

## BREEDING BEHAVIOR OF THE COSCOROBA SWAN (*COSCOROBA COSCOROBA*) IN EL YALI WETLAND, CENTRAL CHILE

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**Resumen.** – **Comportamiento reproductivo del Cisne Coscoroba (*Coscoroba coscoroba*) en el humedal El Yali, Chile central.** – Se observó el comportamiento de parejas durante los períodos de preincubación e incubación, familias e individuos en grupo de Cisne Coscoroba (*Coscoroba coscoroba*) durante Junio a Agosto 2001, Enero 2002, y Junio 2002 a Enero 2003, en el humedal El Yali, Chile. Estimamos que la población local de Cisnes Coscoroba era de aproximadamente 230 a 250 individuos en Julio 2002, de los cuales 34% eran parejas reproductivas que defendían territorios, 29% a 33% eran parejas no territoriales y 33% a 38% eran mayoritariamente individuos jóvenes agrupados. Durante el período de preincubación, los machos y las hembras pasaron proporciones similares de tiempo en alerta, alimentándose, moviéndose, acicalándose, descansando, construyendo nidos y recibiendo agresión, pero los machos fueron más agresivos hacia otros cisnes que las hembras. Durante el período de incubación, los machos pasaron más tiempo moviéndose, acicalándose y siendo agresivos hacia otros cisnes que las hembras. Los machos y las hembras no difirieron en el tiempo que pasaron en alerta, comiendo, construyendo nidos y recibiendo agresión de otros cisnes durante este período. El tamaño del territorio varió de 0,25 a 7,00 ha y algunos nidos estaban ubicados a sólo 10 m de distancia. Los padres acompañaron a sus crías hasta por un año. Siete parejas defendieron territorios todo el año en lagunas con niveles de agua constantes, pero 31 parejas sólo defendieron territorios durante la época reproductiva en pantanos más inestables. Todas las parejas nidificaron fuera de la reserva nacional ubicada dentro del humedal El Yali, y una salina usada para nidificar se secó debido al uso del agua para la agricultura, forzando a algunas parejas a abandonar sus territorios antes y después de la eclosión. Recomendamos protección adicional dentro de la reserva. Además, se necesita mayor comunicación y revisión de los acuerdos entre los dueños y los administradores públicos de estas tierras para conservar el hábitat del Cisne Coscoroba.

**Abstract.** – The behavior of pairs during preincubation and incubation periods, families, and individuals in groups of Coscoroba Swans (*Coscoroba coscoroba*) was observed during June to August 2001, January 2002, and June 2002 to January 2003 in the El Yali wetland, Chile. We estimated the local population of Coscoroba Swans as approximately 230 to 250 individuals in July 2002, of which approximately 34% were breeding pairs defending territories, 29% to 33% were nonterritorial pairs, and 33% to 38% were mostly groups of young birds. During the preincubation period, males and females spent a similar proportion of time alert, feeding, moving, preening, loafing, building nests, and receiving aggression, but males were more aggressive towards other swans than females. During the incubation period, males spent more time

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moving, preening, and being aggressive towards other swans than females. Males and females did not differ in time spent alert, feeding, nest-building or receiving aggression from other swans during this time period. Territory sizes ranged from approximately 0.25 to 7.00 ha, and some nests were only 10 m apart. Cygnets remained with their parents for as long as one year. Seven pairs defended territories year-round in water bodies with permanent water levels, but 31 pairs defended territories only during the breeding season in more unstable marshes. All pairs nested outside of the boundaries of the national reserve located within the El Yali wetland, and one marsh used for nesting dried up due to water use for agriculture, forcing pairs to abandon their territories before and after hatching. We recommend further protection within the national reserve. In addition, better communication and revision of the agreements to conserve this area are needed between private landowners and the public land managers, to conserve the habitat for Coscoroba Swans and other waterbirds. *Accepted 25 August 2007.*

**Key words:** Breeding behavior, Coscoroba Swan, *Coscoroba coscoroba*, Chile.

## INTRODUCTION

The Coscoroba Swan (*Coscoroba coscoroba*) is endemic to southern South America. It is found in Tierra del Fuego and the Falkland Islands north through Chile and Argentina to Paraguay, Uruguay and southern Brazil (Fjeldså & Krabbe 1990). Populations have a patchy distribution and are mainly migratory in the southern part of the range, although details of their migratory movements are unknown (Scott 1972, Rees & Brewer 2005). Birds in the northern part of the range tend to be sedentary (Carboneras 1992).

