

ORNITOLOGIA NEOTROPICAL 21: 383–396, 2010

© The Neotropical Ornithological Society

EFFECTS OF WEATHER AND WATER LEVEL ON REPRODUCTION OF COLONIAL WATERBIRDS IN LAGUNA MAR CHIQUITA - BAÑADOS DEL RÍO DULCE (CENTRAL ARGENTINA)

Ricardo Torres¹, Pablo Michelutti², Jael Dominino³, José León⁴, Arnaldo Mangeaud⁵, Andrés Rodríguez⁶, Cecilia Pozzi⁶, Gonzalo Plencovich⁶, Mariana Pagot⁶, & Gerardo Hillman⁶

¹Museo de Zoología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Vélez Sarsfield 299 (5000) Córdoba, Argentina. E-mail: rtorres444@yahoo.com.ar

²Tucumán 296 (5143) Miramar, Córdoba, Argentina.

³Administración de Parques Nacionales, Delegación Centro, Ricchieri 2298 (5000) Córdoba, Argentina.

⁴Paso de los Andes 95 A (5500) Mendoza, Argentina.

⁵Cátedra de Estadística, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Vélez Sarsfield 299 (5000) Córdoba, Argentina.

⁶Laboratorio de Hidráulica, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Bv. Juan Filloy s/n Ciudad Universitaria (5016) Córdoba, Argentina.

Resumen. – Efectos del clima y el nivel del agua sobre la reproducción de aves acuáticas coloniales en Laguna Mar Chiquita - Bañados del Río Dulce (Argentina Central). – En el presente trabajo se exploró la relación entre factores relacionados al clima y la reproducción de aves acuáticas coloniales en un extenso humedal del centro de Argentina, el sistema Laguna Mar Chiquita - Bañados del Río Dulce. Debido a sus distintos requerimientos ecológicos, las diversas especies presentaron respuestas disímiles a las variaciones de los factores climáticos, los cuales a su vez actúan a distintas escalas espaciales. El éxito reproductivo de casi todas las especies fue negativamente afectado por el viento durante las tormentas que se forman localmente durante el verano. Las variaciones en el nivel del agua, producidas por fenómenos no locales sino ocurridos en la parte alta de la cuenca, a gran distancia del humedal, tuvieron una acción directa sobre el número de especies en colonias. El número de parejas, en cambio, no fue directamente afectado por dichas variaciones, aunque el número de parejas en colonias de la Garcita Azulada (*Butorides striata*) estuvo relacionado al área de hábitat óptimo disponible para la alimentación y nidificación de esta especie, superficie que en definitiva fue regulada por el nivel del agua. La formación de colonias de aves acuáticas estuvo supeditada a niveles estables o con variaciones de hasta 1 m entre un año y el siguiente. Los datos obtenidos presentan implicancias para la biología de la conservación y las estrategias de manejo del agua.

Abstract. – The relationship between climate-related factors in an important extensive wetland of central Argentina (Laguna Mar Chiquita - Bañados del Río Dulce) and colonial waterbirds reproduction was explored. Due to their different ecological requirements, the diverse species responded differently to variations in climatic factors, which in turn interact at different spatial scales. Nesting success of almost all species was negatively affected by storm winds occurring in the region in summer. Water level changes, induced by non-local phenomena occurring in the high basin, at a great distance from the Mar Chiquita–

Dulce River system, had a direct effect on species number in colonies. On the contrary, pair numbers was not directly affected by water level changes, although the pair numbers in the Striated Heron (*Butorides striata*) colonies was related to the area of the feeding and nesting habitat suitable for this species, which was eventually regulated by water level. Waterbirds colony formation depended on water levels that were stable or changed in up to 1 m in consecutive years. The data obtained has implications for biodiversity conservation and water management strategies.

Key words: Mar Chiquita, Bañados del Río Dulce, colonial waterbirds, nesting success, wind, water level.

INTRODUCTION

It is well known that climate is a key factor in the population dynamics of birds, affecting their metabolic rate, behavioral patterns, distribution and movements, nesting success, etc. (Crick 2004, Butler & Taylor 2005; Chambers & Loyns 2006). Birds have to deal with variable climate conditions, both at seasonal and interannual scales, and even with cyclical phenomena at a larger temporal scale (Ware & Thomson 2000, Butler & Taylor 2005). Waterbirds are particularly vulnerable to climate variations (Chambers & Loyns 2006), because they depend on water availability for most of their life requirements; many species, particularly waders, are especially affected by water level changes (Kushlan 1976, 1986, Powell 1987, Dimalaxis & Pyrovetsi 1997, Gawlik 2002).

Understanding the relationship between birds and climate is essential to make predictions on possible future scenarios and to implement mitigation actions accordingly (Crick 2004, Rehfishch *et al.* 2004, Chambers & Loyns 2006). Studies on this subject have been mostly conducted in developed countries that have large databases of meteorological variables and population dynamics of many bird species covering long periods of time. In southern South America such information is scarce or nonexistent. Recently, the results of the first 10 years of the Neotropical Waterbird Census have proved to be a valuable tool for elucidating the movements of several species in this

region (Blanco & Carbonell 2001). Nevertheless, in many places the coverage of the meteorological station network is deficient or its use has been discontinued. Based on fragmentary information, this work attempts to establish the influence of climate-related variables on the reproduction of colonial waterbirds in an extensive and important wetland of central Argentina, the Laguna Mar Chiquita (MC) and Bañados del Río Dulce (BD) system.

METHODS

Study area. The MC-BD system is located in central Argentina (28°50'–31°00'S, 62°10'–63°20'W; Fig. 1). MC is the final collector of the largest South American endorheic basin, with a catchment area of 37,570 km² (Reati *et al.* 1997). The general climate in the basin has been defined as monsoonic subtropical semi-arid, with temperate to warm temperatures and scarce rainfall (700–800 mm) concentrated between October and March. However, rainfall is abundant in the mountains to the west of the basin due to the topographic effect (Bucher *et al.* 2006). Frequent thunderstorms with strong winds of an average maximum speed of over 90 km/h occur in MC-BD system in summer (Fig. 2), with an absolute maximum of almost 137 km/h recorded in January 2003 in the meteorological station of Miramar.

