

MOVEMENT PATTERNS AND POPULATION STRUCTURE OF THE BROWN PELICAN

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Abstract. Interest in monitoring the population viability of the Brown Pelican (*Pelecanus occidentalis*) has recently risen in the context of the species' 2009 delisting as endangered, rapid degradation of nesting habitat, and recent oil spills. To assess the Brown Pelican's patterns of movement (across natal colony, nonnatal colony, and noncolony islands), age and sex structure, and survival probabilities, we banded 1177 chicks in Louisiana from 2007 to 2009. In band-resighting surveys within the Isles Dernieres archipelago from 2008 to 2010, we detected 92 of our banded birds. Neither age nor sex appeared to influence where we observed pelicans resting on beaches across the islands, and we found the highest proportions of pelicans at their natal island. Yet few observations of banded birds suggest either movement outside our study area or mortality. Conditions at colonies and proximity to other sites of loafing or colonies may in part explain the disparity in proportions of resightings of individuals banded on different islands. Finally, the apparent probability of survival of one-year-old pelicans was lower than that of two- and three-year olds. Insights into these trends in movement and survival of young Brown Pelicans can improve future management of colony sites.

Key words: *Brown Pelican, demography, Pelecanus occidentalis, movement, survival, natal site fidelity.*

Patrones de Movimiento y Estructura Poblacional de *Pelecanus occidentalis*

Resumen. Recientemente ha surgido el interés de monitorear la viabilidad poblacional de *Pelecanus occidentalis* como consecuencia del retiro en 2009 de esta especie de la lista de especies amenazadas, de la rápida degradación del hábitat de anidación y de los derrames de petróleo recientes. Para evaluar los patrones de movimiento de *P. occidentalis* (a través de la colonia natal, la colonia no natal y las islas sin colonias), la estructura de edad y sexo, y las probabilidades de supervivencia, anillamos 1177 pichones en Luisiana desde 2007 a 2009. En muestreos de avistaje de aves previamente anilladas, dentro del archipiélago de las Islas Dernieres desde 2008 a 2010, detectamos 92 de nuestras aves anilladas. Ni la edad ni el sexo parecieron influenciar el lugar donde observamos a los pelicanos reposar en las playas a través de las islas, y encontramos las mayores proporciones de pelicanos en sus islas natales. A pesar de esto, pocas observaciones de aves anilladas sugieren la existencia ya sea de movimientos afuera de nuestra área de estudio o mortalidad. Las condiciones de las colonias y la proximidad a otros sitios de descanso o colonias pueden en parte explicar la disparidad en las proporciones de avistajes repetidos de individuos anillados en diferentes islas. Finalmente, la probabilidad aparente de supervivencia de pelicanos de un año de edad fue menor que la de individuos de dos o tres años de edad. Los hallazgos en las tendencias en el movimiento y la supervivencia de los jóvenes de *P. occidentalis* pueden mejorar el futuro manejo de las colonias.

INTRODUCTION

Birds' patterns of movement in the short and long term, influence their population density and distribution, gene flow, and ability to cope with environmental disturbances. Because global climate change is expected to alter habitats (Michener et al. 1997), dispersal may play an increasingly important role in maintaining population viability. Coastal species are particularly vulnerable because of increases in sea level (Antonov et al. 2005, Meehl

et al. 2005, Church and White 2006) and increased frequency and intensity of tropical storms and hurricanes (Webster et al. 2005, Sallenger et al. 2006, Bender et al. 2010). Seabirds that breed on barrier islands are especially at risk (Parnell et al. 1988). Within Louisiana, islands are additionally threatened by elevation loss due to natural sediment compaction (Georgiou et al. 2005, O'Connell et al. 2005, Sallenger et al. 2006) and rapid shoreline erosion (Penland et al. 2005, Miner et al. 2009), which degrade breeding sites.

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The Brown Pelican (*Pelecanus occidentalis*) has a range that extends along the west, east, and gulf coasts of the U.S., and throughout Middle America and the Caribbean (Shields 2002). It is thought that populations breeding in the northern Gulf of Mexico do not migrate because of the region's relatively mild winters (Williams 1974, Schreiber and Mock 1988), while other more northern populations, such as those from South Carolina, migrate south for the winter (Schreiber and Mock 1988). In the northern Gulf of Mexico, the Brown Pelican was historically abundant, particularly within Louisiana, where approximately 50 000 individuals were reported in the early 1900s (Schreiber and Risebrough 1972, King et al. 1977). In the 1950s and 1960s, however, Brown Pelican numbers in Louisiana were severely reduced by pesticide contamination (Nesbitt et al. 1978). Continued contamination ultimately resulted in the extirpation of the species from Louisiana by 1963 (James 1963). To re-establish the Brown Pelican population, 1276 chicks from Florida were translocated to three islands in Louisiana from 1968 to 1980 (Nesbitt et al. 1978, McNease et al. 1984). These translocations provided the foundation for Louisiana's current population (Holm et al. 2003).

Because of the past decrease, the Brown Pelican was placed on the U.S. Fish and Wildlife Service's list of endangered species in 1970, then delisted in 2009 after recovery of the overall population (Levy 2008). The recent delisting has warranted increased monitoring of population viability (USFWS 2009), particularly within Louisiana, where instability of the nesting habitat still poses a threat to reproduction (Visser and Peterson 1994). Yet little is known of the species' basic demographic trends, including what factors regulate demographic processes. Furthermore, interpretation of population trends over time is hindered by contradictory reports in the literature in regard to movement patterns. For instance, several observations suggest Brown Pelicans from nesting colonies in the southern U.S. are relatively sedentary. For example, Schreiber and Mock (1988) reported that no pelicans banded in Florida between 1925 and 1983 were recovered dead in Louisiana, and they suspected that even exchange between the gulf and Atlantic coasts of Florida to be minimal. Limited movement along the northern gulf coast is also supported by Williams' (1974) report that new nesting colonies initiated in Louisiana following the 1963 extirpation were the result of the translocations from 1968 to 1980 rather than of recruits from out of state.

In contrast to these studies, other research suggests considerable long-range movement along the coasts of the southern U.S.. As the pelican population in Louisiana grew following translocations from Florida, Holm et al. (2003) suggested that immigration of individuals from other states as a plausible factor augmenting the population. Long-distance movement of the Brown Pelican has been more definitively demonstrated by the natural formation of a new nesting colony on Gaillard Island, Alabama, in 1983 (Robinson and Dindo

2008)—the first colony ever documented in that state. These birds likely came from Florida (Holm et al. 2003).