Coscoroba Swans reach maturity when they are 2 years old and start breeding at 3 to 4 years (Wilmore 1979). They tend to select small islands of floating vegetation in habitats that include both terrestrial and aquatic areas, mostly in coastal wetlands (Scott 1972, Wilmore 1979). Breeding takes place from June to December, although precise timing varies with location (Rees & Brewer 2005). Todd (1996) reported that the nest is built mostly by the male a month before eggs are laid. Coscoroba Swans lay eggs mainly in June and July, although pairs have been observed sitting on nests at Llancanelo, Argentina, during September and December (Darrieu *et al.* 1989), and pairs produced a second brood in central Chile during December (Brewer & Vilina 2002). Only the female incubates in captivity

(Kojima 1978) and with second broods (Brewer & Vilina 2002). In central Chile, brood size ranges from 2 to 11 cygnets (Y. Vilina *et al.* unpubl.) although clutch sizes have not been documented. Breeding density is quite high in prime habitats, with nests as little as 18 m apart (Gibson 1920, Weller 1967). Coscoroba Swans have been described as highly aggressive and territorial during the breeding season, similar to behavior documented for Mute Swans (*Cygnus olor*) (Johnsgard 1965, Kojima 1978, Wilmore 1979).

In southern Brazil, Coscoroba Swans molt remiges between March and December (Nascimento *et al.* 2001), although Wilmore (1979) reported that parents and mature swans in an undisclosed location had a prolonged molting period from November to April. In central Chile, few parents with broods molted in October and January (Brewer & Vilina 2002) although, in southern Chile, Vuilleumier (1997) noted molting birds during late April.

In Chile, the Coscoroba Swan is listed as an "endangered species" (Glade 1993) and has been reported to be an insufficiently known species of Brazilian fauna, and probably in danger of extinction (Nascimento *et al.* 2001). The greatest threat seems to be the loss of temperate marsh habitats (Wilmore 1979, Carboneras 1992). In this regard, a patchy distribution of small populations

