Response of waterbird colonies in southern Louisiana to recent drought and hurricanes

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Abstract
Although hurricanes have been implicated in causing shifts in waterbird use of individual colonies, little is known about whether or not these effects are consistent across broader areas affected by a storm. We examined the effects of Hurricane Rita, and to a lesser extent Katrina, and a subsequent drought, on the nesting activity of waterbirds across colonies located in southern Louisiana. Using ground counts, we compared changes in numbers of nesting pairs between 2005 and 2006, the years encompassing the hurricanes and drought, with changes between 2004 and 2005. Following the hurricanes, colonies were more likely to become inactive or experience large shifts in numbers of nesting pairs, compared with the period before the hurricanes. Although one third of the surveyed colonies became inactive following the hurricanes, total numbers of nesting birds of most species increased. We hypothesize that these increases were the result of birds shifting from damaged to active colonies. Colony use was negatively associated with the maximum wind speeds experienced at each site, apparently as a result of damage to nesting habitat. There were no associations of colony use with either storm-related flooding or localized rainfall during the drought; however, this may be due to manipulation of water levels by management agencies. Our results suggest that monitoring colonies across a broad area is necessary to understand the influence of hurricanes on the nesting activity of waterbirds.

Introduction
If the world climate continues to warm, the frequency and intensity of hurricanes is expected to increase (Michener et al., 1997; Webster et al., 2005; Holland & Webster, 2007) although the link between climatic change and hurricane severity is uncertain (Donnelly & Woodruff, 2007; Nyberg et al., 2007). An increase in the frequency of intense storms is especially problematic for inhabitants along the northern coast of the Gulf of Mexico, where rapidly rising relative sea levels are leading to increased coastal flooding and saltwater intrusion (Gornitz, 1995). Among the wildlife potentially influenced by hurricanes and associated saltwater intrusion are colonially nesting wading birds (order Ciconiiformes), neotropic cormorant Phalacrocorax brasilianus and anhinga Anhinga anhinga. Although most major storms occur after the cessation of reproduction by these colonially nesting waterbirds, hurricanes have the potential to alter conditions in and around colonies and thereby affect colony success the following breeding season (Shepherd et al., 1991; Michener et al., 1997).

In 2005, southern Louisiana experienced two major hurricanes, Katrina (29 August, maximum wind gusts at a landfall of 209 km h⁻¹) and Rita (24 September, maximum wind gusts at a landfall of 225 km h⁻¹). Extensive areas of coastal Louisiana, well away from areas of high winds, experienced storm-related flooding, with seawater intruding on normally freshwater marshes and rice fields. Following the hurricane season, southern Louisiana experienced a severe drought. The National Weather Service station at Lake Charles Louisiana recorded 34.5 cm of rain between November 1, 2005 and April 30, 2006; the normal average rainfall for this period is 63.9 cm. In spring 2006, amateur and professional ornithologists reported that several large colonies were no longer active. Given the large contribution made by colonies in southern Louisiana to the continental populations of several waterbird species (Martin & Lester, 1990), widespread collapse of colonies in hurricane-affected areas could have implications extending beyond the coastal zone of the state.

A multitude of factors may have affected breeding activity at individual colonies in the season that followed the hurricanes. Storms could alter colony sites, through the destruction of nesting habitat by wind and storm surge (Shepherd et al., 1991). Storm surge could also deposit saltwater in wetlands around colonies. Saltwater could change foraging habitats, resulting in insufficient resources to support the reproductive activity of colonial waterbirds dependent on freshwater invertebrates (Johnston & Bildstein, 1990; Shepherd et al., 1991; Michener et al., 1997).
In Louisiana, saltwater intrusion by storm surges also resulted in massive fish kills in the coastal marshes and swamps. The drought following the hurricane exacerbated this problem as natural rainfall did little to reduce salinities. Due to high salinity, destroyed infrastructure and high fuel costs, many farmers in areas experiencing storm surge did not pump water into fields normally used for rice and crayfish aquaculture. Normally such fields are thought to be responsible for supporting high numbers of wading birds in southern Louisiana (Fleury & Sherry, 1995; Huner, Jeske & Norling 2002). The acreage flooded for rice production in coastal parishes (equivalent to counties in other states) in south-western Louisiana in spring 2006 was 40% of the acreage in 2005 (J. Saichuk, pers. comm.).