Aside from conflicting observations regarding the pelican's patterns of long-distance movement along all southern U.S. coasts, little information exists regarding movements on smaller scales, such as between nesting colonies in the same region. Furthermore, few studies have investigated the role of age in movement, sex ratios, or probabilities of survival. Schreiber and Mock (1988) reported significant differences by age in the Brown Pelican's movement patterns and survivorship. While providing valuable information on the species' demography, those estimates were based on recoveries of dead banded birds and thus provide limited insight into how the long-term demographic patterns of surviving birds affect colony sizes. The lack of estimates of movement and survival makes it difficult to interpret changes observed in the number of pairs of nesting pelicans at the level of the individual colony or set of colonies. For example, Jodice et al. (2007) found a decrease in the numbers of pelican nests in South Carolina from the mid 1980s to 2005 yet lacked data on mortality, emigration, or recruitment that could have helped explain the trend. Neither have movement patterns, behavior, or demographic structure been studied in relation to sex, likely because the species could not be sexed easily prior to recent developments in genetic sexing (Fridolfsson and Ellegren 1999).

Within the context of changing environmental conditions, little is known in regard to how hurricanes and habitat-degradation patterns influence the Brown Pelican's movements. Aside from reports of storm-induced losses of both nests and chicks (Parnell et al. 1988, McNease et al. 1992), it is unclear how subadults (one or two years old) respond in years following hurricanes and associated changes in habitat. As the intensity and frequency of hurricanes in the northern Gulf of Mexico increases with global climate change (Webster et al. 2005, Sallenger et al. 2006, Bender et al. 2010), understanding the influence of hurricanes on the pelican's habitat and population trends could help design management plans to ameliorate the storms' destructive effects.

To increase understanding of the Brown Pelican's movements on the northern gulf coast, we conducted band-resighting and age-structure surveys to determine fidelity to an island, age and sex composition, and individuals' probability of survival. We used these observations to identify factors that may regulate colony size, overall distribution, and the species' long-term viability. This information is needed in light of the 2009 removal of the Brown Pelican from the endangered species list (USFWS 2009) and as an aid to efforts in habitat management and island restoration (Shields 2002, Kulp et al. 2005, Fearnley 2008). A more complete demographic assessment of gulf coast pelican populations allows for an assessment of anthropogenic influences such as the 2010 Deepwater Horizon oil spill (Crone and Tolstoy 2010), an event that resulted in the contamination of more than 1100 km of coastline, primarily in Louisiana (Camilli et al. 2010, Chen and Denison 2011).

METHODS

STUDY SITES

We conducted our research within the Isles Dernieres Barrier Island Refuge, Louisiana (Fig. 1). This archipelago consists of Raccoon, Whiskey, Trinity, and Wine islands, located approximately 3 to 10 km from mainland marsh shore. We also surveyed Orange Island, located 8 km northwest of Wine Island (Fig. 1). This island is not officially named but is known by some local agency personnel as Orange Island. These low-lying (elevation <1 m; Visser et al. 2005) and narrow islands (80 to 500 m wide and 300 m to 12 km long) are vegetated with grasses, herbs, and woody shrubs growing on a sandy substrate. Hester et al. (2005) detailed the plant communities of these barrier islands. The islands lacked human habitation during our study but were heavily used by coastal birds. During our study Brown Pelicans used Whiskey and Trinity islands as resting (loafing) sites only, while Raccoon and Wine islands supported nesting colonies. During the first two years of the study pelicans only loafed on Orange Island but nested there during the final year. Numerous other offshore islands lie to the east of our study site; from Wine Island, the closest potential loafing site is 6 km away (Timbalier Island) and the nearest nesting site is 26 km away (Shallow Bayou Island) (Fig. 1).

BANDING AND SEXING

We banded 1177 chicks from 2007 to 2009. Once chicks had naturally left their nests, we captured individuals by hand before they were able to fly and applied a nine-digit U.S. Geological Survey metal band to one leg and a corresponding three-digit auxiliary color band to the other leg; the color band can be read through a spotting scope. Most chicks were banded

on Raccoon and Wine islands (575 and 539 birds, respectively); in 2007 we also banded 63 chicks on Rabbit Island, within Lake Calcasieu, Louisiana (Fig. 1). We also collected blood samples from 63% ($n = 738$) of banded birds and sexed a subset of them by the methods of Fridolfsson and Ellegren (1999).

BAND-RESIGHTING SURVEYS

We surveyed all islands within the Isles Dernieres approximately biweekly (215 surveys total) from late March to mid July in 2008, 2009, and 2010. Using spotting scopes (Swarovski 20–60 power), we scanned on all loafing individuals for color bands. We walked beaches in all areas of the islands where pelicans were found, and the surveys ended after we scanned all available birds on the beaches, on rock jetties or breakwaters, and within vegetation. Because views of legs, and potential bands, of pelicans perched within vegetation or on nests were almost always obstructed, >99% of the banded birds we observed were on beaches or rocks.

Because of the abundance of pelicans on Raccoon ($n = 50$) and Wine ($n = 53$) islands, surveys there encompassed the entire length of the islands, while surveys on Whiskey ($n = 46$) and Trinity ($n = 51$) islands were restricted to the sandy spits where most pelicans loafed. In 2010, because of limited resources, our 15 surveys included Orange Island only, excluding Rabbit Island and other islands. Surveys extended from 07:00 to 18:00 Central Standard Time, as pelicans were found loafing abundantly over the course of the day, and each island survey lasted from 45 min to 4 hr—larger islands took longer. For each band observation, we recorded coordinates by GPS, island, date, auxiliary band number and color, and age (1, 2, or ≥ 3 years, estimated by plumage characteristics; Shields 2002, Sibley 2000). Ages refer to the number of years after chicks hatched, and hatch-year birds were not recorded in surveys. For all observed pelicans that were banded within the Isles Dernieres, we classified each as either detected at its “natal” island (where the individual was banded and released, e.g., either Raccoon or Wine Island), at a “non-natal colony” island (an island with pelican nesting but not where the individual was hatched, e.g., Raccoon or Wine Island), or on a “non-colony” island (Whiskey and Trinity islands).

