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FACTORS AFFECTING THE NESTING SUCCESS OF THE CATTLE EGRET (*BUBULCUS IBIS*) IN LAGUNA MAR CHIQUITA, CENTRAL ARGENTINA

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Resumen. – Factores que afectan al éxito de nidificación de la Garcita Bueyera (*Bubulcus ibis*) en la Laguna Mar Chiquita, Argentina Central. – Con el objeto de determinar los factores que afectan la productividad de la Garcita Bueyera (*Bubulcus ibis*), se estudió su biología reproductiva en Argentina Central. El estudio fue realizado en colonias en la Laguna Mar Chiquita entre 1993 y 1997. Se observó un fuerte efecto del tamaño inicial de la camada sobre el número de pichones de 3 semanas de edad producidos por nido. El tamaño inicial de la camada, a su vez, estuvo influido principalmente por las pérdidas de huevos debidas a la acción del viento durante las tormentas. La muerte de pichones por inanición o agresión entre hermanos tuvo algún efecto sobre la productividad final, mientras que otras variables (predación, abandono del nido, y estructura de la vegetación) no tuvieron ninguno. El éxito de nidificación varió directamente con la precipitación acumulada durante la estación reproductiva, quizás debido a que la lluvia, a través de la estimulación del crecimiento de las pasturas, habría incrementado el número de Ortópteros, el alimento principal de la Garcita Bueyera, tanto en el área de estudio, como en otras regiones. Los nidos, por lo general, tuvieron una mayor supervivencia durante el período de crianza que durante la incubación, dado que el viento causó mayores pérdidas de huevos que de pichones. Diversas características, tales como el gran número de parejas nidificantes, y una productividad similar a la observada a latitudes cercanas en África, sugieren que la Garcita Bueyera se encuentra bien establecida en la región de Mar Chiquita, la cual representa una importante área de cría en el sur de Sudamérica. *Accepted 7 November 2005.*

Abstract. – The reproductive biology of the Cattle Egret (*Bubulcus ibis*) was studied to determine the factors affecting its productivity in Central Argentina. This study was conducted in the colonies of Laguna Mar Chiquita between 1993 and 1997. A strong effect of brood size on the number of 3-week old nestlings per nest was observed. Brood size, in turn, was influenced mainly by egg losses caused by heavy winds during storms. Death of nestlings due to starvation or sibling aggression had some effect, while other variables (predation, nest abandonment, and vegetation structure) had no effect on final productivity. Nesting success was positively correlated with accumulated rainfall during the breeding season. Rainfall stimulated faster pasture growth, which probably increased the abundance of Orthoptera, the main food item of Cattle Egrets in the study area. Nest survival was generally higher in the chick-stage than in the egg-stage, as winds caused higher losses of eggs than of nestlings. The large numbers of breeding pairs in the colonies and similar productivity to that observed at equivalent latitudes in Africa suggest that the Cattle Egret is well established in the Mar Chiquita region, an important breeding area in southern South America.

Key words: *Bubulcus ibis***,** Cattle Egret, Laguna Mar Chiquita, nesting success, survival, generalized linear models.

INTRODUCTION

The Cattle Egret (*Bubulcus ibis*), a species native to the Old World, has naturally colonized the American continent during the 20th century, providing one of the best documented examples of avian range expansion (Hancock & Elliot 1978, Arendt 1988). In Argentina, Cattle Egrets were not observed until the early 1970´s, when they reached the pampas (Narosky 1973). The pampas region, with extensive pastures supporting livestock, was an ideal habitat for the establishment of this invasive species (Hancock & Elliot 1978). At present, over 30 years later, there is still no information available on the extent of adaptation of egrets to this new habitat.

The reproductive success can be used as a measure of species fitness (Lack 1954, Williams 1966, Burger 1982). Cattle Egret reproduction has been extensively studied in North America (Jenni 1969, Dusi & Dusi 1970, Weber 1975, Maxwell & Kale 1977, Burger 1978, Rodgers 1987, Ranglack *et al.* 1991, Telfair *et al.* 2000), Africa (Bowen *et al.* 1962, Blaker 1969, Siegfried 1972), and Australia (Maddock & Baxter 1991, Baxter 1994, McKilligan 1997). Few studies on the reproductive biology of the Cattle Egret have been conducted in the Neotropics (Lowe-McConnell 1967, Arendt & Arendt 1988), and virtually no studies have been conducted in the southern portion of South America.