Our objective was to examine changes in colony use following hurricanes Rita and Katrina. For the two nesting seasons before the hurricanes, we had made ground counts of colonies across southern Louisiana. Thus we had pre-storm survey data to determine whether the numbers of nesting birds had declined following the hurricanes. Furthermore, because hurricane-induced wind and flooding, as well as effects of the drought, varied across southern Louisiana, it was possible to examine whether these factors influenced nesting activity across a broad landscape rather than at single colonies (e.g. Shepherd et al., 1991).

Materials and methods

Changes in colony use

Censuses were conducted on colonies located in the southern Louisiana parishes of Cameron, Vermillion, Iberia, St Martin and Assumption. This region was most heavily affected by Hurricane Rita, although the eastern portion of the study area experienced high winds and storm surge from Katrina. Colonies chosen for counts were historically active, and accessible by foot, boat or airboat. Most of these colonies could be counted using spotting scopes without the need to enter the colony and disturb nesting birds.

All colonies included in this study were located in a mixture of trees or shrubs growing over and surrounded by water, except for one site that consisted of birds nesting on elevated platforms. All of these nest sites are susceptible to damage during high winds and storm surge. In general, larger bodied species such as great egret Ardea alba, great blue heron A. herodias, roseate spoonbill Platalea ajaja, anhinga and neotropic cormorant nested in trees, while smaller bodied species such as little blue heron Egretta caerulea, cattle egret Bubulcus ibis and snowy egret Egretta thula nested in lower brush. However, there is considerable variation within each species with regard to nest site selection. All the colonies were used by multiple species; however, the composition of the species varied greatly among sites and years.

As part of another study (Green et al., in press), 19 active colonies had been counted from the ground or boats (hereafter referred to as ground counts) in 2004. Efforts were repeated in 2005 but three additional newly established colonies were included. With the exception of one colony that was inaccessible due to hurricane damage, all colonies counted in 2005 were included in the 2006 census. Because we were examining changes in colony use, our comparisons involved colonies active in one year that were sampled again the following year. Therefore our analyses of colony use changes between 2004 and 2005 involved 19 colonies; 21 colonies were used in the 2005 and 2006 comparison. We attempted to count each colony twice, once during the first 3 weeks of May and again in the first 3 weeks of June (two colonies in both 2004 and 2005 were only counted once).

To avoid disturbance of nesting birds, all counts were conducted from the periphery of the colony. All but one colony were counted using the marked subsample method to derive estimates of breeding pairs for each colony (Green et al., in press). This approach has the advantage of estimating the number of birds not observed by a single observer; this bias creates a systematic underestimation of colony size. Two observers, working in tandem, made independent counts of each colony (or multiple subsections of large colonies). Each observer counted the number of nests in each colony independently; however, counts were done at the same time by both observers. The observers counted only occupied nests and assumed that each nest represented one breeding pair. For each nest counted, the location of the nest within the colony was plotted on a colony map. Nest count, nest location within the colony and species composition were then compared between the two observers at the completion of each colony count to determine which nests were counted by both observers. Occupied nests counted by both observers were treated as recaptures for the purpose of estimating the number of breeding pairs that were not detected by either observer. Estimates of the numbers of birds of each species in the colony were made with a Lincoln–Peterson estimator (Chapman, 1951; Seber, 1973). Estimates for nesting pairs made using this approach were typically 31% larger than the average number of birds counted by either observer (Green et al., in press). Estimates were made for individual species except in the case of ibis in the genus Plegadis; observations of Plegadis chihi and Plegadis falcinellus were combined because it was sometimes difficult to differentiate these species. We used these estimated numbers of nesting birds in the analysis reported here, rather than the number counted directly by observers to address systematic undercounting; however, use of either measure of the number of nesting birds did not alter the results of our statistical analysis of annual variation in bird numbers or their association of weather events.