MC is a permanent shallow saline lake of nearly 6000 km² (Reati *et al.* 1997, Rodríguez *et al.* 2006). Affluents of the Dulce River, the

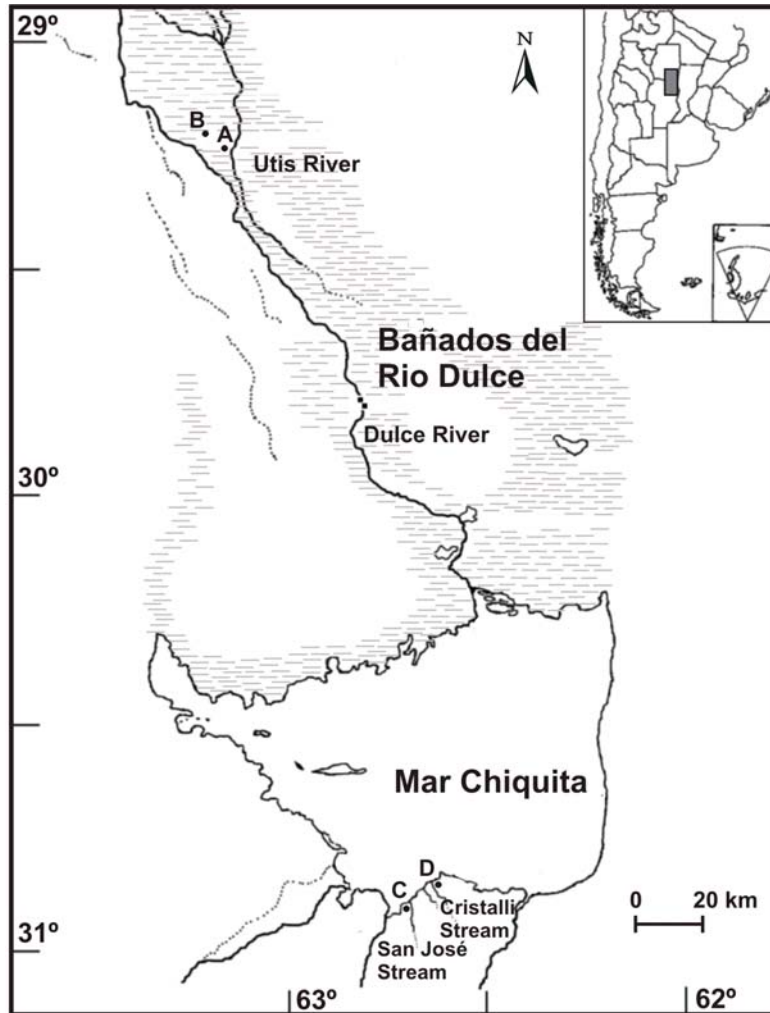


FIG. 1. Geographic location of the Laguna Mar Chiquita – Bañados del Río Dulce system. Black circles indicate relative situation of bird colonies (A: Utis A colony; B: Utis B colony; C: San José colony; D: Cristalli colony).

main tributary, are originated in the mountains to the west of the basin, and the Dulce River ends to the north of MC. Upstream, the Dulce River flow is regulated by a large dam (Embalse de Río Hondo). In its final portion the river floods a great part of the surrounding lands (up to 3500 km², Rodríguez *et al.* 2006) during the summer and autumn, origi-

nating secondary channels and lagoons. Usually, in early winter the water level recedes, and the remnant isolated ponds are dry in early spring. Because there is a marked water deficit at the local level, the water level in MC-BD is mainly controlled by the Dulce River discharge, which depends on the rainfall occurring in the high basin (Rodríguez *et al.* 2006).

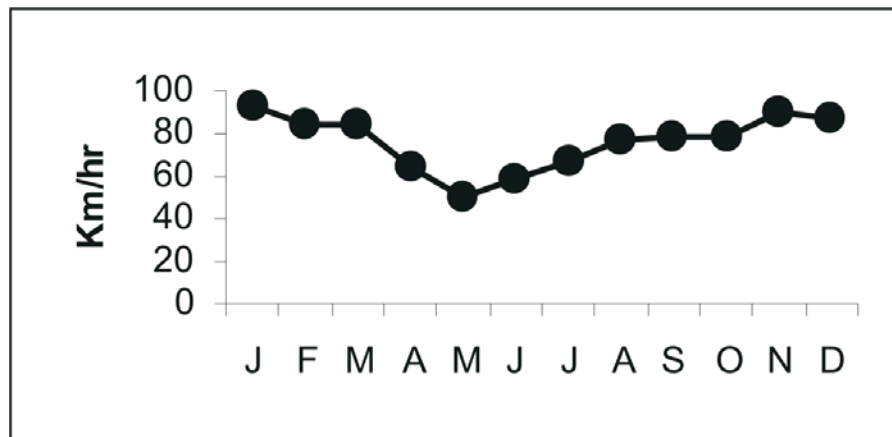


FIG. 2. Mean maximum wind speed in Miramar, Laguna Mar Chiquita, measured in the Miramar Meteorological Station from 2001 to 2005.

Other tributaries and several minor streams flow into MC in the south and southwest coasts (Reati *et al.* 1997). The small flooded area caused by these rivers and streams between October and March is limited by the abrupt slope in those sectors of the coast (RT pers. observ.)

The MC-BD system is characterized by the drastic fluctuations in the flooded area, not only seasonal but also of periods of several years. During the late 1970's, the water level in Mar Chiquita rose notably, increasing the flooded area from 2000 km² to the current values, which were reached in 1982. This increase is related to the rainfall rise in the entire basin (Pasquini *et al.* 2006) and produced changes in the physical characteristics of the lake, mainly in its salt concentration (Piovano *et al.* 2002).