Laguna Mar Chiquita, one of the largest saline lakes in the world (Reati *et al.* 1997), is known for its importance for breeding and wintering waterbirds (Nores 1986, Bucher *et al.* 2000, Morales 2000, Torres & Michelutti 2001, Torres 2004), and was declared Ramsar Site in 2002. The Cattle Egret is abundant and permanent in Laguna Mar Chiquita, moving seasonally throughout the region (Torres & Michelutti 2001). Vegetation in this region was originally dominated by xerophyllous woodlands; however, the conversion of large areas into agricultural and pasture lands transformed its physiognomy, which currently resembles the typical Pampas landscape. Cattle Egret reproduction was studied in colonies in Laguna Mar Chiquita, in order to identify the factors influencing its productivity.

STUDY AREA AND METHODS

Laguna Mar Chiquita and Bañados del Río Dulce comprise a vast wetland located in Central Argentina (26–32ºS, 62–66ºW). Laguna Mar Chiquita (LMC) is a permanent shallow saline lake of nearly 6000 km² (Reati *et al.* 1997). Their main tributaries are the Dulce River in the north, and the Xanaes River in the south. The Dulce River has a large floodplain known as Bañados del Río Dulce, which is inundated during the rainy season (November to March). Precipitation in the rainy season, accounts for 75% of the annual rainfall, which averages between 700–800 mm (Capitanelli 1979). There are also marked year-to-year variations, with wet and dry cycles (Bucher 1992, Reati *et al.* 1997). The mean annual temperature is 18º–19º C. Storms with very strong winds are frequent in the whole area in summer, mainly in January. Vegetation is the typical of chacoan wetlands, including flooded prairies, reeds and other marshy vegetation, in combination with xerophyllous woods and halophyllous shrubs, as described in Luti *et al.* (1979), Menghi & Herrera (1996), and Cabido & Zak (1999).

Systematic samplings were conducted from 1993 to 1997 in two colonies –designated A and B– at the mouth of Xanaes river (30° 55'S, 62° 44'W). These colonies were the

TABLE 1. Pair numbers and nesting species in colonies of Laguna Mar Chiquita.

Colonies	Breeding season	Mean nest density ±SD[1]	Colony area (ha)	Mean estimate of pairs of Cattle Egrets	Other nesting species (pairs)
A	1993–1994	11.60 ± 5.21	6.98	8,097	Great Egret (50) Snowy Egret (4)
B	1993–1994	6.45 ± 1.39	2.10	1,355	None
B	1994–1995	12.29 ± 3.42	8.23	10,115	None
B	1995–1996	15.75 ± 2.20	13.20	20,526	None
B	1995–1996[2]	12.77 ± 3.60	11.84	15,120	None
B	1996–1997	16.57 ± 4.11	16.88	27,970	Great Egret (11)

[1]Mean nest density in 25 plots of 10 x 10 m.
[2]Second nesting in that breeding season.

unique breeding localities in LMC during the study period. The Cattle Egret was the most numerous, and sometimes the only species in these colonies (Table 1). In the 1993–94 breeding season, the birds in colony A nested in dead trees (*Tamarix gallica*). During the same breeding season, new pairs formed colony B, approximately 1 km away from colony A, and used site B in subsequent years (Table 1). In colony B, nests were built on green *Tamarix*, on "Chilcas" (*Baccharis salicifolia*), and occasionally on "Totoras" (*Typha latifolia*) and "Cortaderas" (*Cortaderia* sp.). Nests in both colonies were always constructed over water. Egrets did not use the site of colony A again during the study period. Clutch initiation generally began at the end of November, except in the 1994–95 breeding season, when it began at the end of December. Strong winds completely destroyed nests in colony B while birds were incubating in the 1995–96 breeding season. Later, in February 1996, birds initiated a second attempt, which was successful. Only this second nesting was considered as "1995–96 breeding season" in data analysis.

We marked all nests in ten plots (10 x 10 m) located at 20-m intervals along two randomly selected transects, in each colony and breeding season. We estimated the number of breeding pairs in each colony by averaging nest densities in other 25 randomly selected 10 x 10 m plots , and by extrapolating that mean density to the total colony area, which was determined using hand-held Global Positioning System (GPS) units.

