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SOME ASPECTS OF THE BREEDING BIOLOGY OF ROYAL (THALASSEUS MAXIMUS) AND CAYENNE TERNS (T. SANDVICENSIS EURYGNATHUS) ON ISLA VERDE, URUGUAY

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Resumen. - Algunos aspectos de la biología reproductiva del Gaviotín Real (Thalasseus maximus) y Gaviotín de Pico Amarillo (T. sandvicensis eurygnathus) en Isla Verde, Uruguay. - Presentamos el primer estudio sobre la ecología reproductiva del Gaviotín Real (Thalasseus maximus) y Gaviotín de Pico Amarillo (T. sandvicensis eurygnathus) en Isla Verde (Uruguay) durante la temporada reproductiva de 2005. También analizamos parámetros reproductivos de Gaviotas Cocineras (Larus dominicanus) simpátricas y su tasa de depredación sobre ambas especies de gaviotín. La colonia de gaviotines comenzó su asentamiento durante la segunda semana de Agosto finalizando su reproducción entre el 10-19 de Noviembre. Se estimaron tamaños poblacionales mínimos de 350 parejas de Gaviotín Real y 27 de Gaviotín de Pico Amarillo. Los huevos fueron puestos en el pasto con una densidad de 8,6 nidos/m² ± 1,4 y un tamaño de nidada promedio de 1,03 y 1,00 huevos/nido para el Gaviotín Real y Gaviotín de Pico Amarillo, respectivamente. El período de puesta de la Gaviota Cocinera comenzó entre el 28 de Agosto y el 6 de Septiembre, alcanzando su número máximo de parejas reproductivas (1095, CV = 57,3%) entre el 26 de Septiembre y el 2 de Octubre. Las gaviotas nidificaron sobre todos los sustratos disponibles en la isla (i.e., pasto, conchilla, y rocas), sin embargo la densidad de gaviotas fue más alta en el pasto. Se detectó una gran variabilidad espacial y temporal en la abundancia de nidos de gaviotines. A través de fotografías aéreas se observó que a lo largo de la temporada los nidos eran abandonados en un lado de la colonia en tanto nuevas nidadas eran registradas en el lado opuesto. Las áreas abandonadas por los gaviotines fueron ocupadas por gaviotas. Esta especie fue registrada depredando mayormente sobre huevos de gaviotines a una tasa de 0,03 depredaciones/hora/nido. El éxito reproductivo de los gaviotines fue nulo al final de la temporada. Varios factores podrían haber afectado la reproducción de los gaviotines, sin embargo la depredación por la Gaviota Cocinera sería la causa que mejor explicaría la dinámica observada de esta colonia.

Abstract. – We present the first study of reproductive ecology of a mixed-species colony of Royal Tern (*Thalasseus maximus*) and Cayenne Tern (*T. sandvicensis eurygnathus*) on Isla Verde (Uruguay) during the 2005 breeding season. We also recorded breeding parameters of sympatric kelp gulls (*Larus dominicanus*) and predation rates on both tern species. The terns laying began during the second week of August and the breeding pairs of Royal and Cayenne Tern, respectively. They laid their eggs on the grass with a nest density of 8.6 nests/m² ± 1.4 and mean clutch size was 1.03 and 1.00 for Royal and Cayenne Tern, respectively. They laid their eggs on the grass with a nest density of 8.6 nests/m² ± 1.4 and mean clutch size was 1.03 and 1.00 for Royal and Cayenne Tern, respectively. The laying period of the Kelp Gull began between 28 August and 6 September, reaching the maximum number of breeding pairs (1095, CV = 57.3 %) between 26 September and 2 October. Gulls nested all over the island (i.e., grass, sand-shell, and rocks); however the highest nest density was recorded on the grass. We observed a high spatial and temporal variability in terns breeding pairs. From aerial pictures we could detect that terns were deserting the nest from one side of the colony, while new clutches were recorded on the opposite side throughout the breeding season. Areas that had been abandoned by terns were then occupied by kelp gulls. This species was observed preving mostly

on tern eggs at a rate of 0.03 predations/hour/nest. The terns breeding success was null at the end of the breeding season. As many factors could affect the terns breeding, predation by the Kelp Gull could have been the major cause that explains the dynamic observed. Accepted 4 July 2010.

Key words: Breeding biology, *Larus dominicanus*, predation, *Thalasseus maximus*, *T. sandvicensis eurygnathus*.

