rican Parrot (1985–2000) under the a) best guess, b) optimistic, and c) pessimistic life tables from Snyder *et al.* (1987), and using mean fledging data from 1973–2000 (Wunderle *et al.* 2003), compared to the estimated wild population. Dashed lines represent the maximums and minimums of the simulations.

ticular mortality rate, for each age class, were averaged and then a linear regression of the log-transformed data versus the change in mortality rate performed. The same methodology was used to test the effect of variations in the proportion of females that

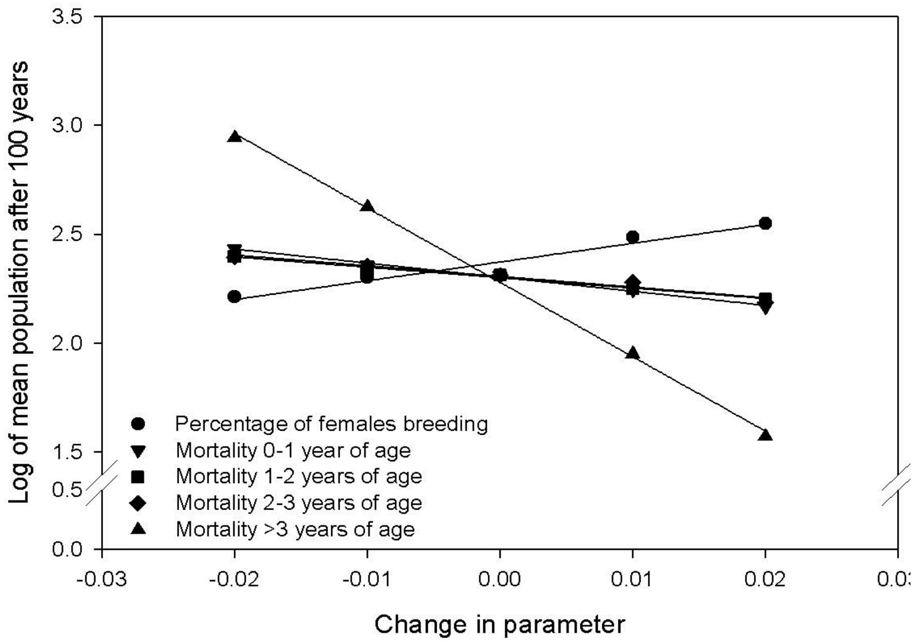

FIG. 3. Linear regression of the Log of the mean simulated population versus the proportional change in mortality by age class and the proportion of females breeding.

breed in a year. The greater the slopes of the regression were, the more sensitive the population was considered to be to changes in a parameter.

RESULTS

The simulations using actual fledging data yielded an average 2000 population of 45 individuals (95% confidence interval = ± 0.31) compared to the estimated 2000 population of 48 birds (Fig. 2). Under the optimistic scenario, the mean predicted 2000 population was 55 birds (95% confidence interval = ± 0.34) and under the pessimistic scenario 28 birds (95% confidence interval = ± 0.25) (Fig. 2). Only under the best guess scenario did all actual population estimates fall with the maximum and minimum range of simulated values (Fig. 2).

Starting with the 2000 estimated population of 48 birds, there is a 4.7% chance that the population will go extinct within 100 years under present management, with a mean population after 100 years of 206 birds (95% confidence interval = ± 10.41), and values ranging from 0–892. Comparatively, under the optimistic scenario the population mean after 100 years was 4009 birds (95% confidence interval = ± 164.6), ranging from 0–15,401 and a 0.2% probability of extinction. Under the pessimistic scenario the 100-year population means was 0 (95% confidence interval = ± 0.01), ranging from 0–5, and an extinction probability of 99.6%.

Under all scenarios, where the population went extinct, the number of fledglings produced per the total number of birds in the population had a mean of 0.142 (95% confidence interval = 0.007). In cases where the population was equal to or below the starting population, but did not go to extinction, the mean ratio of fledglings to the total population was 0.178 (95% confidence interval = 0.002), and where the 100-year population was greater than the starting value, the ratio was 0.188 (95% confidence interval = 0.003). These differences were significantly different (ANOVA $P = 0.000$).

