MODELING BROWN PELICAN POPULATION DYNAMICS IN THE CARIBBEAN

Final report to WindMar Renewable Energy Inc. for the contract:
"Modeling endangered brown pelican populations"

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SUMMARY
We created a population model for the population of Caribbean brown pelicans *Pelecanus occidentalis occidentalis* that is found in Puerto Rico and the U.S. Virgin Islands, and used the model to predict population dynamics under a variety of scenarios. Under the estimated current conditions, the model predicts that the population will decrease rapidly and approach extinction within a few decades. Although limited data were available to us for testing this prediction, the published data that do exist closely match the model's qualitative predictions, although they suggest that the rate of decline in the model is slightly greater than in the real population. We then used the model to determine whether additional pelican mortality due to the proposed WindMar renewable energy facility is likely to exacerbate the population's decline. We examined five scenarios, with differing levels of mortality, derived from the draft Habitat Conservation Plan and a risk assessment conducted by Curry and Kerlinger, LLC. Under all but one scenario the rate of decline was statistically significantly higher than in the basic model, however, the magnitude of the difference was very small and probably not biologically significant. These results suggest that the Caribbean brown pelican is likely to be heading towards extinction under current conditions. Assuming that additional mortality does not greatly exceed that requested in the Habitat Conservation Plan's Incidental Take Permit, the model suggests that the installation of wind turbines near Guayanilla Bay will have only a minor effect on the pelican population. We also conducted a sensitivity analysis to determine whether our results are robust to potential errors in the parameter value estimates. We found that for all of the variables considered, only large errors would result in different conclusions, suggesting that the general findings are likely to be accurate. We also found that the population trajectory is more sensitive to survival parameters than to breeding parameters. Based on the model, increasing the size of the pelican population will not be possible without an increase in the survival of birds after they have fledged. Improved nesting productivity might also be necessary, but is unlikely to be sufficient to attain population increases. Research that would provide better information about survival is needed to refine the model results, and information about the movements of individual pelicans throughout the population would allow one to evaluate details of the model's structure more thoroughly.

INTRODUCTION

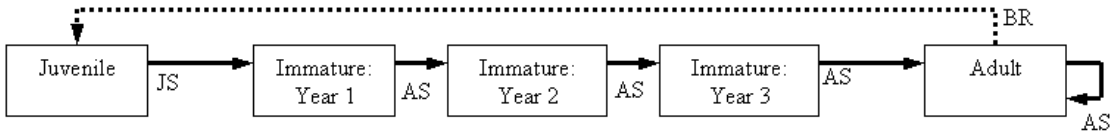
The population of Caribbean brown pelicans *Pelecanus occidentalis occidentalis* that is found in Puerto Rico and the U.S. Virgin Islands is currently listed as endangered under the U.S. Endangered Species Act. The entire population of the Caribbean subspecies is estimated to number approximately 4,800-5,000 pairs (Shields 2002) and is considered to have declined at least 20% since a conservative estimate of 6,200+ pairs was made in the early 1980s (van Halewyn and Norton 1984). At that time, the population found in Puerto Rico and the U.S. Virgin Islands was estimated to number 2,800 individuals (Collazo and Klass 1986). A mean of approximately 2,300 brown pelicans were estimated to winter in Puerto Rico during 1980-1982, declining to less than 600 in 1992-1995 (Collazo et al. 1998).

In this report, we provide an initial attempt to model the dynamics of the pelican population found in Puerto Rico and the U.S. Virgin Islands. Since data is limited, this analysis should be considered preliminary. Nonetheless, the analysis is intended to provide the best possible assessment of the population's likely future given current information. Specifically, we have used the model to (a) predict the likely trajectory for the population under current conditions; (b) estimate the population impact of the projected mortality associated with installation of wind turbines for the proposed WindMar renewable energy project near Guayanilla Bay, Puerto Rico; (c) investigate which aspects of the pelican's population biology are most likely to be important in preventing extinction and facilitating recovery; and (d) determine future research priorities.

METHODS

Model structure

We constructed a stochastic, single population, matrix model to describe the population dynamics of the pelican population. The model subdivides the population into five age classes (Figure 1) and gives the number of individuals in each class. Year to year changes in the number of individuals in each class are determined by multiplying the number present in one year by the estimated survival rate for birds in that age class, to give the number present in the following year. The number of new individuals entering the population is determined by multiplying the estimated number of young produced per nesting attempt by the number of breeding pairs. We assume that there is no immigration or emigration from the population, and that the demographic parameters are not density-dependent. As far as we are aware, no data exist with which to evaluate these two assumptions. Given the limited amount of demographic information that is currently available we felt that it would be inappropriate to make the model any more complex than we have done at the present time.



$$\begin{bmatrix} 0 & 0 & 0 & 0 & BR \\ JS & 0 & 0 & 0 & 0 \\ 0 & AS & 0 & 0 & 0 \\ 0 & 0 & AS & 0 & 0 \\ 0 & 0 & 0 & AS & AS \end{bmatrix} \begin{bmatrix} \text{Juvenile} \\ \text{Immature: Year 1} \\ \text{Immature: Year 2} \\ \text{Immature: Year 3} \\ \text{Adult} \end{bmatrix}$$

Figure 1. Top: A schematic diagram describing the population model. Each box represents a group of individuals of a particular age. Solid arrows represent the movement of individuals from one age class to the next as they age. Once a bird reaches the adult age class they remain in that class unless they die. The dotted line represents the production of new individuals as a result of breeding by adults. Bottom: The matrices used to calculate population size in each simulated year. The matrix on the left includes values for the rates at which individuals move between age classes (also denoted on the corresponding arrows in the top diagram): BR is the number of young produced per nesting pair, JS is the juvenile survival rate, and AS is the survival rate for immatures and adults. The vector on the right includes the number of individuals in each age class. Multiplying these two matrices together gives the number of individuals in each age class for one time step in the future; summing the numbers in the vector on the right gives the total population size.

The model is stochastic, meaning that parameter values are not fixed. Instead, in each year of each simulation, a separate value for each parameter is chosen from a range of plausible values. Values that are thought to be more probable are more likely to be chosen, but all plausible values have some chance of being selected. In biological terms, this means that survival and reproductive rates can vary from year to year in the model, and that although most years will be "average" there is also a chance of unusually good or bad years.

The use of a stochastic model has two consequences. First, because the parameter values picked in each run of the model are chosen from a distribution of plausible values using a randomization procedure, each simulation will produce somewhat different results. Second, because the range of values available for each parameter is based on the range of likely values, the overall pattern across a large number of simulations allows one to estimate both the range of possible outcomes, and the relative probability of different outcomes.

In our analysis we ran 500 simulations, each for a 40 year time period. This time frame is arbitrary and can be changed if desired, but was chosen to balance a desire to assess how population size will change over at least several generations with the need to minimize the compounding errors that could arise if predictions are made too far into the future. For each version of the model we determined whether there was a significant overall pattern of decline using a one-tailed, one-sample *t*-test. Our null hypothesis for these tests was that the population size at the end of 40 years would be equal to, or greater than, the population size at the start; our alternative hypothesis was that the final population size would be significantly less than the

starting population size. By replicating the simulation 500 times we were able to test this hypothesis of no significant decline in population size with a statistical power of $1 - \beta > 0.95$, when $\alpha = 0.05$ and the desired effect size is assumed to be small (0.2) (see Cohen 1988:45-47 for details on how to calculate power for this test). Achieving this level of power is important as it means that we have conducted enough simulations to allow us to accept the null hypothesis of no change should that result arise from a given set of simulations. (If statistical power were low, then it would not be possible to tell whether a non-significant result meant that there was really no effect, or if it simply meant that we did not have enough replication to detect an effect.)

Model parameterization

Relatively little demographic information exists for the Caribbean brown pelican population. Nonetheless, we were able to compile an initial set of parameter estimates from the literature, although not all of these data come from Caribbean birds and some estimates are quite old and may not relate to current population dynamics. For these reasons, the estimates that we have used must be viewed as preliminary and our hope is that our analysis will encourage the collection of the data necessary to obtain more precise, and current, parameter estimates.