One colony, Lake Martin, was too wide to observe all birds from the periphery, making the marked-subsample count method infeasible. This colony was subsampled by making counts from eight fixed points along its periphery. The total number of pairs of each species nesting within 30m of each observation point was determined. Because these counts were made by a single observer, they may be biased downward compared with counts made with the marked-subsample approach; this bias was probably small because all nesting birds within 30m could be easily...
counted. More importantly, colony counts were not compared with each other, but only to other counts from the same colony in different years. Because an individual colony was counted with the same approach every time it was sampled, bias associated with sampling approach would have little effect on our analysis.

For purposes of statistical analysis, counts made in May and June were averaged to obtain one value per year for each colony. While this obscures some seasonal variation in use by individual species, bias in species counts should be the same across colonies used by that species. It would be inappropriate to treat monthly counts as independent observations, and preliminary analysis indicated that separate analysis involving May counts and June counts resulted in the same conclusions as did the analysis of average counts presented here.

Colony changes were assessed using two measures. First, we estimated the proportion of colonies that became inactive from one year to the next. We defined a colony as inactive if it had <2 nesting pairs of waterbirds. We compared the proportion of colonies that became inactive in 2005 with those that became inactive in 2006 using a Fisher’s exact test.

Second, we determined the proportion of colonies that experienced an increase or decrease in numbers of nesting pairs. We established a change in numbers of ≥40% as a threshold to determine which colonies experienced major shifts in numbers. Colonies that changed by <40% were considered to be stable. We chose this threshold because such changes were substantially larger than any potential measurement error associated with our estimates of colony size. This measure of change in colony size included not only colonies that were active one year and failed the next, but also colonies that were active both years but experienced large differences in numbers of nesting pairs. We used a $\chi^2$ test to evaluate the hypothesis that the proportions of colonies experiencing increases or decreases differed between 2004–2005 and 2005–2006.

Environmental correlates of colony use

We made several predictions to examine why some colonies active in 2005 may have failed or decreased in size in 2006. First, we predicted that both the probability of becoming inactive and the number of birds using a colony would be negatively associated with local maximum wind speeds and saltwater intrusion from storm surge. High wind speeds are associated with tree fall and limb damage, which can reduce the quality of nesting habitat (Shepherd et al., 1991). The estimated maximum wind gust experienced by a colony during either of the two hurricanes was obtained from maps from the Louisiana Geographic Information Center, based on data from the National Weather Service.

We predicted that storm surge might affect colony activity because most of these sites were located in areas where normal salinities ranged from fresh to slightly brackish. A rapid change in salinity associated with storm surge could dramatically affect prey populations. To estimate the influence of saltwater intrusion on the colonies, we used maps from the Federal Emergency Management Agency to estimate the proportion of the area around each colony that was flooded by the storm. For this purpose, we defined the area around a colony as that formed by a circle, with a radius of 20 km, centered over the colony. Although there are exceptions (Shepherd et al., 1991), the majority of wading birds nesting at a site typically forage within 20 km of the colony (Smith, 1995; Custer & Galli, 2002; Custer, Suarez & Olsen, 2004).

Because of a drought during the winter and spring of 2005–2006, we predicted that colonies with low rainfall would be more likely to fail or become smaller than colonies where rainfall was more abundant. Rainfall is important in refilling natural wetlands and reducing soil salinities from areas that experience saltwater intrusion. The influence of localized drought conditions was assessed by determining total rainfall between November, 1 2005 and April, 30 2006. We chose this 5 month period because earlier rainfall would have measured the effects of the hurricanes, and later rainfall would have had little impact on colony establishment, which typically occurred before May. We obtained data from the NOAA Climatic Data Center for the National Weather Service recording station located nearest to each colony. A station was located within 21 km of all colonies; most stations were <10 km from a colony. On occasions that a station was inoperative for one or more days during the 5 month sample period, the rainfall recorded at the next closest operable station was included in the estimate of total rainfall.