INTRODUCTION

The reproductive biology of the Royal Tern (Thalasseus maximus) and Cayenne Tern (T. sandvicensis eurygnathus) have been studied in some breeding sites along their distributional range, from North to Southern South America (e.g., Buckley & Buckley 1972, Quintana & Yorio 1997, Branco 2003). These species breed mainly on islands and occasionally on the continental coast. They usually change their breeding sites between years and in cases of high predation rates or human disturbances they can abandon the colony (Buckley & Buckley 1980, Quintana & Yorio 1997). Parental care could last for many months after they have left the colony area (Ashmole & Tovar 1968). During the reproductive season, eggs and chicks can suffer predation, mainly by gulls (Larus spp.) but also by other species of birds such as Blackcrowned Night Heron (Nycticorax nycticorax) and Black Vulture (Coragyps atratus) (Buckley & Buckley 1972, Yorio & Quintana 1997, Branco 2003). In Brazil (Santa Catarina and São Paulo States) and Argentina (Chubut Province), the Kelp Gull (Larus dominicanus) is one of the main predators of eggs and chicks in Royal and Cayenne Tern colonies (Quintana & Yorio 1997, Yorio & Quintana 1997, Branco 2003).

The population status of both species in Argentina and Brazil has been recently reviewed by Yorio & Efe (2008). Although the population size of some colonies is well known, they recommend updating and improving the estimations in this region in order to know the Austral population size of these species.

Seasonal records of frequency and abundance of adults and juveniles of both tern species during the 1960s, lead to the suspicion that they reproduce somewhere along the Uruguayan coast (Escalante 1968, 1970, 1985). In 1997, Cravino et al. (1999) registered for the first time a mixed colony of Royal and Cayenne Terns breeding in sympatry with a Kelp Gull colony on Isla Verde, Rocha Department, Uruguay. Since then, this is the only breeding site known for these tern species in Uruguay and in a wide region of more than 2000 km of Atlantic coast in South America, between the southernmost colonies in Brazil and the northernmost in Argentina. The objective of the present work was to study the reproductive ecology of these tern species during the 2005 breeding season. Particularly, we aim to analyze the spatial and temporal patterns in abundance and some breeding parameters (i.e., nest density, egg size, clutch size, and breeding success). Because of the sympatric breeding with Kelp Gull we also recorded gull population size, nest density, chronology, and predation rates on both tern species.

METHODS

Study area. Isla Verde is located on the east coast (33°56'S, 53°29'W) of Rocha Department, Uruguay. The island has an area of 7.2 ha and it is situated 1450 m off the coast. There are three different habitats on the island: rock, grass (Bermuda grass, *Cynodon dactylon*) and sand with shells (sand-shell). There is also a reed bed of Giant Cane (*Arundo donax*) of 0.14 ha. Close to Isla Verde, there is a small rocky island called Islote Coronilla of about 2.50 ha with some sandshells and a little area of grass (Fig. 1a).

In addition to Royal and Cayenne terns, several waterbirds reproduce on Isla Verde. Kelp Gull breeds all over the area. Snowy Egret (Egretta thula) and Cattle Egret (Bubulcus ibis) breed on a mixed colony on the reed bed. The nesting of the Black-crowned Night Heron and the Great Egret (Ardea alba) has not been confirmed yet, but they have been seen in the reed bed during the reproductive season. American Ovstercatchers (Haematopus palliatus) also breeds on the island and build their nests on the sand-shell. In addition, Isla Verde and its surrounding area is also an important roosting and feeding site for several other bird species, such as South American Tern (Sterna hirundinacea), Common Tern (Sterna hirundo), Olivaceus Cormorant (Phalacrocorax olivaceus), Ruddy Turnstone (Arenaria interpres), Yellowlegs (Tringa melanoleuca, T. flavipes), Solitary Sandpiper (T. solitaria), and Red Knot (Calidris canutus).

Data collection for terns. Between 12 August and 19 November 2005, 12 surveys were carried out on Isla Verde. Given the difficulties to access the island, i.e., sea conditions and logistics, we could carry out field work with a mean of 9 days between surveys (see Table 1).