AGE-STRUCTURE SURVEYS

In addition to band surveys that entailed scanning all possible Brown Pelicans across the entire island, we surveyed two randomly selected, distinct clusters of loafing pelicans (10–136 individuals per island) visit to assess the age structure of the cluster. These surveys encompassed individuals that may or may not have had one of our bands and took place on the same days as the comprehensive band surveys, on Raccoon, Whiskey, Trinity, Wine, and Orange islands, from late March to mid July, 2007 to 2010 (236 total surveys). To ensure individual pelicans were only counted once per survey and island, we surveyed opposite sides of the island on each visit. Within each survey, we tallied pelicans within the designated cluster by their estimated age (1, 2, or ≥ 3 years, as described above) and

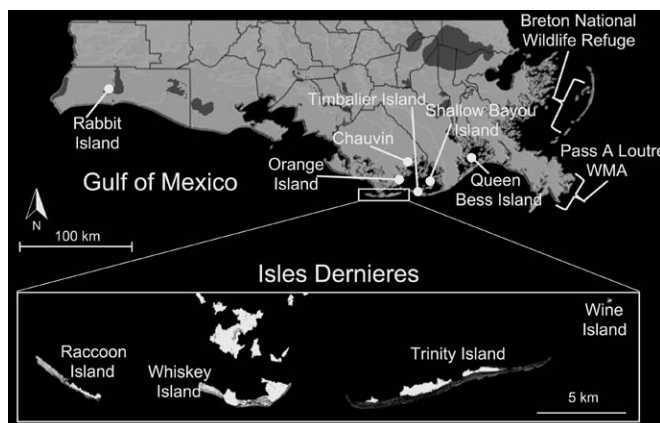


FIGURE 1. Coastline and the Isles Dernieres Barrier Island Refuge (expanded view) of Louisiana. The darker shading of the mainland indicates land, while the lighter shading represents bodies of freshwater. In the expanded view of the Isles Dernieres, the lighter shading represents sandy substrate, the darker shading shows vegetated areas (lighter areas are dominated by grasses and forbs, while darker areas hold dense shrub cover).

whether or not they had one of our bands. Within a cluster, we counted only pelicans whose legs we could see clearly because we wanted to determine what proportion of a random cluster of pelicans our banded pelicans constituted.

ESTIMATION OF AGING ERROR

To assess errors in age determination, we compared ages estimated in the field during band-resighting surveys to their actual ages known from our database and that of the Bird Banding Laboratory (unpubl. data). We then categorized the age of each banded bird, as determined from plumage characteristics by five observers, as correct, underestimated, or overestimated. Using the proportions of individuals in each age class that were incorrectly aged in the field, we adjusted counts of banded and unbanded birds across the three age classes in our age-structure data.

STATISTICAL ANALYSIS

To assess relationships among pelican ages (1, 2, or ≥ 3 years old), sex, and their occurrence at natal, non-natal colony, or non-colony islands, we used log-linear categorical modeling to compare all response-combination frequencies of the fully saturated model (including the three-way interaction) and reduced models (SAS Institute 2008; proc Catmod). We disregarded observations of birds banded on Rabbit Island and at Breton National Wildlife Refuge (NWR) because these sites are outside our survey area, so we were unable to observe them at their “natal” island (resulting in a “structural zero”). Furthermore, we excluded detections of bands at Orange Island because this site was not surveyed in the first two of the three years of our study. Because some banded birds were observed multiple times within a year, to maintain statistical independence, we only used the first location of observation within each year. We used resightings of individuals in subsequent years to allow us to evaluate relationships among the age classes, sexes, and islands.

To assess patterns of loafing across islands with and without colonies, we pooled all data for all ages and both sexes and used chi-squared goodness-of-fit tests (SAS Institute, Inc. 2008; proc Freq). We compared proportions of our observations of banded birds across natal, non-natal colony, or non-colony islands to the proportions of expected if birds expressed no preference for particular islands. We calculated expected values as the product of the proportion of surveys at Raccoon, Whiskey, Trinity, and Wine islands (i.e., survey intensity) and the total number of observations of banded birds, and applied goodness-of-fit tests separately for birds banded on Raccoon and Wine islands. Although the availability of beaches for loafing differed slightly by island, the lack of loafing pelicans on all beaches suggests that available habitat was not a limiting factor in island preference. Also, because Brown Pelicans can fly >100 km while foraging (Walter et al., unpubl. data), the differences in distances between islands should not affect island-preference patterns, as all sites are within the range of possible movement. Finally, for individuals that were observed multiple times

within and across years, we analyzed only a single random observation location.

For banded pelicans observed multiple times, we used chi-squared goodness-of-fit tests to assess whether the proportions of repeated observations (i.e., second to fifth sightings of a particular individual) at the island where the bird was first detected and other islands were equal. We evaluated this question separately for data within a year (62 repeated observations) and across years (25 repeated observations). First, we calculated expected observation values for Raccoon, Whiskey, Trinity, and Wine islands as the product of the proportion of surveys per island and the total number of banded birds observed. Because repeated observations of birds found on Whiskey and Trinity Islands were too few (0–3 observations) for analyses by individual island, we summed all observed and expected counts across islands for an archipelago-wide assessment of observations at the same or different islands. That is, for each repeated observation, the count data used for analyses were either “at the same island” or “at a different island”; the use of these general categories allowed summing observation counts across islands.

To determine if proportions of pelicans that were resighted were independent of where they were banded (Raccoon or Wine Island), we analyzed the data with a chi-squared contingency table analysis. All observations from 2008 to 2010 across Raccoon, Whiskey, Trinity, and Wine islands were pooled for this analysis. Values are means \pm SE, unless otherwise noted. In all statistical analyses, we set $\alpha = 0.05$ as the level of significance.

PROBABILITIES OF SURVIVAL AND RESIGHTING

We also used observations of banded pelicans within the Isles Dernieres to assess probabilities of yearly apparent survival (Φ) and “recapture” (i.e., “resighting” in our study), with a Cormack–Jolly–Seber model of live re-encounters within program MARK (White and Burnham 1999). For each year 2008 to 2010, we considered individuals observed or not within the archipelago (i.e., four “occasions” and three “intervals” when 2007, the year of initial banding, is included). Because we were interested in yearly probabilities of survival, we did not incorporate multiple sightings of an individual during a survey year into the analysis (i.e., we classified pelicans observed more than once as simply present for a particular survey year). The lack of new band sightings during the last third of the summer suggested that surveys over an entire summer were adequate to accurately classify each banded pelican as present or absent within our study area. Because of the infrequency of band detections we did not believe our data were adequate to allow division of a summer’s surveys into multiple periods. We categorized each chick as banded on either Raccoon or Wine Island (i.e., two mutually exclusive groups). We disregarded individuals that were banded on Rabbit Island or at Breton NWR, outside our survey area, and those found dead ($n = 5$), leaving observation data for 1109 birds whose likelihood of detection and survival were theoretically equal.