We used point biserial correlation ($r_{pb}$) to determine if colony inactivity in 2006 was associated with wind speed, storm surge or local rainfall. We used Spearman’s rank correlation ($R$) to examine whether changes in the number of nesting pairs of all wading birds between 2005 and 2006 were associated with wind speed, storm surge or precipitation. This correlation analysis was also conducted for individual species. However, because power of the analysis depends on the number of colonies examined, only species found in at least 15 colonies between 2005 and 2006 were analyzed: great egret, great blue heron, roseate spoonbill and neotropic cormorant.

Results

Changes in colony use

We found that the proportion of previously active colonies that failed in 2006 was higher than the proportion that failed in 2005 (Table 1). Of 19 colonies in 2004, none became inactive in 2005; however, of the 21 active colonies counted in 2005, six became inactive in 2006 (Fisher’s exact test, $P = 0.021$, Table 1).

We observed a similar trend of large shifts in colony size that was observed in colony abandonment. Proportions of colonies experiencing substantial increases and decreases in nesting pairs between 2005 and 2006 were different than between 2004 and 2005 ($\chi^2 = 6.45; P = 0.040$).
2004 and 2005, 58% of colonies were relatively stable, changing by <40% from the previous year (Table 1). Over the same period, 16% of colonies experienced large decreases in size and 26% experienced large increases. Between 2005 and 2006, the period bracketing hurricanes and drought, only 19% of the colonies were relatively stable. Seven colonies (33%) experienced large decreases; this included the six that became inactive (Table 1). More interesting, 48% of the colonies increased their numbers of nesting pairs by >40% of their pre-hurricane numbers.

Although a number of active colonies in 2005 became inactive following the hurricanes and drought, the total number of birds nesting in censused colonies increased by 86% (Table 2). The number of nesting pairs increased for several species. The numbers of nesting great egrets, tricolored herons *Egretta tricolor*, roseate spoonbills, neotropic cormorants and anhingas more than doubled between 2005 and 2006. Some large changes in the numbers of pairs occurred between 2004 and 2005; however, few were as dramatic as those observed between 2005 and 2006 (Table 2).

**Environmental correlates of colony use**

Although 29% of the colonies active in 2005 failed in 2006 (Table 1), the failures were not strongly correlated with weather events. During the two storms, colonies experienced maximum estimated wind speeds ranging between 97 and 177 km h\(^{-1}\). Likelihood that an active colony in 2005 became inactive in 2006 was not positively associated with wind speeds during recent hurricanes (\(r_{pd} = 0.17, P = 0.237\)). The proportion of area around a colony flooded by storm surge varied between 0.1 and 1.0; however, whether a colony became inactive after a hurricane was not positively associated with the degree of storm surge (\(r_{pd} = -0.22, P = 0.670\)). Winter and spring rainfall varied from 28.5 to 45.5 cm. Colony inactivity was not negatively associated with post-hurricane rainfall (\(r_{pd} = 0.01, P = 0.996\)).

There was a significant, negative correlation between wind damage and changes in breeding pairs between 2005 and 2006 (\(n = 21, R = -0.421, P = 0.005\)). There were strong negative associations between wind speed and changes in breeding pairs of great egrets (\(n = 19, R = -0.485, P = 0.018\)) and neotropic cormorants (\(n = 15, R = -0.545, P = 0.018\)). No significant relationships between changes in numbers of breeding pairs and wind speed were found for the great blue heron or roseate spoonbill (\(P > 0.10\)). Similarly, no strong relationships were noted between changes in numbers of nesting birds and local storm surge or local rainfall.