A total of 173 nests were marked in colony A, in the 1993–94 breeding season. In colony B, 66, 107, 82 and 112 nests were marked in the 1993–94, 1994–95, 1995–1996 and 1996–97 breeding seasons, respectively. Marked nests were visited weekly. Nests with broken empty eggshells and no evidence of fallen nestlings were assumed to have been predated. Broken shells were removed after each visit. 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 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 destroyed after storms were attributed to loss 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 a 2-m mirror pole, since the maximum nest height in plots was 2.27 m. Following the method of McArthur & Horn (1961) with modifications, vertical complexity of vegetation was measured during the 1994–95, 1995–96 and 1996–97 breeding seasons in colony B, by counting the number of times that vegetation crossed an imaginary cylinder projected above and below each nest, in strata of 50 cm in height. The imaginary cylinder had the same diameter as the corresponding nest.

Nesting success was calculated using the Mayfield method (Mayfield 1975). The Mayfield method assumes equal survival probabilities throughout the period being measured (Erwin & Custer 1982). Because losses of nests are not always constant among periods of the nesting cycle, success was calculated separately for the egg and chick stages. The length of incubation (23 days) was obtained by averaging the values reported in various studies in North America (Jenni 1969, Weber 1975, Maxwell & Kale 1977). Nestling development was observed until the third week after hatching, because after that time chicks were capable of climbing nearby branches, and this made their assignment to individual nests difficult. Comparisons of nest survival between groups were carried out by the test developed for the Mayfield estimator by Hensler & Nichols (1981).

The correlation between nesting success in each breeding season ($n = 5$) and the corresponding accumulated rainfall and the mean water level was measured by Spearman r coefficient. The two colonies observed in the 1993–94 breeding season were treated as separate breeding events. Water levels and rainfall were obtained from the records of the rangers in Miramar (30º55’ S, 62º41’ W), a coastal town at LMC, 7 km away from the colony sites.

Within a generalized linear modeling framework, multiple regression was applied to explore the factors influencing the productivity of colony B in the 1994–95, 1995–96 and 1996–97 breeding seasons, when vegetation structure data were recorded. Response variable (number of 3-week old nestlings per nest) was modeled with a Poisson distribution and log-linked (McCullagh & Nelder 1989). Independent variables corresponded to nest characteristics (diameter, depth), nest site (height above ground or water, height of corresponding tree or bush, and structural complexity of vegetation in 8 strata of 50 cm in height), clutch date (weeks from date of first egg-laying in sample), clutch size (maximum number of eggs laid), brood size (number of eggs hatched), and mortality factors (number of eggs lost by wind, predation, nest abandonment, and unknown causes, and number of nestlings lost by wind, starvation or sibling aggression, and unknown causes).

The best regression model was obtained by using the stepwise forward method (Montgomery *et al.* 2001). Nests of the same colony, year and clutch date constituted clusters and were obviously correlated and not independent ($r = 0.16$, $t_{(66)} = 1.28$, $P = 0.20$). Then a matrix with an estimated intra-cluster correlation was incorporated into the model (Jiang 2001). Correlation value is an estimation of dependence among clusters. The most parsimonious matrix is the exchangeable type (Littell *et al.* 1996), corresponding to a unique value between nests in the same cluster, and zero between nests in different clusters. We used PROC GENMOD module of SAS 8.01 software.

Model fitness was measured in terms of the residual deviance: the smaller the value, the better the adjustment to the model. Proportion of the explained variability in final models was expressed by values of “pseudo-R^2”, which is equivalent to R^2 of linear models, but is only used for descriptive purposes and does not have an associated statistical test similar to *F* test (McFadden 1979).

Finally, in order to probe the model diagnosis, the validity of a Poisson assumption was checked by plotting deviance residuals against estimated linear predictors, and exam-

TABLE 2. Egg-stage (n = 23 days), chick-stage (n = 21 days), and overall nesting success of Cattle Egrets in Laguna Mar Chiquita[1].