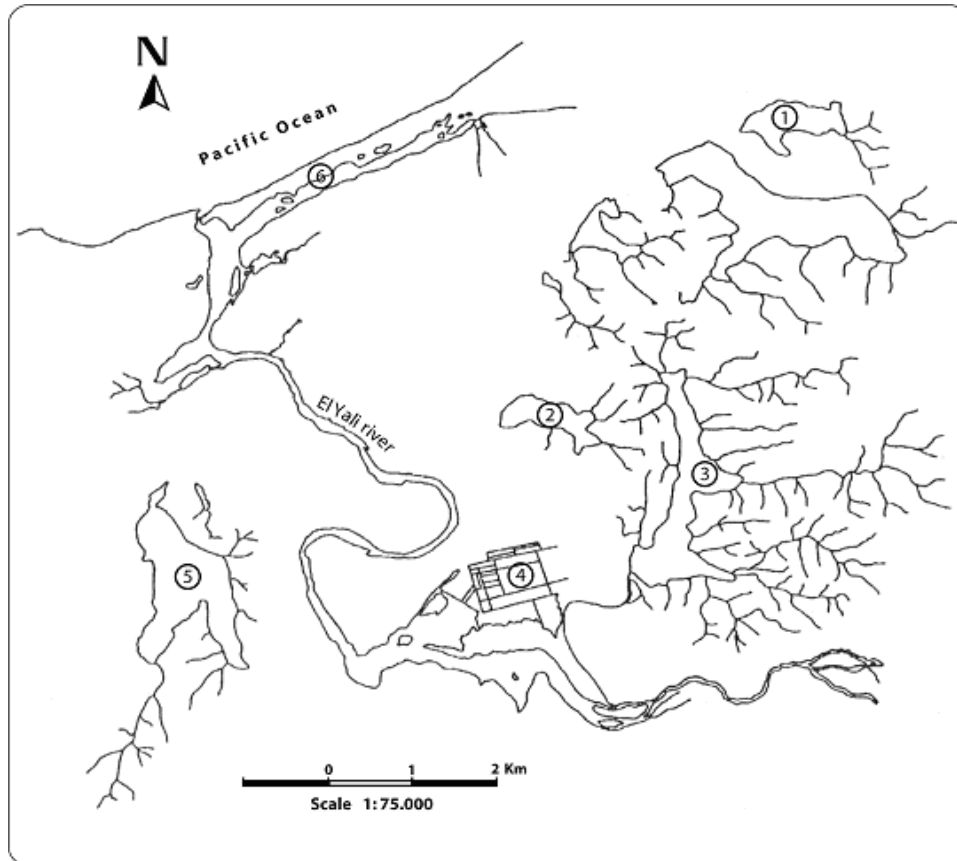


FIG. 1. Study sites at El Yali wetland in central Chile: 1) Laguna Cabildo, 2) Laguna Seca, 3) Tranque Los Molles, 4) Salinas El Convento, 5) Laguna El Rey, and 6) Laguna Costera.

makes this species particularly vulnerable to habitat loss (Rees & Brewer 2005).

Studies on behavioral aspects of the Coscoroba Swan, either in the wild or in captivity, have been purely descriptive or limited in scope. Previous studies of northern and temperate geese and swans have shown that pairs exhibit a division of labor between sexes, particularly during the breeding period (Scott 1977, Lazarus & Inglis 1978, Scott 1980, Sedinger & Raveling 1990, Henson & Cooper 1992, Grant *et al.* 1997, Bollinger & King 2002), and these differences have been attributed to the female's need to acquire, and then

replace, endogenous reserves used for egg formation and maintenance while incubating (Fox & Madsen 1981, Afton & Paulus 1992, Bromley & Jarvis 1993). In the Southern Hemisphere, male Black Swans (*Cygnus atratus*) were found to spend more time incubating than their mates, which appears to contribute to a shorter interclutch interval and the ability to respond to unpredictable favorable breeding conditions (Brugger & Taborsky 1994). The main objectives of this study were to document the breeding behavior of the Coscoroba Swan in the wild in central Chile, and to determine differences in behavior

between sexes during preincubation and incubation periods. We hypothesized that, similar to northern swans, male Coscoroba Swans maintain and defend the territory (Kear 1972) and provide the bulk of nest construction (Evans 1975, Henson & Cooper 1992), and that females spend more time feeding than males during the preincubation period (Henson & Cooper 1992, Grant et al. 1997). Although male incubation behavior has been documented in the Southern Hemisphere Black Swan (Miers & Williams 1969, Brugger & Taborsky 1994) and in several Northern Hemisphere species (e.g., Hawkins 1986, Kriytsov & Mineyev 1991), male Coscoroba Swans have not been reported incubating in the wild nor in captivity. We predicted that during the incubation period, male Coscoroba Swans would continue to maintain the defense of the territory and that the female would spend more time on the nest.

## STUDY AREA AND METHODS

*Study area.* The coastal wetland El Yali (33°47'S, 71°23'W, 520 ha) is located 200 km SW of Santiago, Chile. The area corresponds to the subhumid Mediterranean region, with warm, dry summers and cool, rainy winters. The rainy period generally extends from April to September (Di Castri & Hajek 1976). The average mean annual rainfall is 371 mm, ranging from 127 to 852 mm. The mean annual temperature is 14°C, with means in summer and winter of 19°C and 12°C, respectively. This wetland has been declared a Ramsar site (the Convention on Wetlands of International Importance, especially as waterfowl habitat) because of the great diversity of its aquatic avifauna. However, it is protected only partially by CONAF (Chilean National Forest Corporation) as a National Reserve with human exclusion. The water bodies at El Yali wetland have brackish waters and are surrounded by dunes and beaches. The vegeta-

tion is mainly meadow (pajonal) or emergent aquatic vegetation, low-density thorn shrubs, agriculture fields, and a small remnant of native sclerophyllous forest. The Coscoroba Swans in the El Yali wetland correspond to the northernmost breeding population on the Pacific coast, as a result of a recent range extension (Vilina 1994).