We began developing models with the default fully time-dependent live-encounter model ($\Phi \times \text{time}$) (resighting \times time).

To test for assumptions of fit on this global model, we ran a bootstrap goodness-of-fit test (1000 simulations), which yielded a variance-inflation factor (\hat{c}) of 2.26. For comparison, a median \hat{c} test resulted in $\hat{c} = 1.92$. We used the larger value to adjust \hat{c} conservatively, which allowed all consecutive assessments of models to be based on the adjusted \hat{c} . To explore how various factors might influence an individual's survival, we next designed various biologically plausible models based on different combinations of year, banding cohort, island where banded, and/or age-specific variables determined a priori (Anderson and Burnham 1999). We designated different parameterizations as time dependent, constant within island, or the same across islands, which resulted in 36 candidate models. This set included a null model that estimated single values for Φ and resighting. We used Akaike's information criterion adjusted for small sample size (AIC_c), automatically converted to quasi-likelihood values ($QAIC_c$) via the \hat{c} adjustment, to rank each model (Burnham and Anderson 2002). We considered models with $\Delta QAIC_c$ values < 2 units from the model with the smallest $QAIC_c$ and large model weights (w_i) the best approximating models, given one of the candidate models as the best approximating model of the set (Burnham and Anderson 2002). To account for uncertainty in selection of models, we performed model averaging, which calculates an average value for the models' parameters by averaging over all candidate models. Models with common elements of parameter structure contribute to the averages as a function of their support, based on weight (Burnham et al. 2011).

RESULTS

BAND OBSERVATIONS

We observed 150 uniquely banded individuals within the Isles Dernieres. The majority (57%) of these birds were banded on either Raccoon ($n = 55$) or Wine ($n = 31$) Island, within our study site. The remainder were banded on either Rabbit Island ($n = 6$) 250 km to the west or within the Breton NWR ($n = 58$) 150 km to the east of our survey area (Fig. 1). Because some birds were observed on multiple occasions within and across years, we recorded 231 total observations.

The proportions we observed of pelicans banded at different islands were unequal ($\chi^2_1 = 846.94$, $n = 1176$, $P < 0.001$). Overall we resighted 8% ($\pm <1\%$ SE) of the pelicans we banded, 9% from Raccoon ($\pm 1\%$ SE), 6% from Wine ($\pm 1\%$ SE), and 10% from Rabbit ($\pm 4\%$ SE). Despite relatively few observations, we suspect we detected the majority of banded birds present because sightings of new band numbers declined toward zero near the end of each survey season. Moreover, we continued biweekly searches for bands an average of 18 extra days per year (range 11–24 days) beyond when the last new band was observed.

Despite outreach to the Louisiana birding community for ancillary observations of our banded birds, we only received two reports. Both pelicans were from Raccoon Island and were observed in Louisiana. A one-year-old was observed in Chauvin, and a two-year-old was observed at the Pass a Loutré

Wildlife Management Area, 55 km northeast and 180 km east of Raccoon Island, respectively (Fig. 1).

SEX STRUCTURE

We determined the sex of all individuals observed during band-resighting surveys and for which we had blood samples, finding a sex ratio close to 1:1 (31 females and 30 males). Those individuals plus a sexed random subset of bled and sexed pelicans banded at Raccoon, Wine, and Rabbit islands that we did not resight also resulted in a sex ratio close to 1:1 (233 females and 230 males).

AGE STRUCTURE AND ESTIMATION OF ERROR PROPORTIONS

From our comparisons of field estimates and actual ages of pelicans represented by our 231 observations, we found that, all age classes pooled, 89% of field estimations were correct; 9% were underestimated and 2% were overestimated. Using these percentages per age category, we adjusted our counts before summarizing and analyzing data that were based on estimates of ages in the field. For counts of 1-year-olds we subtracted 17% and added it to the count of 2-year-olds; for counts of 2-year-olds, we appropriated 4% to the count of 1-year-olds and 7% to the \geq three-year-old count; and for counts of birds ≥ 3 years old, we subtracted 3% and added the value to the count of 2-year-olds.

We surveyed a total of 7963 loafing birds within the randomly selected clusters of banded or unbanded pelicans surveyed for age structure, for an average tally of 33.7 loafing individuals per survey (range 10–136). After correction for error of age estimation in the field, proportions of 1- and 2-year-old pelicans (both banded and unbanded) were similar across all years (Fig. 2). There were on average 3.23 (range 2.20–4.28) times more pelicans ≥ 3 years old than 1- or 2-year-old subadults. Furthermore, during 2010 surveys we found an average of $<1\%$

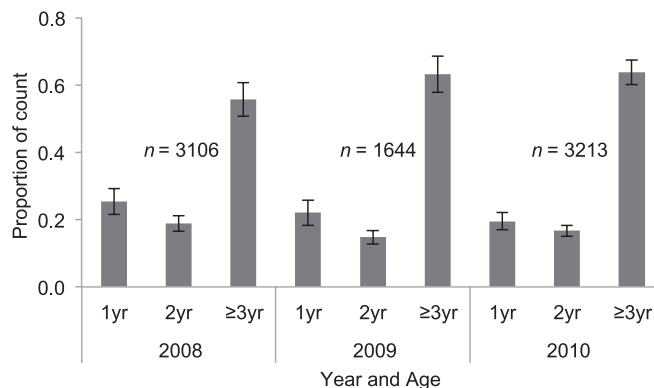


FIGURE 2. Mean proportions of 1-, 2-, and ≥ 3 -year-old Brown Pelicans from 236 surveys during the breeding seasons from 2008 to 2010 on Raccoon, Whiskey, Trinity, Wine, and Orange islands, Louisiana. The birds were aged by plumage characteristics, and counts were adjusted for errors quantified by comparison to birds sexed molecularly. Numbers above bars are numbers of birds counted per year, and error bars are 95% confidence intervals.

($\pm <1$ SE) of pelicans that we had banded (bands from outside our study were not counted).