Reproductive data: Estimates of the number of young produced per nesting attempt were taken from Collazo et al. (1998: Table 2), which summarizes nest success data from five sites in Puerto Rico and the U.S. Virgin Islands. These data were compiled from studies conducted between 1980 and 1982. Collazo et al. (1998) presented the data as 11 separate estimates of the mean – one for each year-site combination. We calculated an overall estimate of the mean, by multiplying each separate mean by the sample size upon which it was based, summing the resulting numbers, and then dividing the total number of young produced over all sites and years by the total number of nests. This process produced a grand mean of 0.98 young per nesting attempt. Because we were unable to obtain the raw data, we could not directly estimate the variance around this mean. In order to obtain a measure of the variability, therefore, we took the original 11 estimates of the mean and set the minimum and the maximum values (0.59 and 2.06 young per nest, respectively) as the 95% confidence interval around the grand mean. Since, the grand mean lies much closer to the minimum than the maximum value, we assumed that the distribution of values was lognormal and calculated the standard deviation that would produce the projected confidence interval. Clearly, this approach can only be assumed to give a crude estimate of the true variance. Access to the original data used by Collazo et al. (1998) would greatly improve our ability to estimate this parameter.

To obtain the mean number of fledglings per nest in a given year, the model randomly picked a number from the lognormal distribution described by the estimated mean and standard deviation. Since brown pelicans very rarely lay more than 4 eggs (Shields 2002), we truncated the lognormal distribution so that larger numbers were not possible.

Although our estimate of reproductive success is based on data from a large number of nests (n = 650) spread over several sites (Collazo et al. 1998), the lack of more recent data, known to be representative of current reproductive activity, is a potential cause for concern. The data we have used, however, match quite closely with the range of values available for the species as a whole, and with the general estimate of about one fledgling per nest (see estimates given in Shields 2002).

In our basic model, we assume that there is an even sex ratio, that each pair makes only one nesting attempt per year, and that all pairs nest. Brown pelicans normally lay only one clutch, but sometimes replace lost clutches. The frequency of relaying has not been quantified in the field, however, and its occurrence is inferred from the behavior of captive birds and extensive renesting after catastrophic colony failures, rather than direct observation of known individuals (Shields 2002). There is also little information on the proportion of the population that breeds each year. As a species, brown pelicans typically begin breeding at age 3-5, although some will breed at an earlier age, and females typically begin breeding earlier than males (Shields 2002). Our basic model assumes that all birds remain in the "immature" class for three years, and begin breeding at age four. After birds begin breeding they are assumed to breed annually until they die. Again, this assumption is consistent with what is currently known about the species, but detailed information on known birds is lacking (Shields 2002).

Survival data: No detailed estimates of age-specific survival rates are available for brown pelicans, and only limited information from band recoveries exists (Shields 2002). Based on an analysis of 3,106 recovered brown pelicans that were banded as juveniles in Florida and the Carolinas between 1925 and 1983, Schreiber and Mock (1988) estimated that only 30% of birds survive their first year, and that less than 2% survive to age 10. Using this information we set the probability of surviving the first year at 0.3. Since only 2% of the original cohort of banded birds survive until they are 10, we estimated that the chance of an immature surviving for a total of nine years was 2/30 (0.0667). Finally, we assumed that survival was constant after the first year of life, which would mean than $x^9 = 0.0667$, where x is the annual survival rate after a bird has survived its first year. Rearranging this equation gives $x = 0.7401$, which we used as the survival rate for adults and immatures. We have no information on variability in annual survival rates, so we simply set the standard deviation equal to 0.1 for all age classes in the basic model, and then tested the effects of sequentially increasing variability as part of our sensitivity analysis.

Clearly, we have made a number of assumptions in estimating survival rates and our estimates must be considered first approximations that need to be verified with better information. Survival estimates based on band recovery data alone have several limitations. For instance, it is not generally possible to differentiate between birds that die and those that leave the study area. Similarly, we do not know whether the recovered birds in Schreiber and Mock's analysis represent a representative sample of all pelicans – especially those currently found in the Caribbean, rather than just those found along the Atlantic coast of the United States during the middle decades of the last century. Yet another problem is that pelicans are known to lose bands through wear after about 12-15 years, suggesting that banding data are likely to underestimate survival unless birds are systematically rebanded before they lose their bands.

Quantitative methods of survival analysis have come a long way since Schreiber and Mock (1988) conducted their analysis, and revisiting their data set using more modern methods and software might provide more precise estimates. It seems likely, however, that better estimates of survival will not be available without new data collection.

Model scenarios

Using our model we examined several different situations. First, we ran the basic model to determine how well it predicted known population estimates, and to predict future population trends under the estimated current conditions. Second, we ran a series of alternate model scenarios, each with additional mortality caused by the installation of a wind farm at Guayanilla, to estimate how much the projected mortality due to collisions with turbines will affect the population trajectory. Last, we conducted a sensitivity analysis in which we systematically altered the parameter values used in the model. This final analysis was used to assess the likely impacts of the paucity of high quality data on our conclusions, and to gain insights into where management might be most effective at increasing the pelican population size.

Basic model: The basic model used the parameter values described previously and was run with an initial population size of 2,800, to match the estimate given in the recovery plan for the Caribbean brown pelican population found in Puerto Rico and the U.S. Virgin Islands (Collazo and Klass 1986). We distributed individuals across age classes according to the stable age distribution that was predicted by the dominant eigenvalue of the population matrix when mean values were used for each parameter. For each of the 500 model runs we determined (a) whether the population declined to less than ten birds, which we considered to be functional extinction, by the 40th year; (b) whether the population declined by the 40th year; (c) the projected size of the population after 40 years; and (d) the population growth rate. Growth rate was calculated from the exponential growth equation by first taking the natural log of each year's population size estimate. Then, for each year, *t*, we calculated the population change over the 2-year period spanning the previous and subsequent years, and divided this change by two to give the change in terms of a single year. Thus, growth in year *t* is defined as $(\ln N_{t+1} - \ln N_{t-1})/2$, and the overall growth rate for a given set of conditions is calculated as the mean across all years and all model runs.

Effects of additional mortality caused by wind turbines: To test for the potential population effects of mortality caused by the proposed wind turbines near Guayanilla Bay, we modified the basic analysis to explore the following potential scenarios:

Scenario 1 (20% annual chance of one turbine death). The draft Habitat Conservation Plan (HCP) prepared by Guarnaccia Associates requests an Incidental Take Permit for eight pelicans over the 40-year lifespan of the WindMar renewable energy project. This mortality rate, translates into an average of one pelican death associated with the wind turbines every five years, or a 20% annual probability of one additional death in the population. To mimic this scenario, we modified our basic model so that every year there was a probability of 0.2 that one additional bird would be removed from the population. In years when there was a turbine-induced death, we selected the age class from which to remove the additional bird at random, with the probability of a bird coming from a given age class determined by the proportion of the total population in that age class.

Scenario 2 (per bird mortality increased by 0.2% for birds at Guayanilla Bay). The "population size dependent HCP" scenario. Our second scenario is also based on the HCP estimate that one pelican will die every five years. Rather than modeling the extra mortality in terms of a given number of additional deaths in each year, however, in this scenario we used the mortality

estimate from the HCP to calculate the additional mortality risk faced by each bird in the vicinity of the WindMar facility. By combining the estimate, from the draft HCP, of approximately 100 pelicans in and around Guayanilla Bay with the estimate that one pelican will be killed by turbines every five years, we calculated that each pelican in this area has an additional mortality risk of 0.2% (i.e., a 20% chance of one death spread across 100 individuals gives an average chance of 20%/100 for each individual). We then applied this additional risk to 100 of the individuals in the model population, or to the whole population if it numbered fewer than 100. This scenario assumes that Guayanilla Bay is favored by pelicans over other sites, and that birds will preferentially gather there, up to a maximum of 100 birds. By making this assumption we may overestimate the population-wide impact of turbine-caused mortality because we assume that birds will always choose Guayanilla Bay over other sites. Evidence suggesting that this assumption is overly-conservative comes from the limited observations conducted at the site. Although approximately 100 pelicans were present at the site during one November visit, no more than 50 pelicans were seen during two other visits (John Guarnaccia *personal communication*). If the typical number of birds present at the site is lower than 100, then this scenario will over-estimate the impact of the turbines.