Observations were made at six sites within the El Yali wetland (Fig. 1). Laguna Cabildo has several small islands with some low vegetation. This site corresponds to a small lagoon (37 ha) with shallow waters (< 2 m) and abundant aquatic floating vegetation. Salinas El Convento is a salt marsh (60 ha) flooded by rainfall during the winter and artificially flooded during most summers. This shallow water salt marsh (< 1 m) lacks aquatic emergent vegetation but has some low terrestrial vegetation. Tranque Los Molles corresponds to a large (83 ha) reservoir with no emergent vegetation. Laguna El Rey is a large lake (106 ha), with an extensive flooded marsh area with abundant emergent vegetation (*Scirpus* sp., *Typha* sp.). Laguna Costera (94 ha) has sandy beaches and floating vegetation. Laguna Seca is a small lagoon flooded only during rainy years. Most of the water bodies where swan territories were established during this study have unstable water levels that depend on the total winter rainfall. Only Laguna Costera and Tranque Los Molles have more permanent water levels. Other species of waterfowl present at this wetland were Black-necked Swan (*Cygnus melancoryphus*), Chiloe Wigeon (*Anas sibilatrix*), Yellow-billed Pintail (*Anas georgica*), Red Shoveler (*Anas platalea*), Cinnamon Teal (*Anas cyanoptera*), White-cheeked Pintail (*Anas bahamensis*), Rosy-billed Pochard (*Netta peposaca*), Argentine Ruddy Duck (*Oxyynra vittata*), Black-headed Duck (*Heteronetta atricapilla*), and Speckled Teal (*Anas flavisrostris*). In July 2001 and 2002, we conducted simultaneous censuses at seven sites in order to

determine the total number of Coscoroba Swans at the wetland. The structure of the population was estimated during behavioral observations.

Pairs, families and individuals in groups were observed during 27 June to 7 August 2001, 13 to 23 January 2002, and 21 June 2002 to 21 January 2003 (Silva-García 2003). We used focal-animal sampling (Altmann 1974) to observe pairs, noting each minute the following behaviors of female and male: alert (extreme head-up), feeding, moving, preening (or bathing), loafing (sleeping and resting), aggression towards others, aggression received, and nest-building. Observations on pairs ceased if the male or female went out of sight, and resumed when both sexes were in sight. Observations were made during different times of day using a 20x spotting scope or binoculars from a distance of 100–700 m. Individual Coscoroba Swans and pairs were identified whenever possible by distinctive plumage and sex (male and female differ in body size, neck length in relation to body size, and voice). In addition, territorial pairs were identified from the area that they defended. Territories were defined by the behavior of pairs and measured to the nearest 0.01 ha using an aerial photo.

We observed 38 territorial pairs for 158 observation periods (from 11 to 90 min in length, for a total of 141 h) during the preincubation period, of which 65.8% were 1 h in length, 9.5% were 0.5–1 h, 20.9% were 0.5 h, 1.9% were < 0.5 h, and 1.9% were > 1 h in length. Sixteen of these pairs were observed for 39 observation periods (from 17 to 60 min in length, for a total of 35 h) during the incubation period, of which 82.1% were 1 h in length, 5.1% were 0.5–1 h length, 7.7% were 0.5 h, and 5.1% were < 0.5 h.