MOVEMENT PATTERNS

We found no evidence to suggest that age or sex were important variables associated with pelicans' occurrence at natal colony, non-natal colony, or non-colony sites, as none of the fully saturated or reduced models in log-linear categorical modeling provided support (for all models $\chi^2_{2-8} = 3.01-7.06$, $n = 66$, $P \geq 0.22$). We did, however, find differences in proportions of loafing banded pelicans at different islands for birds banded on both Raccoon ($\chi^2_3 = 21.59$, $n = 55$, $P < 0.001$) and Wine ($\chi^2_3 = 21.58$, $n = 29$, $P < 0.001$) islands (Fig. 3). On the basis of the combined proportions of total observations of birds banded on Raccoon and Wine islands, pelicans were found 3.14 times more

often at their natal island than at a non-natal colony site and 2.59 times more often at their natal island than at a non-colony island.

Among birds banded within the Isles Dernieres that were observed multiple times, there was a strong association between the island where the bird was first observed and the island where it was subsequently observed, both within ($\chi^2_1 = 76.36$, $n = 62$, $P < 0.001$) and across ($\chi^2_1 = 15.40$, $n = 25$, $P < 0.001$) years. On the basis of overall proportions of multiple resightings, pelicans were observed 2.87 times more often on the same island where first observed within a year and 1.5 times more on the same island across years.

PROBABILITIES OF SURVIVAL AND RESIGHTING

Of our 36 candidate models, seven had $\Delta\text{QAIC}_c < 2$ from the top model (Table 1) and 20 held ΔQAIC_c values < 7 . The model with the smallest QAIC_c value includes separate Φ probabilities for pelicans from Raccoon and Wine islands, while estimates within an island are calculated separately for different years' cohorts (i.e., six different values of Φ are calculated; one each for each group of pelicans banded in 2007, 2008, and 2009, on each of the two islands). Of the other models with $\Delta\text{QAIC}_c < 2$, four others also estimated Φ separately for each cohort. In addition, two models included separate estimates for the age classes 1 year old and 2 and ≥ 3 years old (Table 1). When inference is expanded to models with $\Delta\text{QAIC}_c < 7$, various combinations appear of island, cohort, and age parameterizations that are held constant or are time-dependent. The large number of competing models with various parameterizations suggests Φ is influenced by multiple variables. Therefore, to account for uncertainty in selection of models we provide estimates of probability of survival by island, cohort, and age class (Fig. 4).

For birds banded on Raccoon Island, a trend of decreasing Φ is evident in 1-year-old pelicans of each successive year's cohort (Fig. 4). The trend for individuals banded on Wine Island is similar, yet the reduction in Φ from 2007 to 2008 is greater than that at Raccoon Island. The probability of survival of 2-year-olds is slightly greater for birds from Raccoon Island than for those from Wine Island. When 2- and 3-year-olds are pooled, values of Φ for the two islands are nearly identical. Furthermore, on both Raccoon and Wine islands Φ is generally greater for 2-year-olds and 2- and 3-year-olds pooled than for 1-year-olds. An exception is that in the 2007 cohort values for 1-year olds on Raccoon and Wine Islands are similar, as are values for the 2008 cohort of 2-year olds on Wine Island. Although we identify various trends, particularly decreased probabilities of survival of 1-year olds in the later years of our study, most notably on Wine Island from 2007 to 2008, overlapping confidence intervals suggest differences are not large.

In the top seven models, parameterization of probabilities of resighting also varied (Table 1). Even averaged across all age classes and cohorts, estimates varied by island. The probability of resighting was 0.14 (95% CI 0.05–0.35) for pelicans from Raccoon Island and 0.16 (95% CI 0.05–0.41) for individuals from Wine Island.

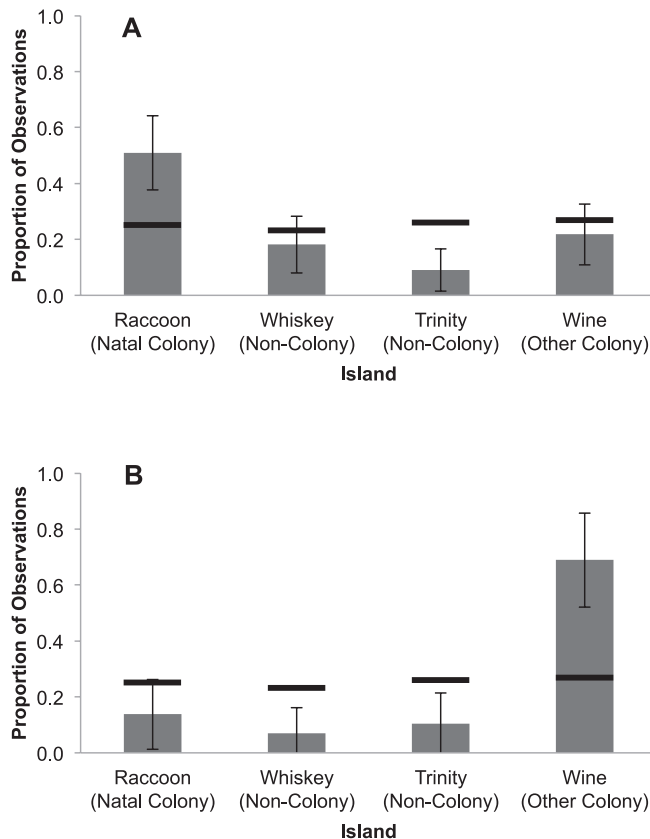


FIGURE 3. Proportions of actual (solid bars) and expected (bold lines) observations of loafing banded Brown Pelicans at islands within the Isles Dernieres archipelago, Louisiana, from 2008 to 2010. "Natal colony" represents an island where chicks were banded and released, "non-natal colony" islands are nesting locations away from an individual's natal island, and "non-colony" islands are areas without nesting. Birds banded on Raccoon (A, 55 observations) and Wine (B, 29 observations) islands were analyzed separately. Expected observation values were calculated as the product of the proportion of surveys at each island (i.e., survey intensity) and the total number of observations of banded birds. Data are from 200 band-resighting surveys, birds were 1 to 3 years old when observed, and error bars are 95% confidence intervals.

TABLE 1. Results of selection of 36 a priori determined and biologically plausible models evaluated to estimate probabilities of apparent survival (Φ) and resighting of Brown Pelicans banded and released on Raccoon and Wine islands within the Isles Dernieres archipelago, Louisiana, from 2007 to 2010. For each survey year (2008–2010) individuals were considered present or absent on the basis of extensive surveys throughout the archipelago from April to June. Estimates for an islands were calculated either separately (“islands diff”) or averaged (“islands same”).