Biogeographically, MC-BD is located in the Chaco region; therefore, the aquatic vegetation is typical of Chacoan wetlands (Sayago 1969, Luti *et al.* 1979, Cabido & Zak 1999, Menghi 2006).

Field work was conducted in two sites:

1. Miramar (30°55'S, 62°04'W). This is the

only coastal town, located on the southern coast of MC. Here the San José and the Cristalli streams flow into the lake (Fig. 1). Stream banks are covered by dense shrubs that are flooded when water level rises. Available rainfall data series of the meteorological station of Miramar include the following periods: January 1986–November 1987, January 1988–August 1993, October 1993, January 1994–June 1996, August–December 1996, April–October 2001, April–May 2002, January–October 2003, January–August 2004, and October 2004–November 2005. Rainfall concentrates between October and April. Monthly water level data were available for the periods: November 1967–October 1997 and February 2001–August 2005. Here, two breeding colonies of the Striated Heron (*Butorides striatus*) were studied.

2. The Utis River (a Dulce River tributary, near the locality of Paso de Los Oscares (29°15'S, 63°11'W; Fig. 1), in northern BD. In this area, grasslands alternate with riparian forests; both are flooded during the wet season (December–May). Waterbird nesting colonies settle on riparian forests or scrublands.

Rainfall has been measured systematically since October 2002 at the nearest meteorological stations: Sumampa (approximately 30 km to the west) and Paso de La Cina (about 70 km to the south). Between 1998 and 2006 the water level was measured, as the distance between surface water and the bridge across Utis River. This measurement was related to the maximum depth of the river at this point. The maximum depth was constant throughout the study period, with the exception of a big water level fall occurred during 2004 and 2005, when the river did not flood the bordering areas. In this site, we studied two colonies of multiple species of herons, egrets, and cormorants.

Field work. Our study was carried out between 1990 and 2004 in Miramar, and between 1998 and 2006 in the Utis river. As colony size in study area varied greatly between sites and years, in the cases that the size of the colonies precludes direct counting of total nest numbers (> 1000 nests), this value was estimated by averaging the number of active nests occurring within 25 randomly selected 100-m² plots, and then multiplying this density value by the area covered by the colony, measured with GPS (Fasola *et al.* 2004). All nests in ten of the 25 plots were marked and visited weekly (MC) or semi-monthly (BD) in order to avoid negative effects of investigator presence on nesting success of birds (Carney & Sydeman 1999). Number of eggs and/or chicks was recorded in each visit. Also, causes of death or loss of eggs and chicks were determined when possible. Nests with broken eggshells and no evidence of fallen nestlings were assumed to have been predated. Eggs that disappeared from tipped or dislodged nests after storms were considered as lost by wind action. Eggs that failed to hatch were opened to determine if they were sterile or if the embryo died before completing development. Clutches with dead embryos in all eggs were

assumed to have been abandoned by parents. Likewise, dead or missing nestlings from nests displaced or dislodged after storms were considered as lost by wind action. Nestlings found dead in nests were assumed to have died of starvation or sibling aggression. The content of all nests was observed directly or with the aid of a 2-m mirror pole.

Analysis of data. Species numbers in colonies and total nest estimates were correlated with changes in annual rainfall and water level at the beginning of clutch. Such analysis addressed only the variation among annual estimates. In Miramar, since Striated Herons fed perching on flooded shrubs at water depths of up to approximately 1 m (Torres 2004), nest number was also correlated with the flooded area between the coastline and up to 1 m deep in an area of 29.70 km², comprising the mouths of the San José and the Cristalli streams. Such flooded area was considered as the potential feeding area of this heron population, and was obtained working on a rectangular grid generated from digitization of the contour lines of the Miramar topographic map (map number 3163-16-4, 1:50,000 scale) of the Instituto Geográfico Militar, and considering the water level at laying, in every breeding season analyzed. This analysis was performed by means of Spring v4.2 software (Cámara *et al.* 1996). In the Utis River area, as in the whole BD, differences in topography of a few centimetres can cause a great difference in flooded area, depending on the changes in water level. There are no topographic maps available with such level of detail for this region. All correlations were performed by means of the Spearman's r coefficient (r_s).

The nesting success of Neotropical Cormorants (*Phalacrocorax brasilianus*), Great Egrets (*Ardea alba*), Cattle Egrets (*Bubulcus ibis*), Striated Herons, and Black-crowned Night Herons (*Nycticorax nycticorax*) was calculated using

the Mayfield method (Mayfield 1975). This method assumes equal survival probabilities throughout the period measured (Erwin & Custer 1982). Nest losses however may vary in different periods of the nesting cycle; thus, success was calculated separately for the egg and chick stages. Incubation lengths (30 days for Neotropical Cormorants, 25 days for Great Egrets, 24 days for Cattle Egrets, 22 days for Striated Herons and 25 days for Black-crowned Night Herons) were obtained from Hancock & Elliot (1978) and Del Hoyo *et al.* (1992). Nestling development was observed until a maximum of 21 days after hatching; after that time, assigning chicks to individual nests became difficult because chicks were already capable of climbing nearby branches. Striated Herons were an exception, since the low nest density allowed us to monitor nestling development until they fledged. Comparisons of nest survival between groups were carried out by the test developed for the Mayfield estimator by Hensler & Nichols (1981).

RESULTS

Miramar. Colonial nesting of Striated Herons occurs in two streams near Miramar: San José and Cristalli Colonies were therefore named San José and Cristalli (Fig. 1). Data of total nest numbers of nine breeding seasons are available for these colonies (breeding seasons from 1990–91 to 1996–97, 2000–01, and 2003–04). Herons nested in only one of the two colony sites each year, with the exception of two breeding seasons in which both sites were used (Fig. 3a). Maximum numbers were 58 active nests in the 1994–95 breeding season, and also 58 pairs in the 2003–04 breeding season. Nesting began in early November (Figs. 4a, b) and fledglings completed development in mid March.