*Statistical analysis.* Data from each observation period were used to calculate percentages of time male and female in each territorial pair

spent exhibiting behaviors in the categories previously described. Percentage time data of multiple observation periods were averaged to obtain means for each territorial male and female. These means were then averaged to obtain overall means and standard errors. Paired t-tests were used to compare time spent alert, feeding, moving, preening, loafing, nest-building, in aggression given to other swans and in aggression received from other individuals between males and females during the preincubation and incubation periods. To maintain the overall level of significance when performing multiple comparisons, we used the Bonferroni method to adjust the alpha level according to Bart *et al.* (1998) by dividing 0.05 by the number of tests performed. Therefore, significance was determined at the 0.006 level.

## RESULTS

*Population numbers and structure.* In a census during July 2001, the total population of Coscoroba Swans at El Yali wetland was 177 individuals, and we estimated the total population to be approximately 230 to 250 individuals in July 2002. We also estimated that, in July 2002, 82 (34%) individuals were in territorial (breeding) pairs, 70 to 80 (29% to 33%) were in non-territorial (non-breeding) pairs, and 80 to 90 (33% to 38%) were moving in groups of variable size. At least 70 % of the latter individuals were young swans with adult plumage that had some remnants of juvenile plumage (some dark spots on the back and wings). In January (2001 and 2002), 3 unpaired females and 10 individuals of unknown sex with no cygnets were observed molting primary feathers.

*Breeding season.* By the time we arrived at the study area in late June 2001 and 2002, some pairs had already started building nests and had established territories. In June 2001, the

TABLE 1. Mean ( $\pm$  SE) percentage of time spent by paired territorial male and female Coscoroba Swans, and mean ( $\pm$  SE) differences between males and females, in various activities during preincubation period. Calculated from means for each territorial male and female. N = 38 pairs.

Sexes	Alert	Feeding	Moving	Preen/bathe	Loaf/sleep	Nest-building	Aggression given	Aggression received
Females	7.7 $\pm$ 1.5	26.4 $\pm$ 4.2	13.3 $\pm$ 1.8	15.7 $\pm$ 2.8	17.0 $\pm$ 2.7	17.4 $\pm$ 4.4	1.8 $\pm$ 0.5	0.1 $\pm$ 0.1
Males	11.5 $\pm$ 2.4	24.8 $\pm$ 4.1	14.0 $\pm$ 2.0	12.8 $\pm$ 2.4	13.8 $\pm$ 2.3	17.9 $\pm$ 4.6	4.2 $\pm$ 0.8	0.3 $\pm$ 0.1
Difference between males and females	-3.7 $\pm$ 2.2	1.5 $\pm$ 2.0	0.6 $\pm$ 1.0	2.9 $\pm$ 1.6	3.2 $\pm$ 1.7	-0.5 $\pm$ 1.8	-2.4 $\pm$ 0.7*	-0.2 $\pm$ 0.1

\*Significant difference ( $P < 0.006$ ) between males and females.

TABLE 2. Mean ( $\pm$  SE) percentage of time spent by male and incubating female Coscoroba Swans, and mean ( $\pm$  SE) differences between males and females, in various activities. Calculated from means for each territorial male and female. N = 16 pairs.

Sexes	Alert	Feeding	Moving	Preen/bathe	Loaf/sleep	Nest-building	Aggression given	Aggression received
Females	8.1 $\pm$ 1.9	4.1 $\pm$ 2.5	7.5 $\pm$ 3.2	3.7 $\pm$ 1.0	65.4 $\pm$ 5.1	9.9 $\pm$ 2.7	0.9 $\pm$ 0.7	0.0 $\pm$ 0.0
Males	22.4 $\pm$ 4.5	7.3 $\pm$ 2.6	16.4 $\pm$ 3.7	11.2 $\pm$ 2.1	27.7 $\pm$ 5.0	5.2 $\pm$ 1.7	9.1 $\pm$ 2.5	0.1 $\pm$ 0.1
Difference between males and females	-14.3 $\pm$ 5.0	-3.1 $\pm$ 2.0	-8.9 $\pm$ 2.7*	-7.5 $\pm$ 2.0*	38.0 $\pm$ 5.4*	4.8 $\pm$ 2.0	8.2 $\pm$ 2.2*	0.1 $\pm$ 0.1

\*Significant difference ( $P < 0.006$ ) between males and incubating females.

water level in Laguna Cabildo was lower than in June 2002, and several small islands were present with territories of ten pairs. During June, July, and August 2001, we observed abundant aggressive interactions and pairs trying to establish new territories on those islands. In June 2002, the water level was higher and the islands had almost disappeared. Only five territorial pairs still had territories, no pairs tried to establish new territories during the following months, and the remaining pairs left when the islands disappeared under water during the spring.