Model ^a	K^b	ΔQAIC_c	Weight	Deviance
Φ (islands diff; cohorts c) re-sight (islands same)	7	0.00	0.15	13.06
Φ (islands same; cohorts t) re-sight (islands same)	7	0.12	0.14	13.18
Φ (islands same; cohorts c) re-sight (islands same)	4	0.70	0.10	19.83
Φ (islands diff; 1yr t, 2,3yr c) re-sight (islands same)	9	0.82	0.10	9.82
Φ (islands diff; cohorts c) re-sight (islands diff; c)	8	1.55	0.07	12.59
Φ (islands same; 1yr s, 2,3yr s) re-sight (islands same)	3	1.68	0.06	22.82
Φ (islands same; cohorts t) re-sight (islands diff; c)	8	1.90	0.06	12.93
Φ (islands diff; 1yr t, 2,3yr c) re-sight (islands diff; c)	10	2.03	0.05	9.00
Φ (islands same; cohorts c) re-sight (islands diff; c)	5	2.34	0.05	19.45
Φ (islands same; 1yr s, 2,3yr t) re-sight (islands same)	4	2.81	0.04	21.93
Φ (islands same; 1yr s, 2,3yr s) re-sight (islands diff; c)	4	3.13	0.03	22.26
Φ (islands diff; 1,2,3yr t) re-sight (islands same)	13	3.51	0.03	4.36
Φ (islands diff; 1, 2,3yr c) re-sight (islands same)	7	4.06	0.02	17.13
Φ (islands same; 1yr s, 2,3yr t) re-sight (islands diff; c)	5	4.25	0.02	21.36
Φ (islands same; 1yr s, 2,3yr s) re-sight (islands diff; t)	8	4.33	0.02	15.37
Φ (islands diff; 1,2,3yr t) re-sight (islands diff; c)	14	4.90	0.01	3.70
Φ (islands diff; 1,2,3yr c) re-sight (islands diff; c)	8	5.81	0.01	16.85
Φ (islands same; 1yr s, 2,3yr t) re-sight (islands diff; t)	9	6.36	0.01	15.37
Φ (islands same) re-sight (islands same)	2	6.46	0.01	29.60
Φ (islands diff; cohorts c) re-sight (islands diff; t)	12	6.72	0.01	9.61
Φ (islands same; cohorts t) re-sight (islands diff; t)	11	7.04	0.00	11.97
Φ (islands diff; 1yr c, 2,3yr t) re-sight (islands same)	7	7.15	0.00	20.21
Φ (islands same) re-sight (islands diff; c)	3	7.65	0.00	28.79
Φ (islands diff; 1,2,3yr t) re-sight (islands diff; t)	16	7.65	0.00	2.34
Φ (islands diff; c) re-sight (islands same)	3	7.92	0.00	29.06
Φ (islands diff; 1yr c, 2,3yr t) re-sight (islands diff; c)	8	8.53	0.00	19.57
Φ (islands same; cohorts c) re-sight (islands diff; t)	9	8.73	0.00	17.74
Φ (islands same) re-sight (islands diff; t)	7	9.18	0.00	22.24
Φ (islands diff; 1,2,3yr c) re-sight (islands diff; t)	12	9.38	0.00	12.27
Φ (islands diff; 1yr t, 2,3yr c) re-sight (islands diff; t)	14	9.43	0.00	8.23
Φ (islands diff; c) re-sight (islands diff; c)	4	9.63	0.00	28.76
Φ (islands diff; t) re-sight (islands same)	7	10.96	0.00	24.02
Φ (islands diff; c) re-sight (islands diff; t)	8	11.19	0.00	22.23
Φ (islands diff; 1yr c, 2,3yr t) re-sight (islands diff; t)	12	11.30	0.00	14.19
Φ (islands diff; t) re-sight (islands diff. c)	8	12.98	0.00	24.01
Φ (islands diff; t) re-sight (islands diff; t)	10	15.15	0.00	22.12

^aLowest QAIC_c = 343.97. Models test for the influence of island, year of banding, and age (1, 2, or ≥ 3 years old). Cohorts = all the Brown Pelicans that belong to the group banded in either 2007, 2008, or 2009; yr = age classes estimated are indicated by groupings of years (1,2,3) followed by yr (meaning years old). Parameterization for model variables proceeding t, c, and s: t (time-dependent) = parameterization differs by year; c (constant) = parameterization is held constant each year but may be the same or differ across islands; s (same) = parameterization is held the same across years and islands.

^b K = number of estimable parameters within the model.

DISCUSSION

ISLAND-USE PATTERNS

Within the Isles Dernieres archipelago we found a strong trend of banded pelicans occurring primarily at their island of their natal colony. This pattern is congruent with the species' tendency for fidelity to the natal site (Shields 2002). Within

Louisiana for instance, marked individuals from the 1968 to 1980 translocations were found nesting at the islands where they were released in subsequent years (Williams 1974). Furthermore, pelicans commonly nest on particular islands, such as Raccoon and Queen Bess, in successive (Fig. 1; Visser and Peterson 1994). This trend has been further supported

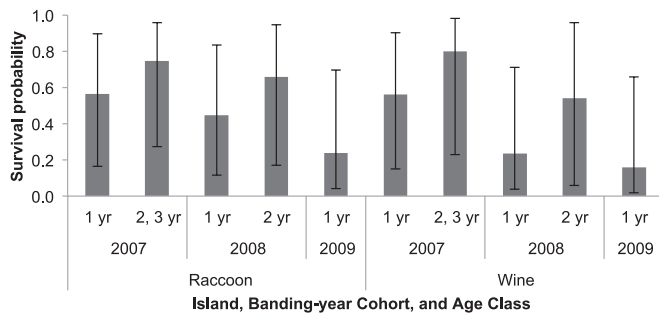


FIGURE 4. Probabilities of apparent survival of Brown Pelicans of cohorts banded in different years and different age classes. Pelicans were banded as chicks from 2007 to 2009 on two islands within the Isles Dernieres archipelago, Louisiana, and individuals' presence or absence was determined yearly via band-resighting surveys within the archipelago from 2008 to 2010. Program MARK was used to compare candidate models, and survival probabilities were derived from model averaging. Nonsymmetrical error bars are 95% confidence intervals back-transformed from the logit scale.

by yearly aerial surveys of coastal colonies in Louisiana (Louisiana Department of Wildlife and Fisheries [LDWF], unpubl. data), although it is unclear if specific colonies are maintained by individuals reared on those islands or by new recruits.