Censuses of breeding pairs, pictures (aerial and from the ground) and direct counts of nests were performed, in order to analyze the spatial and temporal variability of the species abundance. Direct counts were done with binoculars (x10) and telescope (x60) from a two meters high fixed observation point at 30 m distance from the colony, where we had a good view. From this fixed point we took pictures that helped us to improve the precision of our data of number of breeding pairs. In the same way, three aerial surveys were carried out, on 7 September, 22 September, and 11 October 2005, from a 300 m altitude. Then we took pictures with a 4.0 MP digital camera and 37–370 mm lenses. A breeding pair was considered to be any individual in incubating position (Quintana & Yorio 1997) and those which were taking care of a nest, even though they were not settled.

The number of nests, nests per square meter, minimum internest distance, and egg and clutch sizes were estimated from fieldwork within the colony. This information was obtained only on 6 September, 26 September, and 2 October in order to minimize disturbance and negative impact to the terns breeding (see Table 1). Nest density was determined using a 1x1 m quadrant homogeneously set over the colony. Minimum internest distance was recorded from the center of one nest to the center of the nearest. Royal Tern nests were randomly chosen to measure its minimum internest distance, whereas Cayenne Tern nests had to be seek (because of their low abundance, see Results) in sectors where their nests were aggregated. Egg size was measured with calipers to the nearest 0.1 mm. Clutch size was determined for each species as the ratio of the total number of nests with eggs and the total number of eggs from two samples taken with the 1mx1m quadrant (homogeneously set over the colony) in 26 September and 2 October.

Data collection for Kelp Gull. To determine Kelp Gull population size, we estimated nest density within the period of highest abundance (26 September and 2 October 2005). Forty 10x10 m quadrants were homogeneously distributed on each stratum of the island: 15 on the grass, eight on sand-shell, and 17 on the rock. The available surface for nesting was calculated from a satellite picture (Google Earth 5.0). The area of each stratum was: grass 0.62 ha, sand-shell 0.41 ha, and rock 0.65 ha.

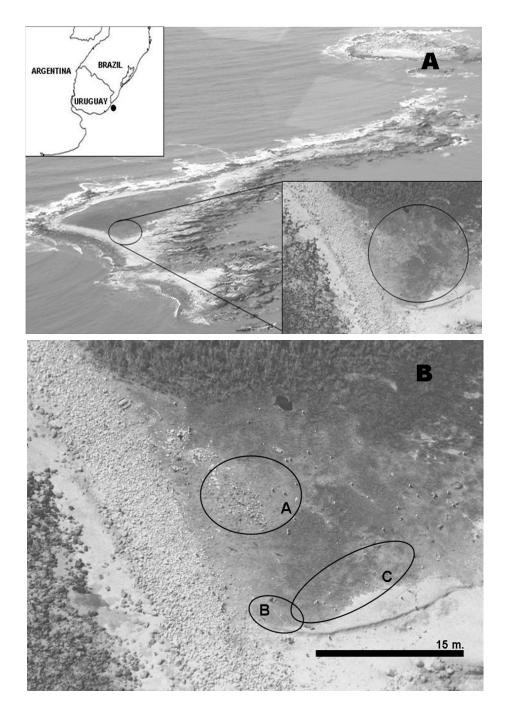


FIG 1. A) Aerial picture of Isla Verde indicating the place where the colony was settled in the 2005 season. B) Picture showing with numbered circles (A–C) the three stages (see text) and the location of the colony.

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Predation by Kelp Gull. Data were taken once Kelp Gull began the laying period on 6 September, until the end of the terns reproductive period, on 10 November. Direct observations were made with binoculars and telescope from the same observation point described above, during 18.6 h spread throughout the breeding season (6 September: 0.3 h, 26 September: 2.5 h, 2 October: 5.3 h, 12 October: 2.0 h, 22 October: 1.5 h, 2 November: 4.0 h, 11 November: 3.0 h). Interactions were quantified considering each aggressive behavior as one attack, classifying them as successful in case of predation, or non-successful. The identity of the attacked species, location in the colony (center or periphery), precedence of the attack (from air or land), and objective of the attack (egg or chick) were also recorded (Yorio & Quintana 1997).

Data analysis. Nest density (nest/m²) and minimum internest distance (cm) of terns were compared between surveys by means of ANOVA and *post hoc* Tukey test as a pairwise test for comparing means.