**Table 1** Numbers of colonies in southern Louisiana becoming inactive or experiencing large changes in the numbers of nesting pairs between 2004 and 2005 and between 2005 and 2006.

<table>
<thead>
<tr>
<th>Species</th>
<th>2004-2005</th>
<th>2005-2006</th>
<th>n</th>
<th>%</th>
<th>n</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colonies sampled</td>
<td>19</td>
<td>21</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Colonies that became inactive(^a)</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>29</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Active colonies that:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Decreased by &gt;40%(^b)</td>
<td>3</td>
<td>16</td>
<td>7</td>
<td>33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Increased by &gt;40%</td>
<td>5</td>
<td>26</td>
<td>10</td>
<td>48</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Changed by &lt;40%</td>
<td>11</td>
<td>58</td>
<td>4</td>
<td>19</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^a\)A colony was considered inactive if it had <2 nesting pairs of waterbirds once the counts from the May and June surveys were averaged together.

\(^b\)Includes colonies that became inactive as well as those that remained active but were much smaller than the previous year.

**Table 2** Numbers of colonies surveyed in southern Louisiana in which a species was actively nesting (\(\geq 2\) nesting pairs) and the total number of nesting pairs, across all colonies, for the 10 most common species.

<table>
<thead>
<tr>
<th>Species</th>
<th>2004(^c)</th>
<th>2004(^d)</th>
<th>2005(^e)</th>
<th>2005(^f)</th>
<th>2006(^g)</th>
<th>2006(^h)</th>
<th>2006(^i)</th>
<th>2006(^j)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Great egret</td>
<td>18</td>
<td>1537</td>
<td>17</td>
<td>1461</td>
<td>18</td>
<td>1747</td>
<td>13</td>
<td>3021</td>
</tr>
<tr>
<td>Great blue heron</td>
<td>7</td>
<td>61</td>
<td>9</td>
<td>84</td>
<td>18</td>
<td>9</td>
<td>86</td>
<td>7</td>
</tr>
<tr>
<td>Little blue heron</td>
<td>6</td>
<td>41</td>
<td>4</td>
<td>66</td>
<td>18</td>
<td>9</td>
<td>3</td>
<td>69</td>
</tr>
<tr>
<td>Snowy egret</td>
<td>13</td>
<td>101</td>
<td>9</td>
<td>133</td>
<td>28</td>
<td>113</td>
<td>6</td>
<td>27</td>
</tr>
<tr>
<td>Cattle egret</td>
<td>14</td>
<td>441</td>
<td>11</td>
<td>598</td>
<td>16</td>
<td>598</td>
<td>11</td>
<td>464</td>
</tr>
<tr>
<td>Tricolored heron</td>
<td>5</td>
<td>20</td>
<td>5</td>
<td>29</td>
<td>5</td>
<td>29</td>
<td>7</td>
<td>119</td>
</tr>
<tr>
<td>Roseate spoonbill</td>
<td>10</td>
<td>105</td>
<td>8</td>
<td>168</td>
<td>18</td>
<td>173</td>
<td>9</td>
<td>392</td>
</tr>
<tr>
<td><em>Plegadis ibis</em>(^c)</td>
<td>2</td>
<td>10</td>
<td>4</td>
<td>25</td>
<td>2</td>
<td>25</td>
<td>6</td>
<td>252</td>
</tr>
<tr>
<td>Neotropic cormorant</td>
<td>11</td>
<td>352</td>
<td>14</td>
<td>553</td>
<td>12</td>
<td>514</td>
<td>8</td>
<td>1406</td>
</tr>
<tr>
<td>Anhinga</td>
<td>7</td>
<td>28</td>
<td>2</td>
<td>14</td>
<td>2</td>
<td>14</td>
<td>4</td>
<td>21</td>
</tr>
<tr>
<td>Total (all species)(^d)</td>
<td>19</td>
<td>2712</td>
<td>19</td>
<td>3218</td>
<td>19</td>
<td>3249</td>
<td>15</td>
<td>6053</td>
</tr>
</tbody>
</table>

\(^c\)Based on 19 colonies sampled in 2004.