While we occasionally found banded pelicans at non-natal colony islands in the proportions expected, they appeared less frequently than expected on non-colony islands that have abundant nesting and loafing habitat. These patterns are in line with the species' gregarious and social habits (Shields 2002). As many colonially nesting seabirds use public information from conspecifics (Forbes and Kaiser 1994, Danchin et al. 1998, Doligez et al. 2002), Brown Pelicans also likely benefit from social information exchange with respect to prey availability, predator avoidance, and general habitat quality. Although previous studies of other waterbirds have reported loafing and foraging locations near the colony (Custer and Osborn 1978, Jodice et al. 2003), it remains unknown whether Brown Pelicans loafing on a particular island are more likely to nest on that island. During our 2010 band-resighting surveys, the birds we banded in 2007 were old enough to reproduce (Shields 2002). Unfortunately, because leg bands were obscured when birds were on nests and our band-resighting data are limited to loafing individuals, we were unable to assess this potential relationship.

Despite uncertainty of the relationship between loafing and nesting, the regular presence of 3-year-old or younger pelicans at non-colony islands suggests habitat away from colony sites holds some value. While foraging, Brown Pelicans must return to land to dry their plumage after approximately 1 hour of repeated dives for prey (Shields 2002). Thus, pelicans we observed at non-colony sites were likely resting during foraging trips, possibly near foraging sites. Although Whiskey and Trinity islands are several kilometers long, pelicans loafed on the sandy, unvegetated spits of the islands almost exclusively;

each island has an eastern and a western spit. Over the course of our study, we observed the complete loss of two spits and considerable erosion of the remaining two. Although we lack data for assessment, we suspect pelicans that previously used the now eroded spits would loaf on available spits at other locations. Although studies of the Brown Pelican commonly focus on stability of nesting habitat (Visser and Peterson 1994, Visser et al. 2005), coastal restoration plans that incidentally protect loafing habitat required during foraging trips could further benefit Brown Pelican conservation. Yet nesting habitat should remain the primary focus of conservation.

INFLUENCE OF AGE AND SEX ON MOVEMENT

Both male and female pelicans loafed at their natal colony island more often than at a non-natal colony island or non-colony island. This is in contrast to the general life-history patterns of many other seabirds in which females disperse more than do males, whose philopatry and territoriality is greater (Kim et al. 2007, Becker et al. 2008, Oro et al. 2011). During breeding, male Brown Pelicans select nest sites and display to attract prospecting females (Shields 2002). If males prefer familiar nesting sites, it may explain why we found them to be most associated with their natal islands. The lack of female-biased movement of Brown Pelicans away from their natal colonies, unlike the pattern observed with most birds (Greenwood 1980), may be a consequence of the dearth of alternative nesting sites. Although coastal islands are abundant in southeast Louisiana, Visser and Peterson (1994) suggested that sites suitable for Brown Pelican colonies are rare. It is also possible that sex-biased dispersal of pelicans, if any, occurs after the third year of age. We are unable to assess potential relationships among sex, natal island, and nest site directly because our band-resighting data are limited to individuals loafing on beaches, not nesting individuals. But for birds loafing on beaches, we found no evidence of sex-biased movement away from their natal island.

There was no influence of age on patterns of island use. Because our band-resighting surveys were restricted to a single archipelago, our data represent natal-site fidelity and not true dispersal to other islands for reproduction. Unfortunately, data regarding age influences on patterns of long-distance movement have been reported only by Schreiber and Mock (1988). On the basis of decades of recoveries of dead banded pelicans, they found differences in movement by age class. Recoveries of banded subadults were on average 689 km from the site of banding in North or South Carolina, while for banded adults this distance was 598 km. These patterns, however, reflect yearly winter migrations to warmer southern environments, not dispersal. Furthermore, these results are based on recoveries of dead birds so do not reflect detailed or complete patterns of yearly movement. Unfortunately, our data do not allow us to investigate movement patterns over the winter or whether our unobserved 3-year-old pelicans dispersed to breed at new locations. Yet, on the basis of observations of individuals aged 1 to 3 years old loafing on beaches, we found no evidence of

age-biased movement away from natal colonies within the Isles Dernieres.

On a statewide scale, our observations of birds banded within the Breton NWR indicate movement of subadult and adult pelicans within Louisiana. Of the 58 individuals from that region that we observed within the Isles Dernieres, 47% were subadults (23 were 1-year olds and four were 2-year olds). If adults frequently loaf near where they nest, our observations of 31 adult birds from the Breton NWR suggest that at least some birds from this site may be nesting in our study area. However, the proportion of the Breton NWR population dispersing to breed in the Isles Dernieres is probably small, given that we observed only 58 of the >11 000 fledglings that have been banded within the refuge over the last decade (Harris, unpubl. data).

ENVIRONMENTAL EFFECTS ON BAND RESIGHTINGS

Although we banded a considerable number of Brown Pelicans, we observed a relatively low proportion of them. To compare our average of <1% of pelicans banded by us and tallied in randomly surveyed groups to the proportion of our banded birds we could have observed, we first estimated the number of birds in the study area on the basis of two adults (individuals 3 or more years old) per nest (3450 nests; LDWF, unpubl. data) and the ratio of 36% 1- or 2-year-olds to 64% adults calculated from our adjusted age-class counts (Fig. 2). The ratio of adults to subadults and the number of nesting adults equates to 10 820 pelicans within the archipelago, provided that all adults were members of nesting pairs. If we assume no unobserved mortality or emigration of banded birds, there should have been 1413 of our banded individuals present (1177 chicks banded on Raccoon and Wine islands, less five of those that died, and 63 banded at Rabbit Island outside our survey area, plus 304 banded surviving chicks that were moved from Raccoon Island to Whiskey Island from 2007 to 2009 as part of a concurrent translocation study [Walter et al. 2013] but were not considered for any other analyses in this study). The proportion of banded birds to the population total (1413 bands/10 820) suggests that we banded approximately 13% of the population by 2010, if all of these assumptions are correct. This is evidently not the case, for we estimated that we should have observed 28.3 times more bands than we did, so unobserved mortality and/or emigration was considerable. Although we observed few banded pelicans, as described above we suspect we encountered the majority of banded pelicans present.

The low rate of detection may be in part due to biases associated with our limited survey area within the Isles Dernieres. Notably, we observed considerably fewer pelicans banded on Wine (6%) than banded on Raccoon (9%). In assessing factors that may have reduced encounters of pelicans from Wine Island, it may be instructive to compare environmental conditions over time on Raccoon and Wine islands and evaluate how conditions may have influenced patterns of band resighting.