This scenario also assumes that the Guayanilla Bay area can support no more than 100 birds (the largest number reported there in recent years according to the draft HCP); if this assumption is relaxed, then it is possible that the population-wide impact would increase because a greater number of birds could be vulnerable to turbines. Evaluating these assumptions is not possible without a better understanding of the quality of different sites used by pelicans, and information on how individual pelicans decide where to spend their time.

Despite our assumptions, the model structure for this scenario is perhaps more realistic than that for the other scenarios because it allows the number of deaths caused by turbines to vary as a function of the local population size. In other words, it assumes that as the number of birds in the vicinity of the WindMar facility changes, so will the number of pelican deaths. The other four scenarios assume that there is a fixed mortality rate, irrespective of the population size. Nonetheless, even this scenario is incomplete because accurately calculating the additional mortality risk to each bird would require that we know more about the use of Guayanilla Bay (e.g., we would need to know the proportion of the entire population that occurs there, which we cannot estimate without a current population estimate, and we would need to know the turnover rate of pelicans in the area). If this information could be gathered we believe that the modeling approach used in this scenario is most likely to provide accurate estimates of the facility's impact on the pelican population.

Scenario 3 (all extra mortality involves juveniles). This scenario mimics scenario 1 but instead of randomly assigning deaths associated with wind turbines across all age classes it assumes that only juveniles are killed by turbines. The inclusion of this scenario recognizes that young birds are potentially more vulnerable than older birds (e.g., because they are less accomplished fliers, or less experienced generally). Although we know nothing about the relative rates at which pelicans of different ages are likely to be killed, the combination of scenarios 1 and 3 should identify the likely range of possible outcomes.

Scenario 4 (0-2 extra deaths each year). The report prepared by Curry and Kerlinger, LLC (Kerlinger 2003) provides detailed information on flight activity of brown pelicans in the vicinity of the WindMar site. This report assessed the risk imposed to brown pelicans by the proposed facility to be "Low-None", which was translated as zero to two deaths caused by turbines a year. To mimic this scenario, we modified the basic model so that there were up to two additional deaths each year, with an equal chance of zero, one and two deaths in any particular year. As with scenario 1, we selected the age class from which to remove each additional bird randomly.

Scenario 5 (2 additional deaths each year). Our final scenario is also based on Kerlinger's (2003) assessment of risk, however, it represents the worse case situation according to that report. For this scenario we assumed that the number of additional deaths was at the upper limit of the projected range, and removed 2 additional individuals from the population every year. Again, the age class from which each bird was taken was determined randomly.

As is pointed out in Kerlinger (2003), even our scenario 5 is not the worst conceivable case, because it is not known how pelicans would respond to turbines. The current risk assessment is based on the observation that pelicans pass through the area where turbines are proposed to stand at a very low rate. Also, based on the field work conducted to date, it is assumed that most observations relate to a relatively small number of individuals (Kerlinger 2003: p.11). If this is the case, then a small proportion of the total pelican population is vulnerable to turbine-induced mortality. It is conceivable, however, that every pelican that occurs in the vicinity of the site might have some very small chance of flying through the turbine zone. If this were the case, then a larger proportion of the population would be vulnerable, albeit with a very low potential risk for each individual. Unfortunately, without detailed information on the movement behavior of individual pelicans it is neither possible to determine whether this scenario is likely, nor to estimate how great the risk would be. Thus, we did not feel that we could derive informed estimates of the additional mortality associated with this "absolute worst case" scenario. Instead, we rely on our sensitivity analysis to provide information on the likely impact of varying mortality rates further.

In order to compare these different scenarios to the basic model, which assumed no mortality due to the WindMar facility, we determined the projected population size at the end of each simulation and used analysis of variance to test whether the final population sizes differed among scenarios. In this analysis, we had six experimental treatments (the basic model and the five scenarios for additional mortality) and 500 replicates of each treatment.

Sensitivity analysis: The third phase of our analysis involved examining the sensitivity of our results to variation in parameter values. Sensitivity analysis serves several functions. First, it allows one to determine how much potential errors in a model and the selected parameter values are likely to influence the model's results. For instance, the exact value of a particular parameter may not be known very precisely, but if there is little variation in the results obtained across the entire range of plausible values, then the results can be considered robust. This same information can also be used to prioritize future data collection, with a greater emphasis placed on collecting better data for those parameters to which the model results are especially sensitive. Finally, sensitivity analysis can be used to identify sets of conditions that result in different qualitative predictions. In the case of a population model, for example, it is useful to be able to

distinguish the suite of conditions that are likely to result in a population decline from the suite that will result in stability or a population increase.

For our sensitivity analysis we systematically varied values of each parameter in the model to span the range of values that we considered plausible, and re-ran the model for each new set of conditions. Initially, we varied values for each parameter separately, then we combined selected parameters to determine the effect of changing both together.

First, we conducted an analysis to test the model's sensitivity to the initial age distribution. For our model, we had little data on the relative number of individuals in each age class and so we used the stable age distribution as derived from the matrix. This calculation gave approximately 764 juveniles, 705 immatures and 1,331 adults. Compared to Collazo's (1986) estimate of 800 breeding adults, our calculations imply either (a) that the age distribution is not stable and that there are fewer adults in the real population, or (b) that only about 60% of the adults breed each year. To determine whether our model was sensitive to the starting age distribution we conducted an analysis in which the 2,800 birds in the population were randomly distributed across the five age classes prior to running the model. This approach was repeated 500 times and a population trajectory determined for each simulation. We then examined the range of outcomes from these 500 simulations and compared them to the results of the basic model.

To investigate the effect of assuming that all adults in the population breed, we sequentially reduced the number of breeders in the population in 10% increments from 100% to 50% in order to extend beyond the estimate that as few as 60% of the adult population may breed (see previous paragraph).

To determine the effect of reproductive output we varied the mean number of young produced per breeding pair from 0 to 4. Clutches of more than 4 eggs are extremely rare (<<1% of all clutches; Shields 2002), so the upper limit that we used assumes both an exceedingly high average clutch size and an extraordinarily high survival of young to fledging. Juvenile survival was varied from a low of 25% to 100% and adult/immature survival was varied from a low of 50% to 100% (Table 1). Clearly the maximum of 100% for each of these survival rates is unrealistic as it assumes that birds never die; nonetheless this value places an absolute upper bound on these parameter values.

In addition to varying the mean values for each parameter, we also investigated how sensitive the model's results are to the standard deviation values associated with breeding success and survival. We varied the standard deviation associated with the mean number of young produced from 1 to 2, and the variance associated with each of the survival estimates from 0.05 to 0.45.

In the real world, parameter values are unlikely to vary in isolation. Examining all possible combinations of parameter value changes is not possible, however, we did conduct one set of analyses in order to examine the combined effects of varying the mean number of young produced and the mean survival rates simultaneously. This combination allowed us to examine the relative contribution of these two variables to population change and to determine combinations of values that are likely to be necessary to prevent further population decline. For this analysis the number of young produced was varied across the same range as was used to

examine sensitivity to this variable alone. Simultaneously, survival rates for all age classes were increased in 10% increments up to the point where adult survival approached 100%.