\(^d\)Based on 21 colonies sampled in 2005.

\(^e\)Based on 21 colonies sampled in 2005 and 2006. Three colonies sampled in 2005–2006 were not surveyed in 2004 because they had been inactive or not discovered; one sampled in 2004–2005 could not be sampled in 2006 due to a hurricane-related closure.

\(^f\)White-faced ibis *Plegadis chihi* and glossy ibis *Plegadis falcinellus* combined.

\(^g\)Includes small numbers of green herons *Butorides virescens*, yellow-crowned night herons *Nyctanassa violacea*, black-crowned night herons *Nycticorax nycticorax* and white ibis *Eudocimus albus* that typically were found in one to two active colonies each year.
Discussion

Changes in colony use

The effects of hurricanes on forest-dwelling species have been widely studied (e.g. Wiley & Wunderle, 1993; Wunderle, 1995; Torres & Leberg, 1996; Greenberg & Lanham, 2001; Tejeda-Cruz & Sutherland, 2005). However, investigations of hurricane impacts on nesting populations of colonial waterbirds are apparently more limited (Shepherd et al., 1991; Michener et al., 1997). Furthermore, these studies focused on the influence of Hurricane Hugo on a large colony in South Carolina. Therefore, little information exists on how a significant storm event might affect the dynamics of multiple colonies across a landscape. The 22 colonies we censused represent 42% of the colonies known to be active in the five parish study area, based on results of an independent aerial survey (Green et al., in press). While a complete ground survey of colonies in the region was not possible, we have a sufficient sample to obtain insight into how the 2005 hurricanes affected regional nesting activity.

Our data strongly suggest that colonies were much less stable between years in which storms occurred than between years before the storms. Although many colonies in southern Louisiana were abandoned following the storms, the remaining colonies increased in size. Colonies that became inactive or experienced large declines in 2006 represented 32% of the colonies known to be active in the five parish study area, based on results of an independent aerial survey (Green et al., in press). While a complete ground survey of colonies in the region was not possible, we have a sufficient sample to obtain insight into how the 2005 hurricanes affected regional nesting activity.

Relocation of birds from one surveyed colony to another does not explain why several species exhibited large increases in numbers of nesting pairs between 2005 and 2006 including great egrets, tricolored herons, roseate spoonbills, Plegadis ibis and neotropic cormorants. It is difficult to explain why some species seemed to have increased in abundance at surveyed colonies while others remained relatively stable. The species with large increases differ greatly in their habitat requirements for foraging and nesting. We suggest that increases at the remaining active colonies were caused by immigrants from colonies we did not survey or from colonies that were outside our immediate study area. It is important to note that our study area represents only about a quarter of the portion of coastal Louisiana affected by the 2005 storms and subsequent drought. Aerial surveys in 2006 indicate that many colonies east of our study area appeared to be abandoned due to drought or hurricane damage (C. Jeske, pers. comm.). This suggests that even a broader area than our five parish study area is needed to assess the effects of severe weather events on waterbird nesting activity.

Environmental correlates of colony use

Of the three environmental factors measured, only maximum wind speed was strongly associated with colony use. Changes in number of nesting birds had a strong negative association with maximum wind speed. All of the censused colonies in the immediate storm track of Hurricane Rita were abandoned. Furthermore, many colonies located to the immediate northeast of the track, where the winds were very strong, were inactive or reduced in size. During counts, we observed much destruction of nesting vegetation at these sites.

Changes in the numbers of two species, great egrets and neotropic cormorants, exhibited declines in areas of high wind speed. It is possible that the tendency of these species to nest high in the canopy at colony sites makes them especially susceptible to wind damage. Shepherd et al. (1991) also reported decreased numbers of nesting great egrets at a colony experiencing wind damage following Hurricane Hugo. However, both the great blue heron and roseate spoonbill also tend to nest high in tree canopies, so other factors might be influencing species-specific use of colonies.