Despite our extensive band-resighting efforts, our surveys that were limited to the Isles Dernieres likely failed to detect individuals that could have flown and remained outside our

study area. Raccoon Island is relatively isolated, and no barrier islands exist to the west within Louisiana. In contrast, several islands lie to the east of Wine Island, including Timbalier Island, only 6 km away. Therefore, on the basis of proximity, pelicans from Wine Island had more loafing locations available to them outside of our study area, which could have resulted in their low rate of detection. This possibility of movement away from natal areas is supported by 43% of our unique band observations being of Brown Pelicans that fledged 150 to 250 km away from the Isles Dernieres (e.g., Rabbit Island and the Breton NWR).

Conditions at the colony may have also influenced the proportions of bands we detected. In fall 2008, after we had completed banding for the year, hurricanes Gustav and Ike severely degraded habitat within the Isles Dernieres. In a concurrent study we assessed the Brown Pelican's use of nest substrates, habitat availability, and land-loss trends and found the hurricanes' effects on Raccoon and Wine islands differed, particularly in regard to availability and use of woody vegetation as nest substrates (Walter et al., unpubl. data). On Raccoon Island, pelicans built nests predominantly in black mangroves (*Avicennia germinans*). Within 1 month following the hurricanes mangroves began to recover, whereas at Wine Island woody vegetation, composed completely of marsh elder (*Iva frutescens*), declined over the following year. Furthermore, hurricane-induced land loss in areas of nesting was much more pervasive on Wine Island than on Raccoon Island.

As Brown Pelicans remaining within our study area expressed natal site fidelity, birds banded on Raccoon and Wine Islands in 2008 and 2009 may have returned to their respective natal islands in subsequent years. Birds returning to Raccoon Island would have found habitat conditions and nesting activity similar to that before the fall 2008 hurricanes and may have been compelled to remain at their natal island. Conversely, birds banded on Wine Island returning to their natal colony would have discovered diminished numbers of pelicans nesting on low-lying and degraded vegetation that rendered nests susceptible to tidal flooding. Although of the rate of nesting by 1- and 2-year-old Brown Pelicans is low (Shields 2002), subadults from the 2008 and 2009 cohorts on Wine were unlikely to breed in 2009 and 2010. In other colonial seabirds, subadults assess environmental conditions through "public information" on active colonies by monitoring numbers of nesting adults and nest success (Atwood and Massey 1988, Forbes and Kaiser 1994), as numbers of nestlings near the end of a breeding season likely offer a better indication of site quality than do numbers of nesting adults at the beginning of the next season (Danchin et al. 1998, Doligez et al. 2002). As nesting adults increasingly avoided unstable conditions on Wine Island in 2009 and 2010, our banded subadult pelicans may have also expressed a similar sensitivity to poor habitat conditions and responded by emigrating out of our study area. If this is the case, it provides a plausible explanation for the number of pelicans from Wine Island being reduced in comparison to those on Raccoon Island.

APPARENT SURVIVAL

Despite uncertainty in estimates due to large confidence intervals, there is an overall trend of decreased apparent survival one of 1-year-old Brown Pelicans in successive years, on the basis of averaging of multiple models that the data support. This potential decrease could be based on a reduced rate of band detection over time that may be due to either chick mortality or emigration outside of our band-survey area. Although our data do not allow us to distinguish between mortality and emigration, differences in emigration between birds hatched on Raccoon and Wine islands, for reasons discussed above, may be at least as plausible as differences in survival. It is also possible that a decline in survival of birds from Wine Island was greater, and particularly for 1-year-olds from 2008; the estimate of survival of this cohort was considerably lower than that of 1-year-olds hatched in 2007. A difference hurricane-induced mortality of pelicans from Raccoon and Wine islands may explain differences in our survival estimates.

The low elevation and vegetation heights on Louisiana's barrier islands offer birds little protection during hurricanes, when chicks may die (McNease et al. 1992). In the fall of 2008, hurricanes Gustav and Ike affected the study sites. Because Hurricane Ike made landfall in Texas more than 350 km west of our study sites (Stormpulse 2008), its effects on Raccoon and Wine islands were likely similar. Hurricane Gustav, in contrast, passed through the middle of the study region (Stormpulse 2008), and the right quadrant of the hurricane passed over Wine Island. Hurricanes in the Northern Hemisphere rotate counterclockwise, so wind speeds and wave heights are typically greatest in the upper right quadrant of a storm's path. Regions lying on this side of hurricanes commonly experience more damage than does the left quadrant (Doyle et al. 1995). All chicks we banded in 2008 were able to fly at the time Hurricane Gustav passed through the Isles Dernieres. Yet if chicks banded on Raccoon and Wine islands that summer were loafing at their respective natal islands, as our study suggests, their mortality at Wine Island may have been greater mortality. If this were the case, it would support our survival estimates for Wine Island being lower than that for Raccoon Island.

At both Raccoon and Wine Islands, probabilities of survival 2- and 3-year-old pelicans were typically greater than those of 1-year-olds. Similarly, Schreiber and Mock (1988) reported that 70% of Brown Pelicans die within the first year after hatching, suggesting younger birds are at a considerable risk of mortality. In our data, the probabilities of survival of 1- and 2-year-olds banded in different years were similar. Yet when we pooled 3-year-olds with two-year olds, the probability of survival of this age class was higher. As mentioned above, these trends must be assessed with caution, given the uncertainty associated with our results. Nevertheless, knowing that younger individuals may be most susceptible to mortality can provide useful information to conservation plans focused on decreasing Brown Pelicans' risk of mortality.

MANAGEMENT APPLICATIONS

In our study, banded birds that remained within our study site were most commonly found at their natal island, suggesting these sites represent habitat more valuable than non-colony sites. Furthermore, other research in Louisiana has found that, despite a landscape comprising several dozen islands, adult Brown Pelicans repeatedly nest on specific islands for several successive years rather than frequently shifting to new islands (Visser and Peterson 1994). Despite the value of maintaining multiple colony sites, in the face of with limited resources for management and restoration it may prove most beneficial to focus conservation efforts on islands with high potential for reproduction and low rates of land loss. However, Brown Pelicans also rested on non-colony islands, suggesting loafing areas also hold habitat value. Fortunately, a wide variety of restoration practices have been successfully implemented to the benefit of maintaining nesting colonies of the Brown Pelican in Louisiana (McNease et al. 1992, Visser and Peterson 1994, Holm et al. 2003, Fearnley 2008).

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