We observed a total of 38 copulations from July to September, 23 of them in territorial pairs and 15 in nonterritorial pairs. These copulations occurred in shallow water. The precopulatory display was repeated head-dipping, usually by both sexes. After some of these displays, the male flew up on the female's back and grasped her nape with his bill. After copulation both males and females stretched the head and neck vertically while calling and opening the wings. However, post-copulatory displays were not always performed. We observed two events of forced extra-pair copulation (FEPC) in August 2001 and January 2002. Both events occurred within the male's territory. In one of the events, a territorial male copulated with a paired nonterritorial female. Her mate aggressively defended her by grasping the other male's nape, but this did not prevent the copulation. After the female was released, she left with her mate. In the other event, a territorial male copulated with an apparently unpaired female that was molting. The female was released after a paired nonterritorial male approached, flapping his wings, and chased the male away. The relationship between the defending paired male and the female was not clear.

*Preincubation period and territoriality.* Most nests

were built on small islands near shore with low terrestrial vegetation, or within emergent vegetation in the marsh of Laguna El Rey. Nests were cone-shaped, made of branches and lined with down, and at least five pairs built more than one nest. Minimum and maximum territory sizes per pair were 0.25 and 7.00 ha, respectively ( $N = 38$ ), and the distance between a nest and the nearest two nests ranged from 10 to 125 m (mean = 46.02 m, S.E. = 9.81,  $N = 22$  nests).

We observed 38 pairs defending territories and nesting at four of the six lakes where the observations were conducted. Of these pairs, 11 had territories at Laguna Cabildo on several small islands, 11 defended territories at El Convento salt marsh, 2 had territories on the shore of Tranque Los Molles, and 14 defended territories at the marsh at Laguna El Rey. All of the sites where Coscoroba Swan pairs nested are located on private lands, outside of the boundaries of the El Yali national reserve.

Males and females did not differ ( $P > 0.006$ ) in proportion of time spent alert, feeding, moving, preening, loafing, nest-building, and in aggression received by other swans (Table 1) during the preincubation period. Territories were defended by both males and females, although males were more aggressive towards conspecifics than were females ( $t = -3.530$ ,  $P = 0.001$ ,  $df = 37$ ).

Seven pairs at Laguna Cabildo defended territories year-round; five of these pairs defended territories for at least 21 months and one defended a territory for at least 23 months, during the study. First arrivals and territory establishment at this lagoon were not documented. Other pairs defended territories for at least 6 to 15 months. These pairs defended the same territories when rearing young, and all of them, except one defending a territory on the lagoon shore, abandoned their territories in the small islands when they were flooded by high water levels during the

winter of 2002. Pairs at El Convento salt marsh defended territories only during the nest-building and incubation periods between July and November 2002. Five of these pairs abandoned their nests and territories before hatching cygnets, when the water levels in the area started to decrease in November. Six pairs and their broods left their territories when this water body dried up due to the use of the water for agriculture in December. During this period, several families with flightless cygnets were observed leaving the salt marsh and walking long distances (1.8 km approximately) over land to Tranque Los Molles. The two pairs with territories at Tranque Los Molles defended them only during nest-building and incubation in October and November, and were last observed in December with their cygnets. In the marsh of El Rey, 14 pairs defended territories, and 12 of them defended a territory during nest-building and incubation from August to October. However, after their broods hatched, they moved to other areas within the same marsh and defended new feeding territories in November in patches of abundant aquatic vegetation that proliferated especially during the spring.