Parameter	Value used in basic model (mean ± SD)	Source for values used in basic model	Range of values used in sensitivity analysis
Initial age distribution	Stable age distribution	Calculated from matrix	500 random assignments of individuals to age classes
Proportion breeding	1	None	0.50-1.00
Annual mean number of young per attempt	0.98 ± 1.461	Collazo et al. 1998	Mean: 0-4 SD: 1-2
Juvenile survival rate	0.3 ± 0.1	Schreiber and Mock 1988	Mean: 0.25-1.00 SD: 0.05-0.45
Adult survival rate	0.74 ± 0.1	Schreiber and Mock 1988	Mean: 0.50-1.00 SD: 0.05-0.45

Table 1. Parameter values used in the basic model and the ranges of values used for the sensitivity analysis.

RESULTS AND DISCUSSION

Predictions under current conditions

The basic model predicts that, under current conditions, the pelican population will decrease rapidly, and approach extinction within the 40 year time frame of the analysis (Figure 2). With an initial population of 2,800, equivalent to the estimated population size when the recovery plan was written for the population (Collazo and Klass 1986), our model predicts that the population size will decline significantly (t_{499} = -1,035, $P << 0.0005$) to only a handful of birds (mean ± SD: 5.0 ± 2.7) after 40 years (equivalent to approximately 20 years from now), with a 95% chance of declining to less than 10 birds within that time frame.

For several reasons, this bleak outlook is likely to be overly pessimistic, but probably only in terms of the speed of the decline and not the eventual outcome. Although we lack very much data with which to test our predictions, the population estimates that are available broadly match the projected trajectory (Figure 2). Collazo et al. (1998) found that the population wintering in Puerto Rico declined by 74%, from an average of 2,289 in 1980-1982 to an average of 593 in 1992-1995. Our model predicts an average decline of 85% over the first 13 years of the simulation (95% prediction interval: 77-93%), suggesting a somewhat faster rate in the model than was observed by Collazo et al. (1998) but not qualitatively different. A recent estimate of approximately 100 pelicans in the vicinity of the WindMar facility (see draft HCP) also suggests that the current Puerto Rican population is likely larger than our current model would predict. Without a complete survey of the population, however, it is impossible to evaluate this assumption fully or to estimate how much our model underestimates the current population size.

Thus, available evidence suggests that our model appears to predict a rate of decline that is slightly faster than that found in the real population.

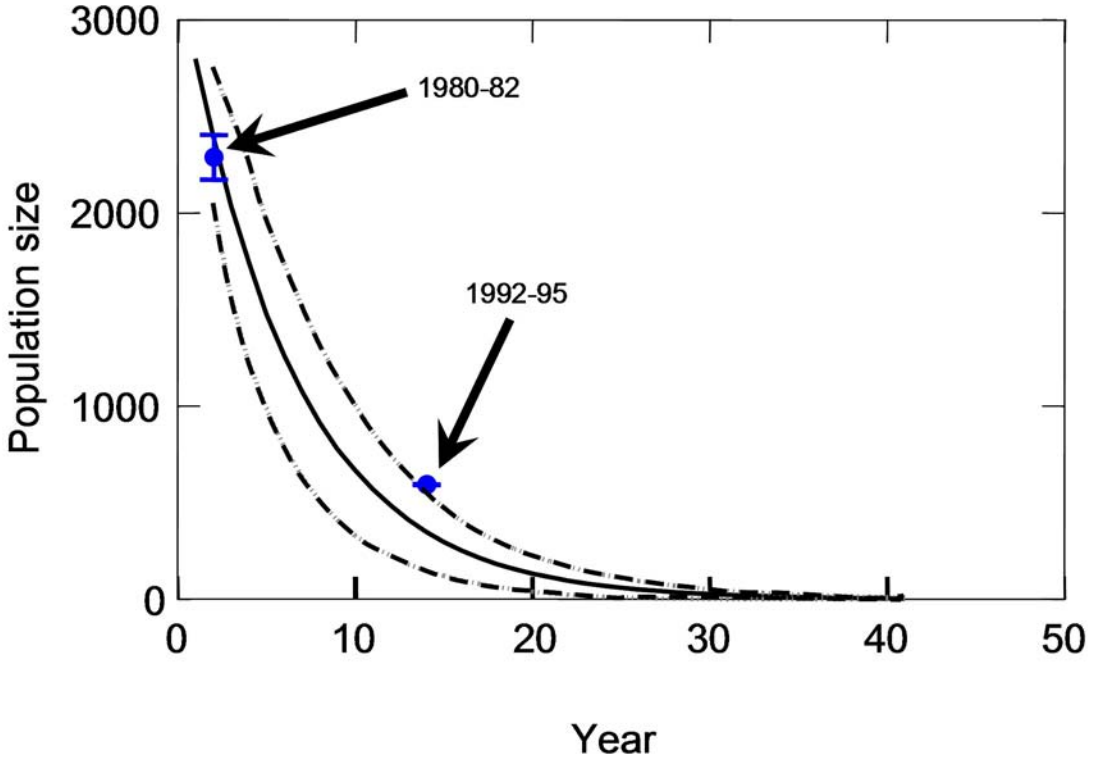


Figure 2. Predicted changes in the size of the Caribbean brown pelican population in Puerto Rico and the U.S. Virgin Islands using the basic model, which simulates current conditions. Initial population size was 2,800 to match the estimated size in the early 1980s (Collazo and Klass 1986). The solid line represents the mean population decline from 500 simulations. The dotted lines show the bounds of the 95% prediction interval around the mean population estimates; 95% of point estimates are expected to lie within this interval. The two circles, indicated by the arrows, show the mean (± SD) number of pelicans counted in Puerto Rico during winter in the early 1980s and early 1990s (from Collazo et al. 1998), and have been lined up against the mid-point of the date range over which they were obtained, assuming that year 1 of the simulation is 1980.

Our overestimate of the rate of population decline could be due to several factors. First, it is likely that our estimates of survival rates are too low because they do not adequately account for the effects of band loss and dispersal. The survival estimates may also be biased because they are based on very limited data and do not come from the population being modeled. Second, given the evidence that nest productivity in some populations can be affected by colony visits by researchers (Anderson and Keith 1980, Shields 2002), it is possible that reproductive rates available in the literature are lower than is typical for unstudied colonies. Third, it is possible that as the population has declined there has been some release from density-dependence that has allowed demographic rates to increase. Nonetheless, the qualitative similarity between our predictions and the empirical data suggest that our model provides a useful first approximation of the population's dynamics.

Predicted effects of the WindMar RE Project

To evaluate the potential impact of the WindMar RE Project we re-ran the basic model under several scenarios that included additional mortality due to the presence of turbines, and compared results obtained under these scenarios to those obtained with the basic model. All of the scenarios produced qualitatively similar results, with differences only in the speed of the decline, which was greater for four of the five scenarios than for the basic model (Table 2).

Analysis of variance showed that the three scenarios based on the draft HCP (1-3) differed in the extent of their deviation from the basic model. Scenario 2, in which additional mortality was linked to the size of the population in the vicinity of the WindMar site, was not significantly different from the basic model. Scenario 3, in which additional mortality was only incurred by juveniles, resulted in a significantly smaller population than the basic model, but did not differ from scenario 2. Scenario 1, in which the mortality risk did not change over time and was randomly distributed across individuals, resulted in a population size that was significantly lower than the basic model and the other two HCP scenarios. Both scenarios 4 and 5 resulted in final populations that were significantly smaller than all of the HCP scenarios. Despite these statistically significant results, the actual differences in mean population size across all scenarios were small and all scenarios resulted in populations that had less than 10 birds on average. Thus, the statistical differences probably have little biologically importance. The one way in which the differences might be biologically significant involves the rate at which the population approaches extinction: although the ultimate outcome does not differ among scenarios, a slower population decline would allow more time for management to reverse the population trend.