	Colony A	Colony B				Total
	1993–94	1993–94	1994–95	1995–96	1996–97	
Egg-stage success	0.46	0.47	0.43	0.85	0.86	0.59
SE	0.010	0.016	0.012	0.009	0.008	0.005
Nest-days	2,324	927	1,606	1,449	1,869	8,176
Chick-stage success	0.91	0.75	0.53	0.68	0.90	0.79
SE	0.007	0.018	0.019	0.014	0.007	0.005
Nest-days	1,603	564	700	1,109	1,652	5,628
Total nesting success	0.41	0.35	0.23	0.58	0.77	0.46
SE	0.008	0.012	0.009	0.010	0.007	0.004
Nest-days	3,927	1,491	2,306	2,558	3,521	13,804

[1]Calculated by the Mayfield method.

ining systematic variations in that plot (McCullagh & Nelder 1989).

RESULTS

The breeding population of Cattle Egrets in LMC increased yearly, almost threefold during the study period (Table 1). The colony sites were occupied mainly by Cattle Egrets, and occasionally by small numbers of other egret species.

Overall nesting success was 0.46 (Table 2). The relationship between nesting success and rainfall was significant (r_S = 0.90, n = 5, P = 0.04). No relationship was observed between nesting success and mean water level (r_S = –0.50, n = 5, P = ns). Total productivity was 1.07 nestlings per nest observed.

Overall chick-stage success was significantly higher than egg-stage success (Z = 26.02, P < 0.0001, Hensler-Nichols test, Table 2) in all the breeding seasons [Z = 26.70, 10.46, 4.43 and 3.67, respectively, for the 1993–94 (A and B colonies), 1994–95 and 1996–97 breeding seasons; P < 0,001 in all cases, Hensler-Nichols test], with the only exception of the 1995–96 season, when egg-stage was more successful (Z = 10.08, P < 0.0001, Hensler-Nichols test, Table 2).

Occasionally, some lost clutches were apparently replaced by new ones. This phenomenon was observed in 18 cases, 4% of total clutches lost. Nesting success of the replaced clutches was 0.15 with 364 nest-days observed, much lower than the total nesting success (Z = –16.15; P < 0.0001; Hensler-Nichols test).

The model selected by stepwise multiple regression analysis indicated a strong effect of brood size on number of 3-week old nestlings per nest (Table 3). A pseudo-R^2 of 0.57 was obtained considering only brood size as an independent variable, i.e., brood size accounted for over 50% of total variability in the final number of nestlings. Death of nestlings by starvation or sibling aggression was the only known mortality factor selected by the model, individually, accounting for less than 3% of the total variability.

When considering brood size at hatching as the dependent variable in the first model, and excluding independent variables that were not relevant (nestlings lost by wind, by starvation, and by unknown causes), eggs lost by

TABLE 3. Stepwise multiple regression analysis for final productivity (number of 3-week old nestlings per nest) and for brood size at hatching of the Cattle Egret, in Laguna Mar Chiquita colonies (n = 301).

Parameters	Estimate	SE	*Z*	*P*	Cumulative Pseudo-R^2
Model for final productivity:					
Intercept	–1.29	0.20	–6.32	< 0.0001	
Brood size at hatching	0.74	0.06	12.17	< 0.0001	0.57
Nestlings lost by unknown causes	–0.75	0.15	–5.11	< 0.0001	0.62
Nestlings lost by starvation or sibling aggression	–0.33	0.06	–5.35	< 0.0001	0.64
Model for brood size at hatching:					
Intercept	–0.28	0.17	–1.67	0.09	
Egg losses by wind	–0.74	0.08	–9.30	< 0.0001	0.49
Clutch size	0.38	0.05	7.90	< 0.0001	0.62

wind was the first variable selected, which accounted for almost 50% of total variability in brood size (Table 3). An effect of clutch size on brood size was also observed.

DISCUSSION

The Mayfield method has not been used before in other studies on Cattle Egret reproduction. Egg success of the Cattle Egret in LMC, like other productivity measures, was considerably low when compared with values from other regions (Table 4). Studies mentioned in Table 4, however, are not directly comparable because the time invested in monitoring nestling survivorship was different. Egg success in LMC (0.37) was similar to values reported in a study from South Africa using a nestling monitoring period of 3 weeks after hatching (Siegfried 1972, Table 4).