Total nest number was not related to water level at the beginning of egg laying ($r_s =$

0.35; $N = 9$; $p > 0.05$). Nevertheless, almost all the reproductive events occurred after falls or rises of the water level < 1 m with respect to the previous year (Fig. 5a). The maximum numbers were reached with inter-annual changes up to 0.4 m; only small colonies (< 20 pairs) occurred with changes greater than 0.8 m. The potential feeding area had a direct effect on the number of nests ($r_s = 0.71$; $N = 9$; $p < 0.05$). No significant relationships between nest numbers and annual rainfall were observed in eight breeding seasons for which there were rainfall data available ($r_s = -0.63$; $N = 8$; $p > 0.05$).

Nesting success was determined in the San José colony during the four breeding seasons comprised between November 1993 and March 1997. Few pairs nested during the reproductive seasons of 1995–96 and 1996–97, which failed during incubation. Nesting success was the same in 1993–94 and in 1994–95 breeding seasons (Table 1). Taking into account both breeding seasons as one group, no significant differences between egg-stage success and chick-stage success ($Z = 0.81$; $p > 0.05$; Hensler-Nichols test) were observed.

Wind was the main loss factor, both during the egg and chick stages (Fig. 6a). Dead embryos were observed in some eggs that did not hatch in the 1993–94 breeding season. A low number of chicks died of starvation or sibling aggression; the causes of the remaining egg and chick losses could not be determined.

Utis river. We studied breeding of Cattle Egret, Great Egret, Black-crowned Night Heron, and Neotropical Cormorant in this area. In addition, Snowy Egrets (*Egretta thula*), Cooi Herons (*Ardea cocoi*), Striated Herons, Wood Storks (*Mycteria americana*) and Roseate Spoonbills (*Platalea ajaja*) also breed here. Birds used two sites to establish breeding colonies in this area. Colonies were located close to the river

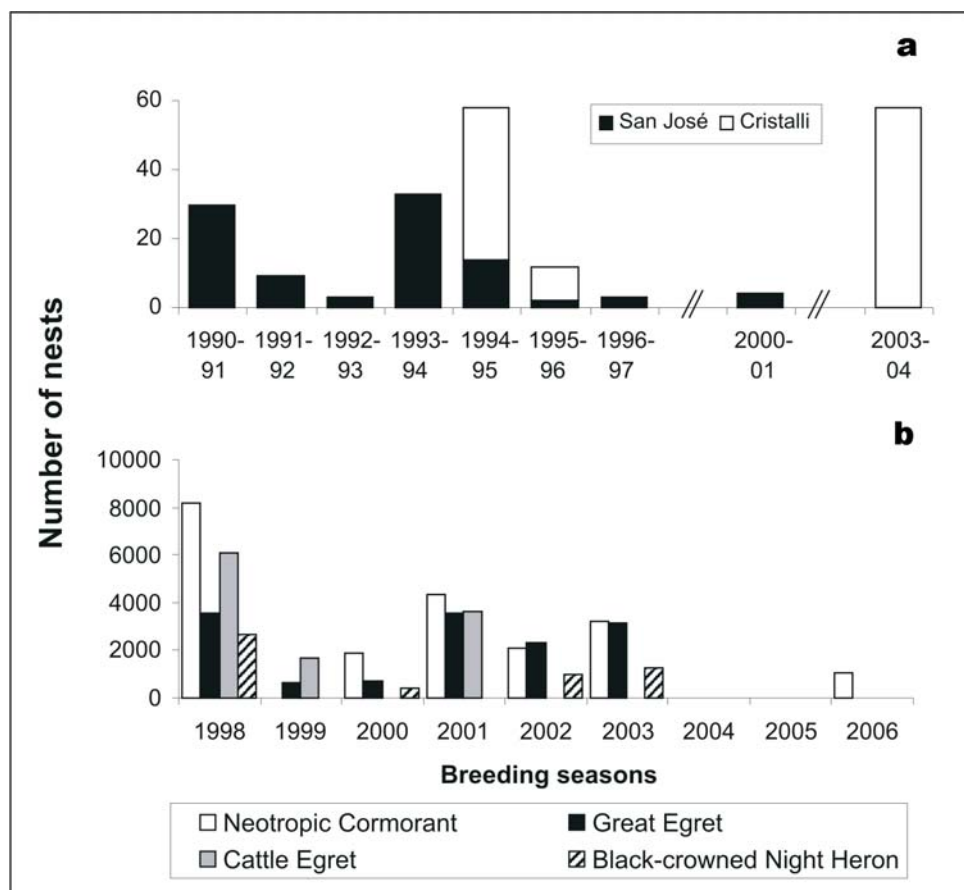


FIG. 3. Number of nests per breeding season, of: a) the Striated Heron in Miramar (San José and Cristalli colonies); and b) diverse species in Utis A (1998 – 2001) and Utis B (2002, 2003 and 2006) colonies.

and were named Utis A and B (Fig. 1). Birds never used these sites simultaneously (Fig. 3b). During 2004 and 2005, due to a severe drought the Utis River did not overflow and no marshland areas were formed; consequently, waterbird breeding colonies were not observed in the area in these years. Maximum estimates for individual species were 8150 nests of Neotropic Cormorants, 3550 nests of Great Egrets, 6050 nests of Cattle Egrets, and 2650 nests of Black-crowned Night Heron (mean nest density in 25 100 m²-plots = 6.52 ± 10.76 for cormorants, 2.84 ± 2.70 for Great

Egrets, 4.84 ± 5.53 for Cattle Egrets, and 2.12 ± 2.67 for Black-crowned Night Heron; colony area = 12.5 ha), all registered in the Utis A colony in 1998 (Fig. 3b). Waterbird colonial species generally began egg laying in this zone in summer; the Black-crowned Night Heron nested at the end of autumn and during winter (Fig. 4c–g). Nevertheless, all the species were observed nesting during the winter in BD outside study span, when food conditions were suitable.

Considering the breeding seasons between 1998 and 2006, the relation between colonial

TABLE 1. Nesting success of Striated Herons in the San José colony (Miramar, Laguna Mar Chiquita) and of Neotropic Cormorants, Great Egrets, Cattle Egrets, and Black-crowned Night Herons in the Utis A colony (Bañados del Río Dulce). ¹ Mean number of 3-week-old nestlings per nest.