Year	Basic model	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
a) Population size (mean ± SD)						
0	2800	2800	2800	2800	2800	2800
10	667.4 ± 173.2	560.6 ± 142.7	583.6 ± 154.5	576.9 ± 144.3	568.4 ± 157.0	567.2 ± 153.5
20	139.4 ± 56.5	117.2 ± 43.3	120.5 ± 48.2	117.5 ± 46.3	107.5 ± 40.6	105.3 ± 47.2
30	25.5 ± 12.7	22.0 ± 11.2	24.4 ± 12.1	24.1 ± 12.5	16.1 ± 12.0	8.4 ± 10.5
40	5.0 ± 2.7[a]	3.2 ± 2.6[c]	4.9 ± 2.7[a,b]	4.7 ± 2.9[b]	0.2 ± 0.8[d]	0[d]
b) Probability of fewer than 10 individuals						
40	95%	97%	95%	95%	100%	100%

Table 2. Results of simulations that include additional mortality caused by the WindMar RE project. Section (a) gives the mean population size at 10 year intervals under each of the different scenarios. Section (b) gives the percent of simulations in which the pelican population had declined to less than 10 birds by the end of 40 years. Mean population sizes in year 40 were compared among scenarios using analysis of variance. Overall, treatments differed significantly ($F_{5,2994} = 509.2$, $P < 0.001$). Significant pairwise differences, determined using Tukey's post-hoc test, are indicated by the superscript letters in the table. Values with the same letter are not significantly different, whereas values with different letters do differ.

Sensitivity analysis

For our sensitivity analysis we systematically varied the values used for each parameter in the model to determine the impact of changing each parameter on the population's dynamics. First we examined the effect of different starting age distributions. By randomly selecting different starting distributions from the full range of possibilities our analysis explored the full range of potential starting scenarios, including very unlikely ones (such as a population that almost entirely constitutes juveniles, or just adults). A very wide range of possible population sizes are found during the first few years of the simulations. In some scenarios, the population plummets in the first few years – these are likely to be scenarios in which the majority of birds in the population are assumed to be juveniles, which have a relatively high mortality rate that causes a lot of deaths during the first few years of the simulation. In other scenarios, the population initially increases because the population is dominated by adults, which have relatively low mortality rates. Within a few years, however, as the age distribution in each model run stabilizes, the different scenarios all take on the same character of steady decline towards a very small number of birds. These results show that the initial age distribution does qualitatively affect the model results over very short time frames of only a few years. But, that the qualitative results over the longer time frames more relevant to managers are very similar regardless of the model's starting conditions. Under current conditions, therefore, it seems that an accurate understanding of the age distribution is important for estimating the speed over which the population will decline, but not the overall pattern of population change.

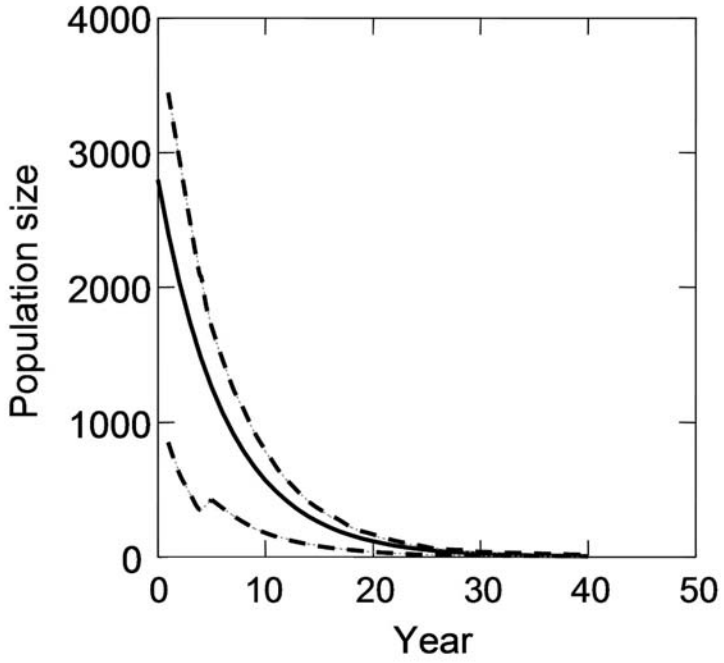


Figure 3. Results of 500 simulations in which individuals were randomly distributed across age classes to explore the likely consequences of errors in the initial age distribution used in our basic model. The solid line represents the population trajectory from the basic model and the dotted lines show the outer bounds of the zone within which the 500 simulated trajectories lie.

Another assumption of our basic model was that all of the adults in the population breed on an annual basis. We have no data to support or refute this assumption, but empirical evidence suggests that the number of breeders is only about 60% of the number of adults predicted for a stable age distribution using our matrix model (see Methods). When we varied the proportion of birds that breed each year, however, we found that there was little effect on the model results (Figure 4). For all scenarios, the population declined to an average population size of less than 10 individuals within 40 years (Figure 4c).

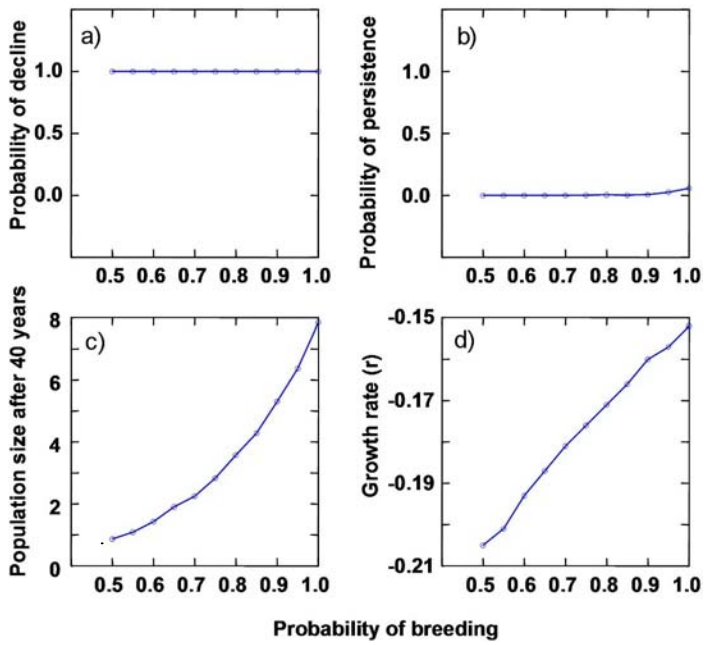


Figure 4. Effects of varying the proportion of adults that breed each year. The basic model assumes that the probability of breeding is 1.0 (i.e., all adults breed every year). Each panel shows a different type of model output: (a) probability that the population declines over the 40 year simulation, (b) probability that the population persists (i.e., more than 10 individuals remain) after 40 years, (c) population size after 40 years, averaged over 500 simulations, (d) average population growth rate averaged over 500 simulations (a growth rate of zero implies a stable population).

Varying the number of young produced by each nesting pair did not influence the overall population trajectory; even at highly unrealistic levels of > 3 young produced per pair, the population still declined in all simulations (Figure 5a). The magnitude of the decline, however, did vary for different reproductive rates. As the average number of young produced by each pair increased above its current level of about 1, there was a sharp increase in the chance of the population persisting for 40 years, a concomitant increase in the population size at the end of the simulations, and an increasingly less negative growth rate (Figures 5b-d, respectively). These results suggest that if one could increase the productivity of the population within a realistic range (e.g., to approximately 2 young per pair, the maximum recorded for the population; Collazo et al. 1998) then a clear effect on the population trajectory is possible. Such an increase in reproductive success, however, would not be sufficient to reverse the projected population decline, and would still result in a population that is so small as to be very vulnerable to

extinction (Figure 5c). As with the other variables previously discussed, these results suggest that errors in our estimates of the population's average productivity are unlikely to have resulted in qualitatively different conclusions from those we have presented.