*Incubation and some aspects of parental care.*

Females were observed sitting on nests during the period from July to December. No males were observed sitting on a nest. Females spent significantly more time loafing than did males during the incubation period, and they only loafed while sitting on the nest ( $t = 6.957$ ,  $P < 0.0001$ ,  $df = 15$ , Table 2). Males spent significantly more time moving, preening, and in aggression towards other swans than females ( $t = -3.332$ ,  $P = 0.005$ ;  $t = -3.659$ ,  $P = 0.002$ , and  $t = -3.795$ ,  $P = 0.002$ ; all  $df = 15$ ). Males and females did not differ, in time spent alert, feeding, nest-building or receiving aggression from other swans ( $P > 0.006$ ).

The first broods were observed in October 2002 at the marsh of Laguna El Rey. Newly hatched broods were observed until January 2003 when the study ended. Brood size ranged from 1 to 10 cygnets (mean = 5.32, S.E. = 0.431,  $N = 41$ ). One brood of 10 was seen to result from brood amalgamation. Two broods only a few days old, one with three cygnets and the other with seven, got mixed during feeding. Parents became involved in prolonged aggressive interactions, but they were unsuccessful in separating the broods and, after several hours, the mixed brood stayed with one of the pairs. We observed no occurrences of double brooding.

Both parents led young and defended them from approaching individuals of Coscoroba Swans or other species such as Black-necked Swans or ducks. We observed four different attempts of predation on newly hatched broods by Kelp Gulls (*Larus dominicanus*) and, in these cases, parents adopted an aggressive position with head up and wings raised. Most families that were observed in Laguna Cabildo in January 2002 had disbanded by June 2002 when cygnets were at least 8 to 9 months old. One pair with cygnets that had hatched in September or October 2001 remained with the cygnets until September 2002. This pair left the lagoon when their territory on one of the islands was flooded, but their cygnets stayed at that lagoon, moving together with other small groups of juveniles. A similar case was registered for a pair with one cygnet that possibly hatched during December 2001. The parents remained with their cygnet until August 2002. In both cases, parental aggression towards juveniles was evident from near the beginning of the breeding season in July 2002, and at times cygnets were observed to move independently from their parents. Neither pair could be followed to determine if they bred successfully in the next breeding season.



## DISCUSSION

The Coscoroba Swan population at El Yali wetland, central Chile, showed an extended breeding season, with a prolonged nesting period from June to December. We registered few broods hatching in January. These observations coincide with descriptions for other regions in the species' range (Rees & Brewer 2005), and with descriptions of a prolonged breeding season for populations of Black-necked Swans in Chile (Schlatter *et al.* 1991). This possibly relates to the extended period of favorable conditions in temperate wetlands.

Todd (1996) reported that the nest is built mostly by males a month before eggs are laid. However, in this study, we found that males and females spent the same proportion of time building the nest during the preincubation and incubation periods. These results differ from what has been described for swans in the Northern Hemisphere. Male Trumpeter Swans (*Cygnus buccinator*) spend twice as much time as females in nest-building behavior during the preincubation period (Henson & Cooper 1992). A similar division of labor was observed in a pair of captive Tundra Swans (*Cygnus columbianus*) (Evans 1977). In Trumpeter and Tundra swans, males provide the bulk of nest construction and perform other duties that include territory defense (Kear 1972) and sitting on eggs during female incubation recess (Hawkins 1986) to allow their mates to maximize food intake. During the preincubation period, male Coscoroba Swans were significantly more aggressive than their mates. Therefore, male Coscoroba Swans shared nest-building during the preincubation period and specialized in territorial defense to protect females, feeding sites, and probably nest material in a habitat where nests can be only 10 m apart.