Species/seasons	Egg-stage nest success (nest-days)	Chick-stage nest success (nest-days)	Nesting success (nest-days)	Nestlings per nest ¹ ± SD
Striated Heron				
1993–94 (N = 33)	0.70 (413)	0.57 (742)	0.39 (1155)	1.15 ± 1.21
1994–95 (N = 14)	0.62 (221)	0.63 (182)	0.39 (403)	0.64 ± 0.94
Neotropic Cormorant				
1998 (N = 97)	0.50 (1277)	0.80 (928)	0.40 (2,205)	0.67 ± 0.98
Great Egret				
1999 (N = 30)	0.39 (336)	0.76 (196)	0.30 (532)	0.97 ± 1.13
Cattle Egret				
1999 (N = 64)	0.58 (651)	0.80 (707)	0.47 (1358)	0.93 ± 0.92
Black-crowned Night Heron				
1998 (N = 30)	0.39 (301)	0.94 (262)	0.37 (563)	1.13 ± 1.10
2000 (N = 30)	0.52 (385)	1.00 (280)	0.52 (665)	1.23 ± 1.01

species number and water level at the beginning of egg laying was marginally significant ($r_s = 0.67$; $N = 9$; $p = 0.051$). In contrast, the number of breeding pairs was not influenced by variations in water level in the Utis River ($r_s = 0.42$; $N = 9$; $p > 0.05$). All the reproductive events occurred when water depth was between 3.5 and 4.5 m in the Utis River (Fig. 5c). Most nesting events occurred with changes in water level below 0.5 m (Fig. 5b). No reproductive events occurred during the big water level fall of more than 1.5 m in 2004, and in the following year, when water level remained low, with very little variation with respect to the previous year. In 2006, water level returned to the usual values, increasing almost 2 m and allowing recolonization by breeding colonial waterbirds. This was the only reproductive event occurring after a drastic change in water level (Fig. 5c). Relationships between rainfall and numbers of species and nests were not considered due to the low time coverage of rainfall data at the Sumampa and Paso de la Cina meteorological stations.

Wind was the main mortality factor identified in Neotropic Cormorants, Great Egrets, and Cattle Egrets, both during incubation and at the chick stage (Fig. 6b). Some clutches in the Utis A colony were lost because of nest abandonment by parents, notably in Black-crowned Night Herons. Also, in this species the highest percentages of predated eggs and losses of nestlings by starvation or sibling aggression were observed.

DISCUSSION

Effects of storm winds and other mortality factors. Winds were the main cause of egg losses in most of the colonial species evaluated. In contrast, because of their clinging ability nestlings had a higher probability of surviving to wind effects. Predation, and climate constraints to a lesser degree, are the most frequent causes of egg losses throughout the distribution range of the species considered in this study (Maxwell & Kale 1977, Burger 1982, Kaiser & Reid 1987, Hothem & Hatch 2004). Egg losses caused by wind in MC-BD

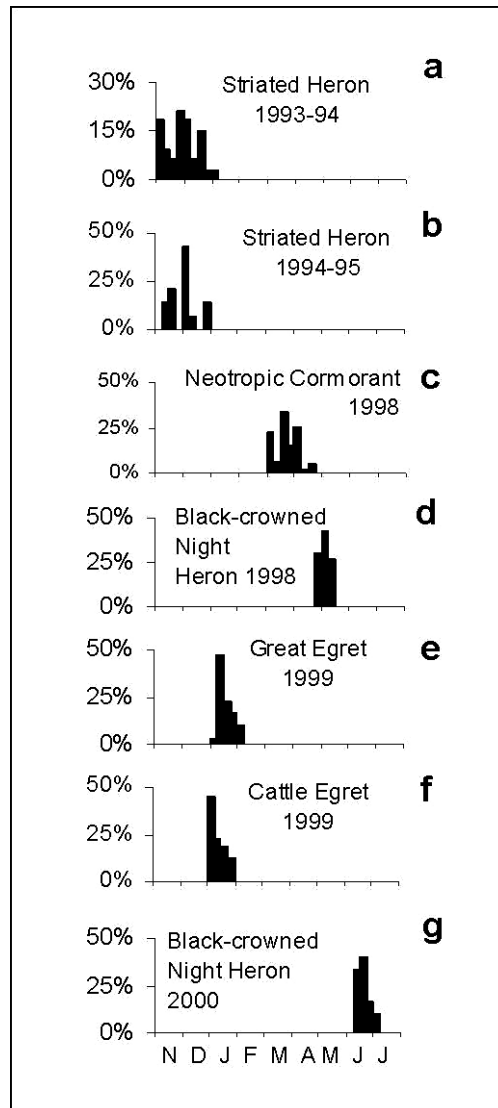


FIG. 4. Laying chronology (weekly percentage of laying pairs) of colonial waterbird species in San José Colony (a–b), Miramar, Laguna Mar Chiquita, and in Utis A colony (c–g), Bañados del Río Dulce.

largely exceeded those attributable to predation and other factors, which only represented a small proportion of all egg losses. Black-crowned Night Heron was the only species that was not affected by wind. During the

study span, egg-laying in this species occurred between late April and early July, i.e., when the maximum average wind speed is below 70 km/h (Fig. 2); in contrast, egg-laying in the other species usually occurred between