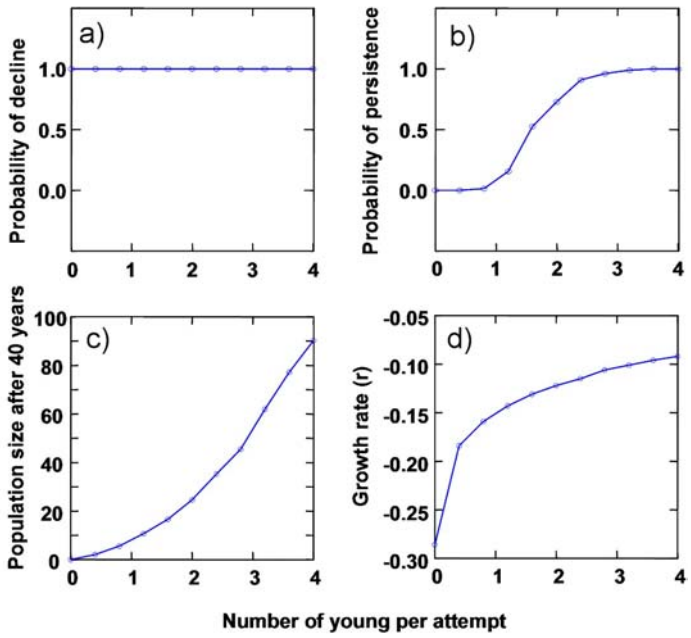


Figure 5. Effects of varying the average number of young produced by each breeding pair. The basic model assumes that 0.98 young are produced per nesting attempt. The four panels mirror those in Figure 4.

As one would predict for a long-lived species, the population trajectory was most sensitive to variation in survival rates, especially survival of adults but also survival during the first year of life. Increasing juvenile survival alone, however, was not sufficient to produce positive population growth and increasing populations in our simulations (Figure 6a). Even moderate increases in the juvenile survival rate (e.g., an increase to 50% survival), however, created a notable increase in the chance that the population would persist for 40 years (Figure 6b), and similar increases in juvenile survival rate had a much larger effect on the population size after 40 years than any of the variables previously considered in this sensitivity analysis. For comparison, an increase in productivity to 2 fledglings per nest, is predicted to result in a population size of approximately 25 pelicans after 40 years. In contrast, increasing juvenile survival to 50% would result in a population about twice as large. Neither change alters the overall pattern of decline, but reducing first year mortality appears likely to have a bigger population impact than increasing reproductive output.

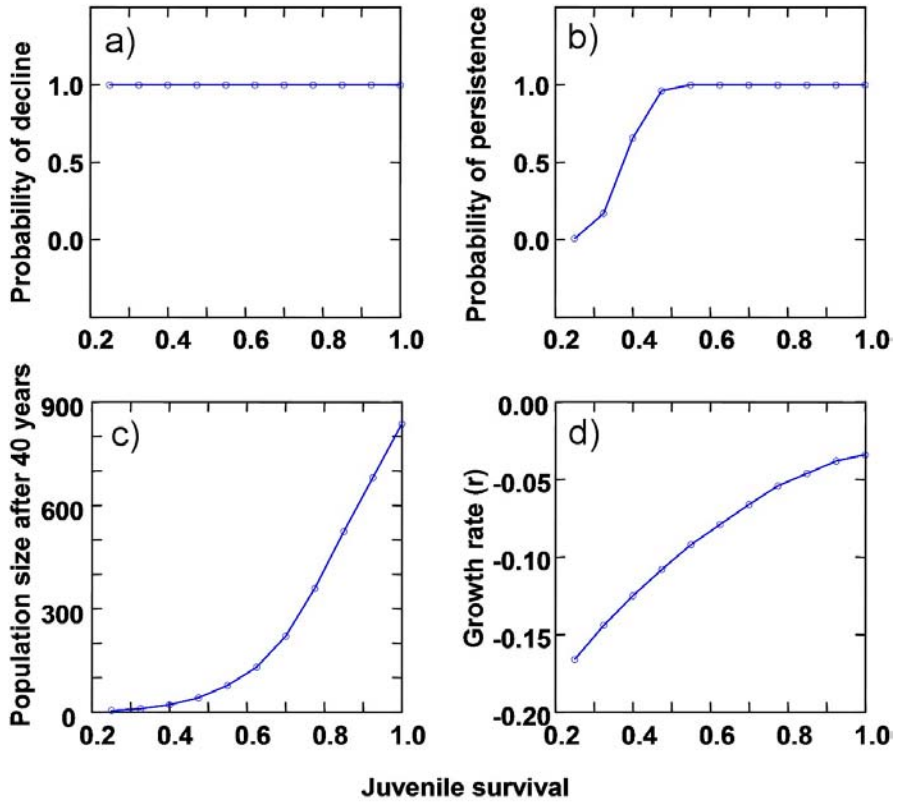


Figure 6. Effects of varying the juvenile survival rate. The basic model assumes that there is a 0.3 chance of a bird surviving its first year after fledging. The four panels mirror those in Figure 4.

Even more important than juvenile survival, was adult survival. Among those variables examined, this was the only one for which it was possible to obtain an increasing population (compare the (a) panels in Figures 4-7). Even so, we found that the adult survival rate needed to be increased above 90% to result in a reduced chance of population decline (Figure 7a) and that the average population growth rate did not exceed zero unless the adult survival rate approached 95% (Figure 7d). More modest increases in adult survival did produce final population sizes substantially larger than were found when increasing productivity or juvenile survival within plausible ranges. For instance, increasing the adult survival rate to somewhere between 0.85 and 0.9 resulted in an ending population size in the hundreds (Figure 7c), whereas an equivalent increase (either proportionate, or absolute) in the juvenile survival rate resulted in a final population size in the tens (Figure 6c). Based on this comparison among variables, it is clear that increasing adult survival is likely to be key to reversing the decline of the pelican population, and that obtaining more accurate model results is contingent on better data on the survival of pelicans in the population.

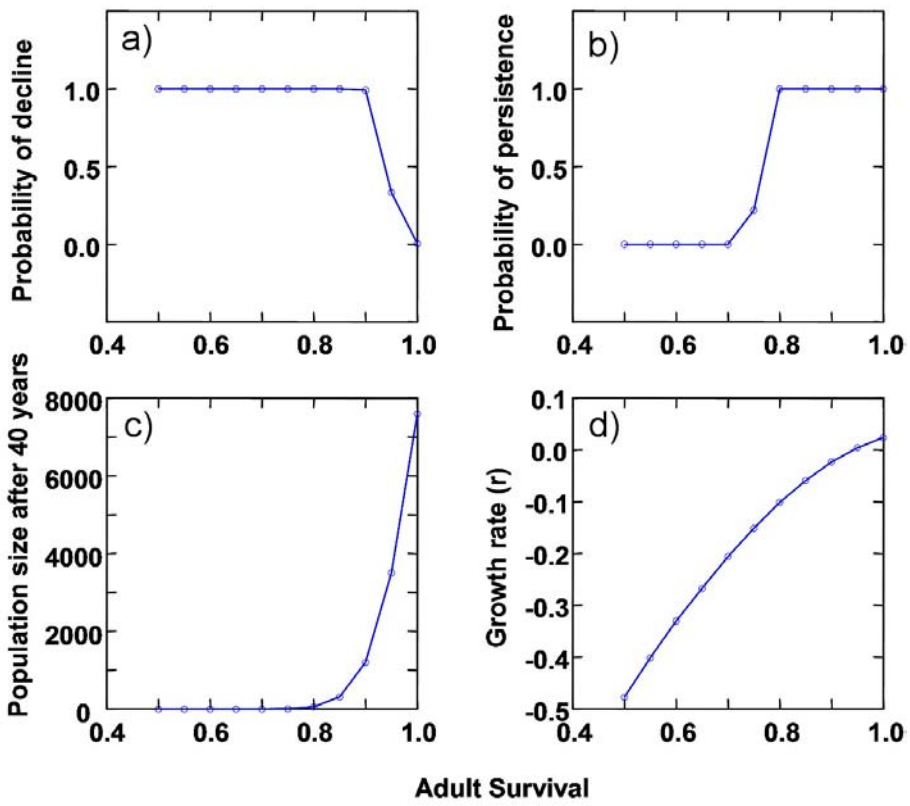


Figure 7. Effects of varying the survival rate of immatures and adults. The basic model assumes that once a bird has survived its first year after fledging, it will have an annual survival rate of 0.74. The four panels mirror those in Figure 4.