Using the pre-recovery effort (pre-1973) fledging data, there was a 99.9% probability of extinction after 100 years, with a range of 0–5 individuals, using the best guess mortality estimates. Even under the optimistic scenario, there was a 96.5% probability of extinction after 100 years with a maximum population of 17 birds. Using the pessimistic scenario extinction probability was 100%.

The model was sensitive to changes in mortality across all age classes, but most sensitive to changes in mortality of mature individuals (age class 4; Fig. 3). The simulated population was also highly sensitive to the proportion of females breeding (Fig. 3).

DISCUSSION

The optimistic and pessimistic estimates of mortality provided by Snyder *et al.* (1987) were intended to bracket their best guess estimates by including the extremes in mortality. Based upon the modeling, at least in the short term, these estimates appear to do that, with the results using the best guess scenario fitting the population estimates most closely. The best guess scenario was the only one of the three where the simulated extremes in population size always include the population estimates. It is difficult, however, to make meaningful comparisons between the simulations and the population estimates because population estimation of the parrot is poorly executed, without accounting for differences in detectability (e.g., differences among observers, number of observers, period of the year, weather conditions), and not presented with confidence intervals (United States Fish & Wildlife Service 1999, Wunderle 1996).

Given the behavior of the model using the actual fledging data, and the relative security in mortality estimates (see methods), it can be inferred that of the three scenarios, the model run under the best guess scenario best simulates the actual population. This is further highlighted when the model was run to simulate 100-years. The optimistic scenario produces a population growth that is unrealistically rapid compared to the historic dynamics of the population. Conversely, under the pessimistic scenario, population growth is negative with the majority of model runs resulting in extinction.

If the assumptions and the data used in the model are representative of the population of the Puerto Rican Parrot, there is an approximately 5% likelihood that the population will go extinct under the present intensive management. Moreover, the modeling indicates the precarious position the species was in prior to the recovery effort, and that the decline of the parrot population starting in the 1950's was inevitable when viewed in the context of intensive nest robbing activities (Snyder *et al.* 1987), and most likely would have led to extinction without intervention.

The model suggests that there is a 6.8% probability of reaching the population goal of 500 individuals within the next 100 years (United States Fish & Wildlife Service 1999). Based on this, the goals of the recovery effort may be overly ambitious. Moreover, this is dependent upon a continuation of intensive nest management successfully maximizing nest success, which may not be feasible at larger population sizes.

The sensitivity of the model to adult mortality is not unexpected given the *K*-selected evolutionary strategy of parrots (Pianka

1970). A caveat, however, is that lost individuals from nesting pairs are usually replaced by a non-breeding individual, which should buffer the sensitivity of the population to adult mortality (Snyder *et al.* 1987). If this were the case, this would also make fledging success even more significant within the context of the population recovery.

Increased mortality may explain the greatest departure of the model predictions from the actual data, which occurs during the second half of the 1990's. The sensitivity of the model to the proportion of females breeding, which ultimately leads to increased recruitment, may also explain these differences. Nest guarding during this period was considerably reduced compared to the earlier period of the recovery effort, which may have led to overestimates in fledgling success (Wunderle *et al.* 2003). Equally plausible is a higher than normal mortality immediately after fledging, which went undetected.

The recovery of the parrot population that has occurred to date is largely, if not solely, a function of increased nest success and fledgling rates stemming from nest guarding, the elimination of nest robbing, nest modifications, exclusion of bees, parasite control, and fostering of captive bred chicks into wild nests (Snyder *et al.* 1987, United States Fish & Wildlife Service 1999). Based upon the modeling, this is the most effective and practical path to increase the population. Continuation of these practices, and intensification if possible, particularly in synchronizing nesting of captive birds with the wild population to maximize the number of chicks fostered into wild nests, is imperative for maintaining the species.

Considering the expense associated with nest management, it is obvious that, as the population grows, there will not be the ability to maintain the same level of management intensity per nest as presently exists. At what threshold the population may be large enough to maintain itself is conjectural, however, the modeling does suggest that a minimum mean fledging ratio of approximately one recruited bird per six birds in the population per year is necessary for maintaining a population size and about one recruited bird per five birds in the population per year for an increase in the population. The usefulness of this measure is questionable, however, without validation and better estimation of population size.