Although we hypothesize that vegetation damage due to wind speeds affected colony activity following the hurricanes, we do not have direct measures of wind damage, and it is possible that wind speeds were associated with some other environmental changes that affected the birds. We also do not want to completely discount the influence of saltwater intrusion and drought. We saw no statistical evidence that these factors were associated with bird use of colonies, but suggest that the complexities of the landscape of coastal Louisiana may have obscured the potential importance of these factors relating to foraging habitat. Of 17 colonies located within 65 km of Rita’s storm track, 11 that remained active in 2006 were located in large impoundments managed by the US Fish and Wildlife Service and Louisiana Department of Wildlife and Fisheries. Some of these impoundments were managed to reduce salinity through drawdowns after initial storm surges; subsequent pumping of freshwater and other approaches were used to restore water levels in the impoundments. These actions probably helped restore foraging habitats damaged by saltwater intrusion as well as maintained water below colonies at some sites. Maintenance of foraging habitats would be especially important during a time when many rice and crayfish farmers were not able to flood their fields. Thus, colony dynamics in the coastal zone of Louisiana was likely influenced not only by the hurricanes and drought, but also by post-hurricane management of water levels.

The increased number of Plegadis ibis in censused colonies is of special interest because nesting ibis are apparently sensitive to drought and saltwater intrusion (Bildstein et al., 1990; Shepherd et al., 1991; Michener et al., 1997), and ibis are heavily dependent upon rice and crayfish aquaculture (Fleury & Sherry, 1995). Thus we expected their numbers to decrease in response to hurricanes. We suspect that increases...
in ibis following the hurricanes were the result of individuals abandoning nesting sites located in stands of bulrush \((Juncus\; spp.\; and\; Scirpus\; spp.)\). We could not count ibis nesting in bulrush with our approach, because it would have involved entering colonies and caused extensive disturbance of birds. Bulrush stands, that had supported large numbers of nesting \(Plegadis\) ibis, were heavily damaged by high winds and storm surge. This damage could have forced ibis to nest in shrubs and trees where we could count them.

Our interpretation of changes in colony use among years assumes they reflect differences in choices of breeding site selection and not variation in recruitment or mortality patterns. We make this assumption because we have no reason to believe that hurricanes and drought would lead to higher net population growth between 2005 and 2006 than occurred between 2004 and 2005. One might hypothesize that high winds might have caused mortality, explaining the negative correlation between changes in colony size between 2005 and 2006 with positive wind speed. However, the storms and drought did not occur until after the 2005 nesting season and there were no records of widespread mortality of any of the study species following the storm or during the drought. Birds using colonies are highly vagile and most probably avoided storms and drought through movement. Although our ability to interpret the trends in numbers of breeding pairs would be strengthened by estimates of net productivity of each site, the more parsimonious explanation for our results is that they are due to shifts in regional nesting activity from sites damaged by high winds to less damaged colony sites.

To understand the effects of the hurricanes on nesting activity, our analysis relies heavily on comparison of changes occurring between two years before the hurricanes. This is not ideal as it is impossible to know whether the 2004–2005 period represents a typical pair of years in terms of colony stability. At best, we conclude that the two sets of years experienced very different levels of colony dynamics, and can speculate on the nature of the differences; however, long time-series are needed to better distinguish between the effects of random fluctuations and more extreme weather events (Hsieh \textit{et al.}, 2005). Furthermore, given the varied responses of colonies in hurricane- and drought-impacted areas, it is clear that studies that monitor individual colonies will provide little information on the dynamics of colonial nesting bird populations following major weather/climate events. Our understanding of the influence of changing weather on regional colony dynamics will be greatly improved by long temporal series of high-quality census data from the majority of colonies in the region. Given the threats that coastal regions are likely to experience in the coming years due to predicted climate change and sea level rise, it is important that we begin to develop this dataset.

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