In addition to altering the mean values for each parameter we also investigated the effect of changing the amount of variability in both productivity and survival. In both cases, the values used for the standard deviations of these parameters had little effect on the overall pattern observed in the simulations (Figures 8 and 9). It is plausible that investigating a much larger range of values would lead to different conclusions, but it appears that our very poor knowledge of the correct values for these parameters is not a major problem under current conditions. If one wanted to examine a range of scenarios in which the basic model produced results that were less clear cut (i.e., if the basic model resulted in a population growth rate close to zero), then better estimates of these parameter values might be more important.

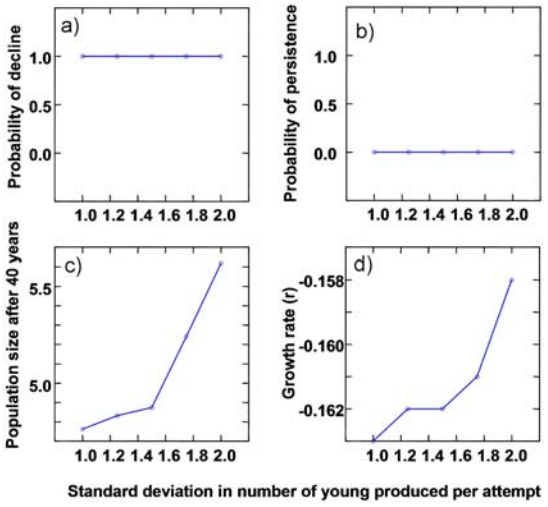


Figure 8. Effects of varying the standard deviation for the average number of young produced by each nesting pair. The basic model uses a value of 1.46. The four panels mirror those in Figure 4.

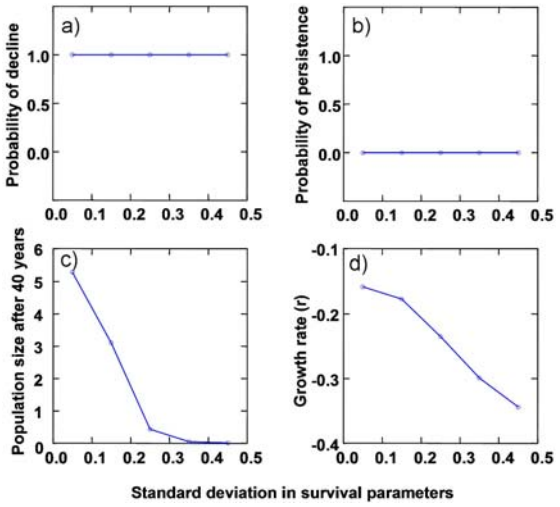


Figure 9. Effects of varying the standard deviation for the juvenile and adult survival rates. Both standard deviations are set equal and are varied simultaneously. The basic model uses a value of 0.1. The four panels mirror those in Figure 4.

The final phase of our sensitivity analysis involved investigating the joint effect of altering both breeding and survival rates simultaneously. This analysis gives combinations of values for these parameters that are predicted to result in an increasing population. Given the amount that individual parameter values have to be increased to obtain results that indicate an increasing population, it appears likely that management activities will have to target multiple aspects of the species' biology if they are to succeed in meeting recovery goals.

If we assume that it is unrealistic to increase productivity above a mean of two young per nesting pair, then it becomes apparent that survival rates will also need to increase by at least 10% (such that juvenile survival is at least 33% and immature/adult survival is at least 81%) to achieve a stable or increasing population (Figure 10). If even this increase in productivity is not possible, then one can use this graph to estimate how high survival will need to be to obtain positive population growth. For instance, if it were concluded that no improvement in productivity were possible, then the graph shows that all survival rates must be increased by at least 20% (i.e., juvenile survival > 36%; immature/adult survival > 89%) before the population can be expected to increase.

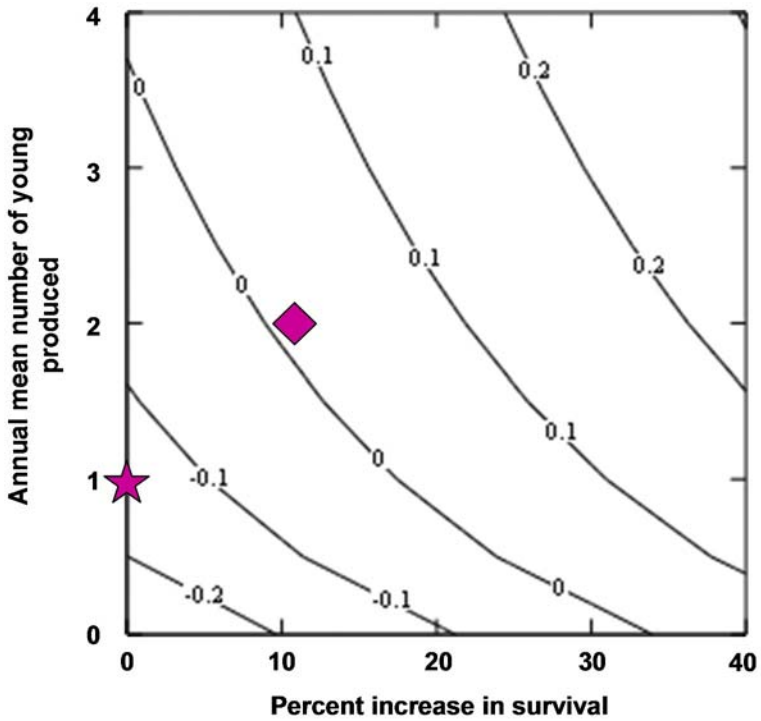


Figure 10. Effects of varying the breeding rate and survival rates simultaneously. Moving from left to right across the graph represents changing conditions so that average survival of all age classes increases by the given percentage; adult survival can only be increased by a maximum of 35%, which is equivalent to increasing adult survival to almost 100%. Moving from the bottom to the top of the graph represents an increase in average nest productivity. Each contour line represents all the points at which the population growth rate is equal to the value labeling the contour. Points on the graph which lie above and to the right of the contour labeled with zeros indicate combinations of breeding and survival rates that will result in an increasing population. Points below and left of this contour represent conditions that will result in a declining population. The star represents the conditions estimated for our basic model of current conditions; at this point on the graph the population growth rate is negative and the population will decline. The diamond represents a point where nests produce an average of two young per pair and survival rates have been increased by just over 10%; this combination produces a positive growth rate and suggests that this combination of values will be sufficient to create a population increase.

To summarize, our sensitivity analysis suggests that varying each parameter within the range of plausible values has little effect on the overall pattern of population decline predicted by our basic model. The rate of decline, and thus the magnitude of the population reduction over the 40 year time frame of our simulations, however, are affected. Varying survival parameters has more influence on the model results than does varying reproductive parameters, and the model is most sensitive to estimates of post-juvenile (adult) survival. Consequently, it is most likely that any mismatch between our model and actual population changes derive from the paucity of survival information. Collecting such data, should thus be an important research priority.

The sensitivity analysis also suggests several conclusions of relevance to managers. First, the discovery that the model results are not particularly sensitive to breeding parameters, suggests that management geared towards increasing reproductive success – at least when done in

isolation – is unlikely to be successful at increasing the population size. Even unrealistically high increases in reproductive rates are insufficient to produce positive population growth. In our model, adult survival was the only variable that, alone, could be increased to the point where the population increased, and even this effect could only be accomplished with much higher survival rates than those used for our basic model. Clearly, it is important to not only obtain better estimates of pelican survival, but also understand what factors cause mortality and determine what could be done to ameliorate these impacts.