To analyze predation interactions we defined the "absolute predation rate" (*APR*) as the number of predation events per hour of observation. Also "predation rate" was defined as the number of predation events relative to the potential prey or peripheral nests (see Yorio & Quintana 1997). Peripheral nests were estimated using pictures taken from the ground (fixed observation point) relative to each survey. The mean predation rate (*PR*) was estimated by the formula:

$$PR = \frac{\sum_{i=1}^{n} Pi / hri / PNi}{n}$$

where PR is the ratio between the number of predation events (P) in each sample (i) and to

the amount of h observed (hn) relative to the peripheral nests (PN), averaged by the sample size (n).

The population size of Kelp Gull (\overline{N}) was estimated by a stratified sampling analysis

$$\overline{N} = \sum W_e * N_e$$

where W_e is the weight of each stratum (i.e., grass, rock, and sand-shell) relative to all the possible sample units, and N_e is the mean number of nests per stratum (Greenwood 1996). Differences among strata were tested using ANOVA and *post hoc* Tukey test.

Results are presented as mean \pm standard deviation (SD). Statistical analyses were performed with the software Past v 1.74 (Hammer *et al.* 2001).

RESULTS

Breeding of terns. Reproductive activity began in July, when Royal Tern flocks were seen in the continental coast doing courtship feeding, terrestrial displays, and mating. The laying period began on the second week of August when four nests with eggs and 50 adult Royal Terns were recorded (Table 1). By the end of August, 350 pairs of Royal Tern and seven of Cayenne Tern were observed in a mixed colony. One month later, on 22 September, the entire colony had been moved to an adjacent site. Finally, on 12 October, the colony had been moved again to a position adjacent to the last one. These three stages in the spatial and temporal changes in breeding pairs were distinguished as A, B, and C (Table 1, Fig. 1b). Although the limited sampling frequency, field observations and aerial pictures suggest that the colony was progressively moving throughout the grass. This means that terns were deserting from one side of the colony while new clutches had been laid on the

TABLE 1. Number of Royal and Cayenne Tern pairs throughout the 2005 reproductive season. Substrate for nesting and sampling methods are also shown. DC: direct count, GPA: analysis of pictures taken from the ground, APA: analysis of aerial pictures, WC: work within the colony. * Total number of breeding pairs (species could not be discriminated).

Date	Royal Tern pairs	Cayenne Tern pairs	Substrate	Sampling method
Stage A				
12 Aug	4	0	grass	DC
20 Aug	76	3	grass	DC, GPA
28 Aug	350	7	grass	DC, GPA
6 Sep	220	20	grass	DC, GPA, APA, WC
Stage B				
22 Sep	100*	100*	grass	APA
26 Sep	222	27	grass	DC, GPA, WC
2 Oct	278	25	grass/sand-shell	DC, GPA, WC
Stage C				
12 Oct	200	15	grass/sand-shell	DC, GPA, APA
22 Oct	300	11	grass	DC, GPA
2 Nov	130	10	grass	DC
10 Nov	16	1	grass	DC, GPA
19 Nov	0	0		-

opposite side. Areas that had been abandoned by terns were then occupied by Kelp Gulls.

We could not distinguish the relaying pairs from those which laid for the first time in the subsequent stages of the colony, making it difficult to estimate population sizes. Thus, we estimated the minimum population sizes based on the maximum number of breeding pairs recorded during the study period. Therefore, the minimum population sizes were estimated in 350 pairs and 27 pairs for Royal and Cayenne terns, respectively (Table 1).

Most terns laid their eggs on the Bermuda grass during the season, but in the B and C stages some nests were located on the bare soil. On 12 October, 13 Royal Tern and one Cayenne Tern were recorded breeding on Islote Coronilla with their eggs laid on the grass. In subsequent surveys, they were not observed again.

The number of nests per square meter was 8.6 nests/m² \pm 1.4 (N = 43, range 6–12).

No statistical differences were observed throughout the breeding season (ANOVA $F_{2,43} = 0.87$, P > 0.05). The minimum internest distance between Cayenne Terns showed no significant variation through the season. Nevertheless, we detected that the Royal Terns inter-nest distance decreased towards 26 September and 2 October (Table 2).