To assess the effectiveness of nest management requires increased rigor in population estimation so that the impacts of management efforts can be quantitatively evaluated. Moreover, the modeling highlights the need for a refinement in survival estimates. Both these ends can be facilitated via radio tagging.

The techniques for capturing and radiotagging *Amazona* are well worked out (Meyers 1994, 1996) and radio transmitters have been utilized on Puerto Rican Parrots, Yellow-shouldered Parrots (*Amazona barbadensis*), White-fronted Parrots (*Amazona albifrons*), Orange-winged Parrots (*Amazona amazonica*), Red-crowned Parrots (*Amazona viridigenalis*), and Hispaniola Parrots (*Amazona ventralis*) without any apparent negative effects (Lindsey *et al.* 1994, Meyers 1996, Meyers *et al.* 1996, Sanz & Grajal 1998, Collazo *et al.* 2003). Based upon the success in the radio-tagging parrots, the low risk involved, and the high value of the data obtained from well-executed telemetry projects, such studies should be a priority of the recovery effort.

ACKNOWLEDGMENTS

J. M. Meyers, J. P. Carroll, and three anonymous reviewers provided helpful comments on the manuscript. This research was supported through grants from the National Aeronautics and Space Administration Experimental Program to Stimulate Competitive Research (NCC5-215) and from the

National Science Foundation (DEB-9411973) to the Institute for Tropical Ecosystem Studies, University of Puerto Rico and the International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest.

REFERENCES

Collazo, J. A., T. H. White, Jr., F. J. Vilella, & S. A. Guerrero. 2003. Survival of captive-reared Hispaniolan Parrots released in Parque Nacional del Este, Dominican Republic. Condor 105: 198–207.

Lacy, R. C., N. R. Flesness, & U. S. Seal. 1989. Puerto Rican Parrot population viability analysis. Captive Breeding Specialist Group, Apple Valley, Minnesota.

Lindsey, G. D., W. J. Arendt, & J. Kalina. 1994. Survival and causes of mortality in juvenile Puerto Rican Parrots. J. Field Ornithol. 63: 466–472.

Meyers, J. M. 1994. Improved capture techniques for psittacines. Wildl. Soc. Bull. 22: 511–516.

Meyers, J. M. 1996. Evaluation of 3 radio transmitters and collar designs for *Amazona*. Wildl. Soc. Bull. 24: 15–20.

Meyers, J. M., W. J. Arendt, & G. D. Lindsey. 1996. Survival of radio-collared nestling Puerto Rican Parrots. Wilson Bull. 108: 159–163.

Pianka E. R. 1970. On r and K selection. Am. Nat. 104: 592–97.

Sanz, V., & A. Grajal. 1998. Successful reintroduction of captive-raised Yellow-shouldered Amazon parrots on Margarita Island, Venezuela. Conserv. Biol. 12: 430–441.

Scatena, F. N., & M. C. Larsen. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. Biotropica 23: 364–372.

Snyder, N. F. R., J. W. Wiley, & C. B. Kepler. 1987. The parrots of Luquillo: Natural history and conservation of the Puerto Rican Parrot. Western Foundation of Vertebrate Zoology, Los Angeles, California.

Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. J. Wildl. Manage. 61: 261–270.

U.S. Fish and Wildlife Service. 1999. Puerto Rican Parrot (*Amazona vittata*) revised technical/agency draft recovery plan. U.S. Fish and Wildlife Service , Atlanta, Georgia.

Wunderle, Jr., J. W. 1996. Guiding principles and recommendations for the recovery of the endangered Puerto Rican Parrot. Unpubl. report. USDA Forest Service International Institute of Tropical Forestry, Río Piedras, Puerto Rico.

Wunderle, Jr., J. W., N. F. R. Snyder, B. Muiznieks, J. W. Wiley, & J. M. Meyers. 2003. Histories of Puerto Rican Parrot nests in the Caribbean National Forest/Luquillo Experimental Forest, 1973–2000. IITF-GTR-21, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.