Lastly, given that high survival rates must be achieved in order to reverse population declines, it seems likely that a "mixed strategy" that involves management activities that will increase both survival and reproductive success might be necessary in order to stabilize the population size and meet recovery goals.

One final point to make is that our sensitivity analysis only investigates the effects of varying model parameter values. Additional factors, involving the model's underlying structure and assumptions, could also influence the results. One clear possibility is that density dependent processes might exist in the natural population that are not accounted for in the model. For instance, it is plausible that as the population declines, survival rates might increase due to a reduction in competition for resources. On the other hand, if colony size has an important influence on nesting success (e.g., by reducing predation risk), a reduction in overall population size could result in lower reproductive success than we have modeled. To our knowledge, no data exist to address these issues, but their inclusion in the model would be possible if such information were gathered.

RESEARCH PRIORITIES

Clearly there is much that is not known about Caribbean brown pelicans, and there are many areas where additional research would make it easier to manage the population. Based on the model, however, there appear to be two major areas where additional research would be especially fruitful.

First, we know very little about survival rates or about the factors that influence mortality. Improving our estimates of survival in the years after pelicans leave the nest would increase our ability to interpret the results of the model scenarios described in this report, and would allow us to better evaluate the impact of additional mortality due to wind turbines and other causes. Understanding more about the current causes of death in the population will likely be key to identifying management activities that could be used to help increase the population's size.

Currently, one can only speculate on what the major causes of mortality might be. Direct persecution – in the form of egg and young collection from nests, shooting of adults, and nest destruction – all occur, although the frequency of these activities and their population-level impacts are unknown (van Halewyn and Norton 1984, Shields 2002). Accidental killing through entanglement in fishing gear is a major source of mortality in the Atlantic U.S. population, affecting hundreds of birds annually (Shields 2002). Again, however, is it unclear how serious a problem this is for Caribbean populations. Pesticides have been implicated in the deaths of Caribbean pelicans (van Halewyn and Norton 1984, Shields 2002), but studies of organochlorine pesticide and mercury residue levels in eggs and eggshell thinning do not indicate that Caribbean

pelicans are affected by these chemicals (Collazo et al. 1998). Yet another possibility is that mortality is elevated simply because of a reduction in the food supply. Elsewhere in the species' range, it is suggested that prey availability regulates population levels, although this effect is proposed to operate primarily via its influence on reproduction rates (Shields 2002). Little is known about the factors that determine the availability of prey to pelicans in the Atlantic, Gulf of Mexico and Caribbean (Shields 2002). Distinguishing among these and other potential sources of mortality is likely to be a necessary component of any attempt to recover the species in the Caribbean.

Although the traditional approach to collecting mortality information would be a large-scale banding program, it is not clear that this would be the best solution as it would likely require an enormous effort to band enough birds and take many years to gather sufficient information to refine parameter estimates. Perhaps more effective would be more focused telemetry studies that target fewer individuals, but gather much more detailed information about them. Other unconventional approaches also exist that might allow one to estimate survival rates from the population's age structure (e.g. recent work on various species, shows that telomere shortening can be used to provide approximate ages in many bird species; Vleck et al. 2003). Even if more traditional, well-tested, approaches are used we would recommend that these alternatives be considered as supplemental methods of data collection, in the interests of obtaining the necessary information as quickly as possible.

The second area where research would be especially valuable involves understanding the manner in which individual pelicans move around both within the vicinity of Guayanilla Bay, and more generally throughout the region. This information would allow one to test a number of the assumptions in the model that it is currently impossible to address. Perhaps most importantly it might enable us to improve the way that the model describes the mechanism by which any additional mortality caused by turbines is imposed upon the population. For instance, if we could determine what portion of the population is actually vulnerable to turbine mortality, we could more effectively direct this mortality to the appropriate portion of the model population. If this information were available, one could model the way that mortality is likely to change as the population's size changes in a manner similar to that described in our "scenario 2" (see Methods: Model scenarios). This research would require the study of birds that are individually-identifiable in the field. Clearly, telemetry is one potential method that could provide the necessary information. With sufficient planning, this work could be combined with that proposed previously to improve our knowledge of survival patterns in order to address both sets of question at once.

There are various other areas of research that would be fruitful to explore, and these should probably be considered as a secondary tier of priorities. Currently, our model assumes that there is no emigration from, or immigration into, the population that occurs in Puerto Rico and the U.S. Virgin Islands. This assumption, however, is untested and there is likely to be at least some movement in and out of the population. It may be possible to address this question through banding or other marking studies; studies of population genetics provide another possibility. Another major assumption of our model is that there are no density dependent effects on any of the main model parameters. Testing this assumption is likely to be difficult without a long-term commitment to monitoring productivity and survival rates over many years, but it may be

possible to make some headway through shorter term studies (e.g., by comparing reproductive rates in colonies that differ in size). In general, our model suggests that management to increase reproductive output should not be the highest priority, but the model also suggests that it may be necessary to combine breeding season management with other activities. With this in mind, experimental studies that would allow one to determine why productivity varies among sites and years could provide insights into the reasons for past declines, and determine what management activities could help improve the situation. For example, experimental food supplementation might provide a means of testing whether the food supply limits productivity. Also, our different model scenarios suggest that the age structure of any birds that are killed by turbines will influence the population trajectory (i.e., compare scenarios 1 and 3). Therefore, the collection of data on the ages of birds killed by turbines should be a priority in any studies of turbine mortality conducted at other sites where turbines and pelicans co-occur, or at the WindMar site should turbines be installed. The larger the differences in survival rates between age classes, the more important this information will be.

Lastly, we note that the lack of comprehensive population estimates, collected at regular and frequent intervals for the entire population, limit the ease with which models such as ours can be tested, as well as clearly limiting our understanding of how the population's size is changing. Devising and implementing a regular population-wide monitoring program would help rectify this situation.

CONCLUSIONS

Our model predicts that the Caribbean brown pelican has been decreasing in recent decades, and that this decrease is likely to continue. Limited survey data support our model's predictions, although they suggest that the true rate of decline is slightly lower than the model would suggest. Incorporating the additional mortality that is anticipated to arise as a result of the installation of turbines at the WindMar RE facility slightly increases the rate of the population decline, but only by a small margin. If the Incidental Take Permit request in the draft HCP underestimates actual mortality then the rate of population decline in the model will be underestimated as well; again, however, the difference between the scenarios that we have modeled is slight. In short, our models suggest that the population is likely to decline substantially with or without the proposed facility.

Sensitivity analysis suggests that our results are robust to plausible errors in the model's parameter values. The model is much more sensitive to changes in survival parameters than breeding parameters. We presume that our estimates of adult survival are too low, because very little information was available to estimate this parameter and the types of data that were available frequently cause underestimates. This difference would account for the discrepancy between the model's predictions and published population estimates. Even when accounting for errors in our survival estimates, our general conclusions are unlikely to change unless true survival is much greater than available estimates suggest.

Simply improving breeding conditions in the model, within a range of plausible values, did not result in a population that was self-sustaining. Improving the status of the Caribbean brown pelican population in Puerto Rico and the U.S. Virgin Islands, therefore, would seem to require management activities that improve survival rates. If the demographic rates used in our model

are representative of those currently found in the real population, achieving a sufficient increase in survival rates to reverse population declines will probably be difficult. Consequently, it is likely that efforts to improve survival will need to be coupled with management to increase breeding productivity.

Currently, we do not have good estimates of survival rates, nor do we know what factors influence post-fledging survival in this population. Investigating these two factors is critical if we are to devise methods for effectively managing the population and improving its status. Equally, there is a need to obtain better information about the behavioral decisions made by individual pelicans when selecting habitat and moving between sites. This information would allow us to improve the structure of our population model so that it can more effectively estimate the impact of environmental changes, such as mortality due to wind turbines, that might influence the population. Finally, the limited number of comprehensive population censuses restricts the extent to which population models can be tested, and without these tests it is difficult to fully evaluate the model output and improve on the model's design.

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