Cayenne Tern clutch size was 1.00 eggs/ nest in both random samples (26 September: N = 18; 2 October: N = 10). Royal Tern clutch size on 26 September was 1.01 eggs/ nest (N = 110) and on 2 October 1.04 eggs/ nest (N = 114), averaging 1.03 eggs/nest. The percentage of Royal Tern 2-egg clutches in both surveys was 0.9% and 4.4%, respectively (average: 2.7%). Nevertheless, in the first survey (6 September) three nests with 3-egg clutches of Royal Tern were observed. Average egg sizes of both species are shown in Table 3. Only four chicks were observed hatched, one of which was seen predated by a

TABLE 2. Minimum internest distances between Cayenne and Royal Tern nests. *ANOVA: ($F_{2,14}$ = 1.20, P > 0.05); **ANOVA: ($F_{2,37}$ = 9.46, P < 0.01); ** Tukey test: 6–26 September: Q = 5.65, P < 0.01, 6 September–2 October: Q = 4.50, P < 0.01; 26 September–2 October: Q = 0.65, P > 0.05.

Species	Mean cm (\pm SD)	Date
Cayenne Tern*	24.8 (± 7.5)	6 Sep
	$27.0 (\pm 2.4)$	26 Sep
	$29.4 (\pm 2.7)$	2 Oct
Royal Tern**	$38.8 (\pm 5.7)$	6 Sep
	31.8 (± 3.3)	26 Sep
	32.6 (± 3.4)	2 Oct

Kelp Gull on 22 October (see below). A total breeding failure was recorded by the end of the season (2 November).

Kelp Gull breeding. From field observations and aerial photographs we determined that the clutch initiation date of Kelp Gulls was between 28 August and 6 September. The highest peak of nests occurred between 26 September and 2 October. Kelp Gulls built their nests on the grass, sand-shell, and rocks. Average nest density was significantly higher in the grass $(11.3 \pm 5.7 \text{ nests}/100 \text{ m}^2)$ than on rock $(3.2 \pm 2.6 \text{ nests}/100 \text{m}^2)$ and sand-shell $(4.6 \pm 2.6 \text{ nests}/100 \text{ m}^2)$ ($F_{2,40} = 16.90$, P <0.01, N = 40; Tukey post hoc: grass-sand Q =5.67, P < 0.01; grass-rock Q = 6.90, P < 0.01; sand-rock Q = 1.24, P > 0.05). Kelp Gull population size was estimated as 1095 (CV = 57.3 %) breeding pairs.

Predation by Kelp Gull. A total of 52 attacks performed by Kelp Gull were recorded (2.8 attacks/h) of which 11 (21.2%) were successful predation events (10 eggs and 1 chick). Ground attacks mainly occurred towards peripheral nests (92.3%), and secondary to central nests (1.9%); some aerial attacks to central nests (5.8%) were also observed. The highest rate of attacks (18.02 attacks/h) occurred at the beginning of the gulls laying period (on 6 September).

Predation rate (*PR*) was 0.03 ± 0.06 predations/h/nest, but was variable throughout the season. The highest *PR* (0.17 predation/h/ nest) was recorded in the last survey (10 November) when there were less than 20 pairs in the colony (see Table 1). The absolute predation rate (*APR*) was 0.59 ± 0.67 predations/h. All except one attack were towards Royal Terns (98.1%). However, some egg shells of Cayenne Tern were observed on 2 November at the periphery of the colony, where Kelp Gull attacks were previously recorded.

DISCUSSION

Information about seabird populations and the location of their breeding sites is scarce in Uruguay (Escalante 1991). Here, we present the first results of the reproductive biology of seabirds done in this country, obtaining the chronology and some important parameters of the nesting of Royal and Cayenne terns (i.e., minimum population, clutch and eggs sizes, and nest density) and Kelp Gull (i.e., population size, nest density, and attack and predation rates towards breeding terns).

Breeding of terns. The terns' reproductive chronology recorded here agrees with Escalante (1968, 1970, 1985, 1991) who suggested that these species could breed in Uruguay or in the region during the spring. We could confirm this intermediate reproductive schedule between Brazilian (May–August) and Argentinean colonies (November–February) following a latitudinal gradient. This relevant finding was also suggested by Cravino *et al.* (1999) who recorded incubating adult terns and a recently formed crèche on October 1997 on Isla Verde. Egg laying date is proximately determined by many factors, such as climate,

TABLE 3. Average egg sizes of Royal and Cayenne Terns.

Species	Length mm (± SD)	Width mm (± SD)	Ν
Cayenne Tern	64.5 (± 1.5)	44.3 (± 0.9)	43
Royal Tern	52.5 (± 1.7)	37.5 (± 1.8)	24

food availability, territory quality, behavior of the mate, age, and body condition. However, responses to photoperiod had been experimentally proposed as the principal mechanism responsible of local adaptive variation in laying date (Lambrechts *et al.* 1997).