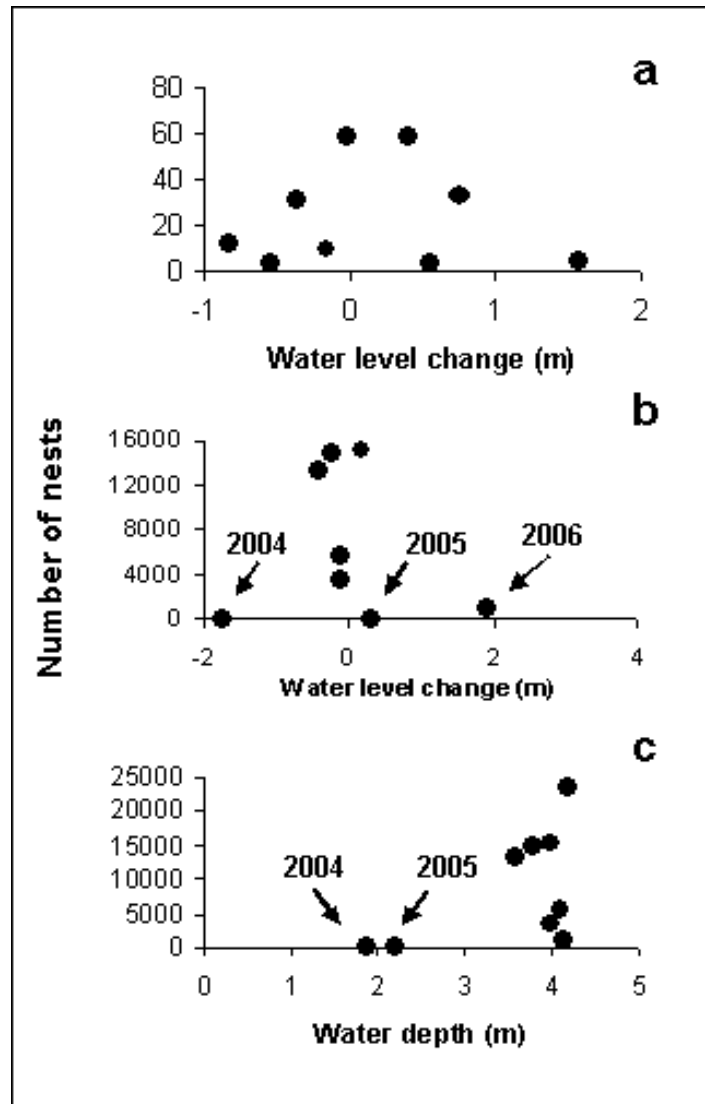


FIG. 5. Nest numbers in colonies, in relation to water level changes in consecutive years in (a) Miramar, San José and Cristalli colonies pooled, and (b) the Utis River (all colonies pooled), and in relation to water depth at laying in the Utis River (c). The 2004, 2005 and 2006 breeding seasons in the Utis River are remarked, because its special characteristics (see text for explanations).

November and March, when the wind exceeds (sometimes to a great extent) 80 km/h. Due to the absence of losses by wind, the mortality factors that had low incidence in

most of the species had an important effect in the Black-crowned Night Heron.

Since wind had a low incidence during the chick stage, all the species were more

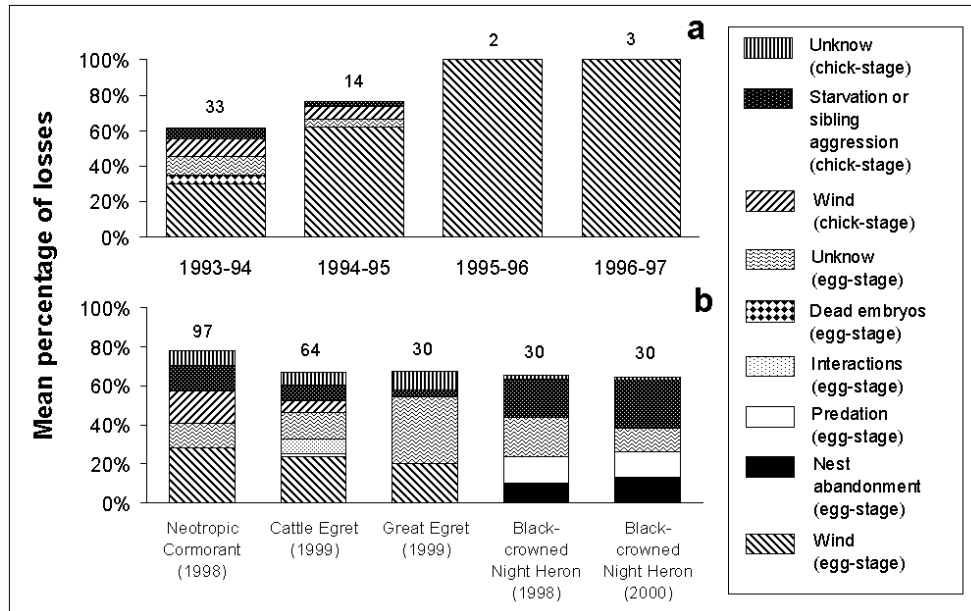


FIG. 6. Mean percentage of losses per nest and per cause for: a) Striated Herons in San José colony, Miramar, Mar Chiquita; and b) Neotropic Cormorants and three heron species in Utis A colony, Bañados del Río Dulce, in different breeding seasons. Numbers above columns indicates sample size (coinciding in “a” with total nest numbers).

successful at this stage than during incubation, with the notable exception of the Striated Heron, whose nestlings died of starvation or sibling aggression in large numbers. The latter mortality factor affected all the species considered, and in general had a low effect on final productivity. The Black-crowned Night Heron had the highest performance during the chick stage. In the 2000 breeding season, after a successful egg stage during which all nests produced at least one hatchling, this species reached the highest value of nesting success of all species examined.

Effects of local rainfall. As water level fluctuations in the MC-BD system do not depend on local rainfall but on rainfall in the high basin of the Dulce River, colonial waterbirds in this region should not be

largely affected by local rainfall fluctuations. In fact, annual precipitation did not influence the pair numbers of Striated Herons in Miramar. Nevertheless, a strong relationship was previously detected between Cattle Egret nesting success and local rainfall in MC, probably due a positive effect of rainfall on prey populations (Torres & Mangeaud 2006).