In our study area, mortality was higher during the incubation period, resulting in lower success than during the chick-stage. Winds during the incubation period accounted for almost 50% of the total variability in brood size. The structural complexity of the vegetation had no effect on final productivity, and therefore was an ineffective wind barrier. Because of their clinging ability, nestlings had a higher probability of surviving wind. In the atypical 1995–96 breeding season, during the second incubation period that began in February 1996, no storms occurred (pers. observ.) and, in contrast to the other years, birds showed higher success in the egg-stage than in the chick-stage. This suggests a relatively small influence of other limiting factors such as predation. Wind was the main cause of egg losses reported by Blaker (1969) in Paarl, South Africa.

Death by starvation and sibling competition during the chick-stage is also often mentioned, (Blaker 1969, Jenni 1969, Siegfried 1972, McKilligan 1985, Ploger & Mock 1986). Such mortality, which also occurred in our study area, indicates certain restrictions in food availability (Inoue 1985, Drummond 2001). In Australia, McKilligan (1997) suggested that rainfall, through its action on pastures, increases populations of Acrididae, enhancing the survival of nestlings and nesting success. Such a phenomenon also occurred in LMC where Orthoptera are the main food item of Cattle Egret nestlings (Torres & Gutiérrez 1999), and a direct relationship was observed between rainfall and nesting success.

Predation in LMC had no effect both on brood size and the final number of nestlings. The identity of predators raiding marked

TABLE 4. Productivity of Cattle Egrets in different regions.

Sites	Egg success[1]	Nestlings produced per observed nest	Nestling development monitored to	References
Accra (Ghana)	0.28*	–	14 days	Bowen et al. (1962)
Paarl (South Africa)	0.34	0.86*	21 days	Siegfried (1972)
Alabama (USA)	–	0.36*	26 days	Dusi & Dusi (1970)
Alabama (USA)	0.38	1.11	12 days	Ranglack et al. (1991)
Florida (USA)	0.82*	–	14 days	Jenni (1969)
Florida (USA)	0.71	1.80	fledging	Weber (1975)
Florida (USA)	0.69	2.10*	10 days	Maxwell & Kale (1977)
Florida (USA)	0.48	1.30	14 days	Rodgers (1987)
New Jersey (USA)	0.74	–	14 days	Burger (1978)
Laguna Mar Chiquita (Argentina)	0.37	1.07	21 days	This study
New South Wales (Australia)	–	1.60–2.00	fledging	Baxter (1994)

[1]Stated as proportion of eggs that produced nestling.
*Based on data in original publication.

nests is unknown; however, we consider that Crested Caracaras (*Polyborus plancus*), Black Vultures (*Coragyps_atratus*), and Brown-hooded Gulls (*Larus maculipennis*) are probably egg predators in our study area. Predation on chicks by Crested Caracaras was observed in unmarked nests on two occasions. Some studies indicate that other birds are usually predators (Blaker 1969, Jenni 1969, Siegfried 1972, Maxwell & Kale 1977, Ranglack *et al.* 1991).

Nest abandonment in the early incubation stage may be caused by disturbance generated by researcher activities in the colonies (Jenni 1969). During our study in LMC, adults left the nests temporarily, leaving them exposed to predators; it is possible that some predation events were produced by that disturbance.

In LMC, breeding populations increased almost threefold in four breeding seasons. According to Arendt (1988), certain characteristics act synergistically to cause such rapid growth, e.g., immigration from other areas, the capacity of 1-year old Cattle Egrets to breed, and the pre-adaptation to diverse habitats types, often created by humans. In this study a high resilience after catastrophic losses was also observed. In the 1995–96 breeding season, after total losses of clutches by wind, 83% of pairs returned to breed, and subsequently achieved one of the highest values of nesting success observed during this study.

The maximum number estimated in LMC (c. 28,000 pairs in January of 1997) was even higher than that estimated for the whole country in February of the same year during the Neotropical waterbird census [35,240 individuals (or 17,620 pairs), Nores & Serra 2001]. Although the census coverage was not complete, the numbers observed suggest that LMC is the most important area for Cattle Egret breeding, at least in Argentina.

Hancock & Elliott (1978) considered Argentine pampas as an ideal habitat for Cattle Egret immigration. The large numbers reported in this study, with productivity similar to that reported from localities of similar latitude in Africa (the original home of this subspecies), appears to support this suggestion.

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