Some breeding parameters observed on Isla Verde colony are different than other breeding grounds, but generally fit with the life history characteristics of these Thalasseus species. Royal Tern and Cayenne Tern bred in lower density (nest/m²) on Isla Verde than other mixed species colonies, such as Punta León colony in Patagonia (9.8-11.1 nests/m² Quintana & Yorio 1997). By contrast, T. maximus colonies in the northern hemisphere breed less aggregately (6.8-7.4 nests/m² in Buckley & Buckley 1972) than in Uruguay. Despite these small differences, the density recorded in this colony is as high as most of the Thalasseus genus colonies (Buckley & Buckley 1972). Nesting in high densities has been proposed as an antipredator mechanism and even as one factor shaping colonial breeding (Danchin & Wagner 1997). Accordingly, the observed reduction of inter-nest distances of Royal Tern throughout the season could have occurred to minimize predation and the rate of attacks.

Egg sizes were similar compared with those reported by Cravino *et al.* (1999) for the same colony. The results were also in accordant with Buckley & Buckley (1972) in the northern limit of the distribution in North America and with Branco (2003) in Santa Catarina (Brazil). However, Ansingh *et al.* (1960) reported egg sizes that were on average 2 mm smaller, both in width and length, from a tropical colony in Curacao (Netherlands Antilles).

As far as we know, Royal Tern 3-egg clutches have not been previously reported in the literature. Nevertheless, the possibility that an individual could accidentally move or abandon eggs, or maybe incubate clutches of more than one female, cannot be rejected (Buckley & Buckley 1972). However, the average clutch size of Royal Tern and Cayenne Tern was the same (one egg) as reported elsewhere (e.g., Ansingh *et al.* 1960, Buckley & Buckley 1972, Quintana & Yorio 1997, Branco 2003).

Predation by Kelp Gull. When predation occurs toward peripheral nests, the shape and size of the colony have a key role in the reproductive success (Langham & Hulsman 1986, Yorio & Quintana 1997). Because of the border effect caused by the perimeter/area ratio, the smaller the colony the bigger the negative effect of predation on peripheral nests. Thus, the relative small size of the Isla Verde tern colony could be one of the factors that could have been operating in the recorded failure of breeding success.

Preliminary, our results suggest that the high rate of Kelp Gull attacks at the beginning of the terns reproductive season and the reduction in tern abundance detected may not be related to gull feeding behavior only. Terns laid their eggs on the grass where most gulls built their nests. Kelp Gull laying period overlapped in time with the highest reduction in tern abundance (see Table 1). The abundance of tern breeding pairs had still been decreasing until 26 September when kelp gulls reached its highest abundance. These observations and the occupation of the abandoned tern nest sites by kelp gulls (see Results) allow us to hypothesize that the terns' reproductive cycle could also be affected by space competition with gulls. Although this interaction has not been detected yet among these species, high densities of kelp gulls could negatively affect the terns' egg-laying period (see Quintana & Yorio 1998).

Other causes could have also affected the observed dynamics and tern breeding success, such as extreme weather conditions (flooding and strong winds), research disturbance, or egg collection by humans. There was a storm during the breeding period but we did not detect any kind of destruction over the colony after that. No evidence of nest desertion was detected immediately after the field work within the colony. Although egg harvest was common in both Isla Verde and Islote Coronilla some decades ago, it appeared not to be the case during 2005 breeding season. Currently, access to the island is restricted by law. Unfortunately, predation by the Blackcrowned Night Heron could not be evaluated because this species is principally nocturnal and we could not stay at night on the island.

Remarks on the Uruguayan terns populations. The Royal Tern breeding population in Uruguay could be considered of concern in the region. First, the minimum estimated population size of Royal Tern in Uruguay is intermediate between Argentinean and Brazilian colonies. Although the biggest colonies are in Patagonia, Argentina, the Punta León colony size was estimated as only 450 Royal Tern pairs (Yorio & Efe 2008). The other colonies have not been censused or the populations have not been distinguished yet, but they are supposed to comprise between 633-7135 breeding pairs (Yorio & Efe 2008). Second, this is the only colony in a wide area of more than 2000 km of Atlantic coast. Without considering the degree of its reproductive isolation, the viability of this colony could be important for the conservation of the Austral Royal Tern population. Concerning the Cayenne Tern, there are many colonies in the region and some have important breeding population sizes, for example Espírito Santo in Brazil and Banco Culebra in Argentina with 6500 and 700 pairs, respectively (Yorio & Efe 2008). Comparatively, the estimated population size of this species on Isla Verde is small.