Effects of water level fluctuations. For many water-bird species throughout the world, water level is one of the main variables that affects feeding and reproduction (Kushlan 1986, Powell 1987, David 1994, Briggs *et al.* 1997, Dimalaxis & Pyrovetsi 1997, Kingsford & Johnson 1998, Duncan *et al.* 1999, Gawlik 2002, Russell *et al.* 2002). Water level influences wading birds directly by determining the depth at which they can feed, or indirectly, by deter-

mining the extension of suitable feeding habitats. In Utis A colony, a direct effect of water level on species number was observed but not on breeding pairs number. This suggests that in this site the rise in water level, rather than increasing the availability of the same type of feeding habitat, promote the coexistence of more diverse habitats, increasing the offer for more species with different requirements. In Miramar, water level did not affect the number of breeding pairs of the Striated Heron directly; however, it did so indirectly through its influence on the species' potential feeding area. Some studies of other heron species (Gibbs 1991, Farinha & Leitão 1996, Baxter & Fairweather 1998) also found relationships between the availability of feeding habitats and the number of nests. Furthermore, both in the Utis River and in Miramar, colony formation mainly depended on stable water levels or levels with small inter-annual changes, suggesting that habitat predictability plays a key role on colony establishment and site fidelity.

Implications for conservation. MC-BD is a very important wetland for the congregation and nesting of many species of waterbirds (Torres & Michelutti 2005). Consequently, a portion of the wetland is protected at both provincial and international levels. One of the most important efforts was the inclusion of the system as Ramsar Site in 2002. The site protects almost the entire MC, and a small portion of the BD. Many ecosystem processes in MC-BD, however, are regulated by events that occur at a great distance from the wetland. Protection and management of this wetland system, therefore, should not be conducted only at the local scale but at a much greater spatial scale. Our results can contribute to devise possible management strategies of river discharge and water level to maximize abundance, richness, and nesting success of colonial waterbirds.

Inter-annual water changes of up to 1 m favour the establishment of colonies in the whole area. In the particular case of the Utis River, colonies occur only with variations in water depth between 3.5 and 4.5 m. In BD, also, winter nesting of most colonial species normally occurs if floods remain until the beginning of winter (RT pers. observ.), as was the case of the Black-crowned Night Heron in this study; this phenomenon has also been observed in nearby wetlands, as Bañados de Figueroa (Olrog 1965). The possibility of breeding in late autumn and even in winter, when winds are not so strong, is therefore a factor to take into account. If water recession begins as late as at the beginning of winter, the remaining ponds take longer to dry off than if water recession begins earlier, since the temperature and thus the evaporation levels are lower than in autumn. Therefore, a water management strategy that maximizes colony establishment would be one that ensures a minimal discharge so that at least the areas surrounding the nesting sites would remain flooded until early winter.

ACKNOWLEDGMENTS

We thank Alfredo Ponce for his invaluable aid. Gabriel Schelotto, Jorge Juárez, Raúl Vaca, Gabriela Martínez, Andrea Caselli, Andrés Losada, Gustavo Giovanetti, Julieta Sánchez, Alejandra Giantomassi, Julio Vallejo and Bernardo Parizek collaborated with field work. Comments and suggestions of two anonymous reviewers improved the manuscript. This study was partially supported by Secretaría de Ciencia y Técnica (Córdoba, Argentina), grant N° 89/96, 177/97, 05/M002 and 05/M042; CONICOR, grant N° 3990 PID 41/97 and 4529 OPD 91/98; FONCyT PICTOR Redes, grant N° 20251-5, and the Administración de Parques Nacionales de Argentina.

REFERENCES

- Baxter, G. S., & P. G. Fairweather. 1998. Does available foraging area, location or colony character control size of multispecies egret colonies? *Wildl. Res.* 25: 23–32.
- Blanco, D. E., & M. Carbonell (eds.) 2001. *The Neotropical Waterbird Census. The first 10 years: 1990–1999.* Wetlands International, Buenos Aires, Argentina, & Duck Unlimited, Inc., Memphis, Tennessee.
- Bucher, E. H., G. Gavier Pizarro, & E. D. Curto. 2006. Síntesis geográfica. Pp. 15–27 *in* Bucher, E. H. (ed.). *Bañados del Río Dulce y Laguna Mar Chiquita (Córdoba, Argentina).* Academia Nacional de Ciencias, Córdoba, Argentina.
- Burger, J. 1982. An overview of proximate factors affecting nesting success in colonial birds: concluding remarks and summary of panel discussion. *Colon. Waterbirds* 5: 58–65.
- Butler, R. W., & W. Taylor. 2005. A review of climate change impacts on birds. USDA Forest Service Gen. Tech. Rep. PSW-GTR-191: 1107–1109.
- Cabido, M. R., & M. R. Zak. 1999. Vegetación del norte de Córdoba. Secretaría de Agricultura, Ganadería y Recursos Revocables de Córdoba, Córdoba, Argentina.
- Camara, G., R. C. Sousa, U. M. Freitas, & J. Garrido. 1996. SPRING: Integrating remote sensing and GIS by object oriented data modeling. *Computer & Graphics* 20: 395–403.
- Carney, K. M., & W. J. Sydeman. 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22: 68–79.
- Chambers, L. E., & R. H. Loyns. 2006. The influence of climate variability on numbers of three waterbirds species in Western Port, Victoria, 1973–2002. *Int. J. Biometeorol.* 50: 292–304.
- Crick, H. Q. P. 2004. The impact of climate change on birds. *Ibis* 146: 48–56.
- David, P. G. 1994. Wading bird use of Lake Okeechobee relative to fluctuating water levels. *Wilson Bull.* 106: 719–732.
- Del Hoyo, J., A. Ellis, & J. Sargatal (eds.) 1992. Handbook of the birds of the World. Volume 1: Ostrich to ducks. Lynx Edicions, Barcelona, Spain.
- Dimalaxis, A., & M. Pyrovetsi. 1997. Effect of water level fluctuations on wading bird foraging habitat use at an irrigation reservoir, Lake Kerkin, Greece. *Colon. Waterbirds* 20: 244–255.
- Duncan, P., A. J. M. Hewison, S. Houe, R. Rosoux, T. Tournebize, F. Dubs, F. Burel, & V. Bretagnolle. 1999. Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. *J. Appl. Ecol.* 36:11–23.
- Erwin, R. M., & T. W. Custer. 1982. Estimating nesting success in colonial waterbirds: an evaluation. *Colon. Waterbirds* 5: 49–56.
- Farinha, J. C., & D. Leitao. 1996. The size of heron colonies in Portugal in relation to foraging habitat. *Colon. Waterbirds* 19: 108–114.
- Fasola, M., P. Galeotti, N. Dai, Y. Dong, & Y. Zhang. 2004. Large numbers of breeding egrets and herons in china. *Waterbirds* 27: 126–128.
- Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. *Ecol. Monogr.* 72: 329–346.
- Gibbs, J. P. 1991. Spatial relationships between nesting colonies and foraging areas of Great Blue Herons. *Auk* 108: 764–770.
- Hancock, J., & H. Elliot. 1978. *The herons of the world.* Harper & Row, New York, New York.
- Hensler, G. L., & J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. *Wilson Bull.* 93: 42–53.
- Hothem, R. L., & D. Hatch. 2004. Nesting success of the Black-crowned Night Heron at Alcatraz Island, San Francisco Bay, California, 1990–2002. *Waterbirds* 27: 112–125.
- Kaiser, M. S., & F. A. Reid. 1987. A comparison of Green-backed Heron nesting in two freshwater ecosystems. *Colon. Waterbirds* 10: 78–83.
- Kingsford, R. T., & W. Johnson. 1998. Impact of water diversion on colonially-nesting waterbirds in the Macquarie Marshes of arid Australia. *Colon. Waterbirds* 21: 159–170.
- Kushlan, J. A. 1976. Wading bird predation in a seasonally fluctuating pond. *Auk* 93: 464–476.
- Kushlan, J. A. 1986. Responses of wading birds to seasonally fluctuating water levels: strategies and their limits. *Colon. Waterbirds* 9: 155–162.
- Luti, R., M. Solís, F. M. Galera, N. Müller de Fer-