Knowledge of the degree of genetic relationship between breeding populations of both species in the region is required to detect management priorities for the Uruguayan colony. However, while this information is not available, a high degree of caution must be taken due to their small population size and geographic isolation.

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REFERENCES

- Ashmole, N. P., & H. Tovar. 1968. Prolonged parental care in Royal Terns and other birds. Auk 85: 90–100.
- Ansingh, F. H., H. J Koelers, P. A. Van Der Werf, & K. H. Voous. 1960. The breeding of the Cayenne or Yellow-billed Sandwich Tern in Curaçao in 1958. Ardea 48: 51–65.
- Branco, J. O. 2003. Reprodução de Sterna hirundinacea Lesson e S. eurgenatha Saunders (Aves, Laridae), no litoral de Santa Catarina, Brasil. Rev. Bras. Zool. 20: 655–659.
- Buckley, F. G., & P. A. Buckley. 1972. The breeding ecology of Royal Terns Sterna (Thalasseus) maxima maxima. Ibis 114: 344–359.
- Buckley, F. G., & P. A. Buckley. 1980. Habitat selection and marine birds. Pp. 69–112 *in* Burger, J., B. L. Olla, & H. E. Winn (eds). Behavior of marine animals. Plenum Press, New York, New York.
- Cravino, J. L., E. Arballo, & A. Ponce de León. 1999. Isla Verde, Uruguay: sitio de reproducción de tres especies de gaviotines (*Thalasseus maximus, sandvicensis eurygnatha y Sterna hirundinacea*) en el Atlántico Sudoccidental. Resúmenes del VI Congreso Ornitol. Neotrop., Monterrey, México.
- Danchin, E., & R. H. Wagner 1997. The evolution of coloniality: the emergence of new perspectives. Trends. Ecol. Evol. 12: 342–347.
- Escalante, R. 1968. Notes on the Royal Tern in Uruguay. Condor 70: 243–247.
- Escalante, R. 1970. Notes on the Cayenne Tern in Uruguay. Condor 72: 89–94.
- Escalante, R. 1985. Taxonomy and conservation of austral-breeding Royal Terns. Pp. 935–942 *in* Buckey, P. A., M. S. Foster, E. S. Morton, R. S. Ridgely, & F. Buckely (eds). Neotropical Orni-

thology. Ornithol. Monogr. 36.

- Escalante, R. 1991. Status and conservation of seabirds breeding in Uruguay. Pp. 159–164 in Croxal, J. P. (ed.). Seabird status and conservation: a supplement. ICBP 11. Publisher, Cambridge, UK.
- Greenwood, J. J. D. 2004. Basic techniques. Pp. 11– 110 *in* Sutherland, W. J. (ed.). Ecological census techniques. Cambridge Univ. Press, Cambridge, UK.
- Hammer, Ø., D. A. T. Harper, & P. D. Ryan 2001. PAST: Paleontological statistics software package for education and data analysis. Paleontol. Electron. 4: 9.
- Lambrechts, M. M., J. Blondel, M. Maistre, & P. Perret. 1997. A single response mechanism is responsible for evolutionary adaptive variation in a birds laying date. Proc. Natl. Acad. Sci. 94: 5153–5155.
- Langham, N. P., & K. Hulsman. 1986. The breeding biology of the Crested Tern Sterna bergii. Emu 86: 23–32.
- Quintana, F., & P. M. Yorio. 1997. Breeding biology of Royal and Cayenne terns at a mixed-species colony in Patagonia. Wilson Bull. 109: 650–662.
- Quintana, F., & P. M. Yorio. 1998. Competition for nest sites between Kelp Gulls (*Larus dominicanus*) and terns (*Sterna maxima* and *S. eurygnatha*) in Patagonia. Auk 115: 1068–1071.
- Yorio, P., & F. Quintana. 1997. Predation by Kelp Gulls Larus dominicanus at a mixed-species colony of Royal Terns Sterna maxima and Cayenne Tern Sterna eurygnatha in Patagonia. Ibis 139: 536–541.
- Yorio, P., & M. A. Efe. 2008. Population status of Royal and Cayenne Terns breeding in Argentina and Brazil. Waterbirds 31: 561–570.