- reira, M. Berzal, M. Nores, M. Herrera, & J. C. Barrera. 1979. Vegetación. Pp. 279–368 in Vázquez, J. R., R. Miatello, & M. Roqué (eds.). Geografía física de la provincia de Córdoba. Editorial Boldt, Buenos Aires, Argentina.
- [Mayfield, H. F. 1975. Suggestion for calculating nest success. *Wilson Bull.* 87: 456–466.](#)
- Maxwell, G. R., & H. W. Kale. 1977. Breeding biology of five species of herons in coastal Florida. *Auk* 94: 689–700.
- Menghi, M. 2006. Vegetación. Pp. 173–189 in Bucher, E. H. (ed.). Bañados del Río Dulce y Laguna Mar Chiquita (Córdoba, Argentina). Academia Nacional de Ciencias, Córdoba, Argentina.
- Olrog, C. C. 1965. Diferencias en el ciclo sexual de algunas aves. *Hornero* 10: 269–272.
- Pasquini, A. I., K. L. Lecomte, E. L. Piovano, & P. J. Depetris. 2006. Recent rainfall and runoff variability in Central Argentina. *Quat. Int.* 158: 127–139.
- Piovano, E. L., D. Ariztegui, & S. Damatto Moreiras. 2002. Recent environmental changes in Laguna Mar Chiquita (Central Argentina): a sedimentary model for a highly variable saline lake. *Sedimentology* 49: 1371–1384.
- [Powell, V. N. G. 1987. Habitat use by wading birds in a subtropical estuary: implications of hydrography. *Auk* 104: 740–749.](#)
- Reati, G. J., M. Florín, G. J. Fernández, & C. Montes. 1997. The Laguna de Mar Chiquita (Córdoba, Argentina): a little know, secularly fluctuating, saline lake. *Int. J. Salt Lake Res.* 5: 187–219.
- Rehfish, M. M., G. E. Austin, S. N. Freeman, M. J. S. Armitage, & N. H. K. Burton. 2004. The possible impact of climate change on the future distributions and numbers of waders on Britain's non-estuarine coast. *Ibis* 146: 70–81.
- Rodríguez, A., M. R. Pagot, G. D. Hillman, C. E. Pozzi, G. E. Plencovich, G. Caamaño Nelly, C. E. Oroná, E. Curto, & E. H. Bucher. 2006. Modelo de simulación hidrológica. Pp. 57–77 in Bucher, E. H. (ed.). Bañados del Río Dulce y Laguna Mar Chiquita (Córdoba, Argentina). Academia Nacional de Ciencias, Córdoba, Argentina.
- Rusell, G. J., O. L. Bass, & S. L. Pimm. 2002. The effects of hydrological patterns and breeding-season flooding on the numbers and distribution of wading birds in Everglades National Park. *Anim. Conserv.* 5: 185–199.
- [Sayago, M. 1969. Estudio fitogeográfico del norte de Córdoba. *Bol. Acad. Nac. Cienc. \(Córdoba\)* 46: 123–285.](#)
- Torres, R. 2004. Biología de la nidificación de aves acuáticas coloniales en la Laguna Mar Chiquita y Bañados del Río Dulce. Tesis Doc., Univ. Nacional de Córdoba, Córdoba, Argentina.
- Torres, R., & P. Michelutti. 2005. Reserva de Uso Múltiple Bañados del Río Dulce y Laguna Mar Chiquita. Pp. 134–137 in Di Giacomo, A. S. (ed.). Áreas importantes para la conservación de las aves en Argentina. Sitios prioritarios para la conservación de la biodiversidad. Temas de Naturaleza y Conservación N° 5. Aves Argentina/Asociación Ornitológica del Plata, Buenos Aires, Argentina.
- Torres, R., & A. Mangeaud. 2006. Factors affecting the nesting success of the Cattle Egret (*Bubulcus ibis*) in laguna Mar Chiquita, Central Argentina. *Ornitol. Neotrop.* 17: 63–71.
- Ware, D. M., & R. E. Thomson. 2000. Interannual to multidecadal timescale climate variations in the Northeast Pacific. *J. Climate* 13: 3209–3220.