These activities of the male mate decrease the female's need to spend time in nest-building, and behavior and energy in aggressive

interactions during the preincubation period, which probably allows her to accumulate reserves more efficiently. However, we did not find differences in the proportion of time males and females spent feeding during the preincubation or incubation period. In the Northern Hemisphere, Trumpeter Swan females fed 48% and 42% of the time during the prelaying period (Henson & Cooper 1992, Grant *et al.* 1997, respectively), while, in Coscoroba Swans, we found that females only fed 26% of the time during the same period. This difference may be explained by the more prolonged favorable conditions that are not restricted by extreme seasonal changes in temperate Mediterranean habitats like the El Yali wetland, so that southern female swans are not forced to acquire their nutritional requirements for reproduction during a short period of time. Furthermore, this population is sedentary and does not have to face an energetically-costly spring migration before trying to breed or an autumn migration after the breeding season like northern species of swans. Therefore, nonmigratory Southern Hemisphere female swans might not be so constrained as northern female or migratory southern female swans to feed and build up or restore protein and lipid reserves in a limited time when conditions are favorable, either before the breeding season or before migration.

During the incubation period, females spent the majority (65%) of their time incubating eggs. Males spent a greater proportion of the time being aggressive towards other swans than females, and they were still involved in nest construction. Anserinae females maintain high levels of incubation constancy to minimize the length of the incubation period and protect against predators and adverse weather (Aldrich & Raveling 1983, Owen & Black 1990, Afton & Paulus 1992). However, females still need to take feeding recesses, which increase the risk of

predation on eggs. Therefore, male Coscoroba Swans, as in other swan species, act more aggressively than do females during the incubation period to protect their immediate reproductive interests, the eggs, and their long-term interests, the females (Henson & Cooper 1992). High levels of male aggressiveness towards intruders may also allow females to feed for longer periods during incubation, although we did not quantify the length of female feeding bouts in this study.

In a previous study at the same wetland, pairs were observed incubating a second clutch while tending cygnets during October 2000 (Brewer & Vilina 2002). We did not observe evidence of double brooding for those pairs or other pairs in subsequent breeding seasons (2001–2002, 2002–2003). Further studies are needed to determine factors favoring or preventing double brooding in this species, but the continued availability of nest sites as affected by water levels is likely to be a factor.

We observed the occurrence of one brood amalgamation. This phenomenon has been described in Black Swans (Bowler 2005), Trumpeter Swans (Mitchell & Rotella 1997), Whooper Swans (*Cygnus cygnus*) (Rees *et al.* 1990) and Mute Swans (Meng & Parkin 1991), but has not been described previously for Coscoroba Swans. The observation that 5 of 41 broods observed during the study had 10 cygnets suggests that either brood sizes are larger than published clutch size data would indicate, or that brood amalgamation is not uncommon.

We observed only a few birds molting wing feathers during January 2001 and January 2002, none of which were accompanying broods. We did not note any other bird molting between June and January 2002. This study did not cover the period between February and May but, in southern Chile, individuals molted during late April (Vuilleumier 1997). It is possible that most of the popula-

tion of Coscoroba Swan in El Yali wetland molts between January and June, but further observations are needed to confirm this.

Offspring remained with both parents until fledging, (wild cygnets begin flying at 13 weeks), with family bonds typically persisting for another month. However, we found that offspring remained with both parents as long as one year in one case and 8–9 months in another case at Laguna Cabildo.

The pre- and postcopulatory displays we observed were similar to that described previously for the species (Johnsgard 1965, Wilmore 1979) except that the female also performed repeated head dipping before copulation on some occasions. Forced extra-pair copulations (FEPCs) appear to be part of a secondary mating strategy in some species of waterfowl but are apparently absent in some taxa, and range from rare to common in others (McKinney & Evarts 1998). This behavior has not been described previously for Coscoroba Swan or any other swan species. We only observed two events of FEPC during the study, which suggests that this strategy is occasional in Coscoroba Swan. Further information is necessary to understand the factors promoting or excluding FEPC as part of a male's mating system in this species.

Most northern swans-Bewick's (*Cygnus bewickii*), Whooper, Tundra and Trumpeter-defend territories only during the breeding season, and copulation, nesting, brood rearing, and foraging of adults and young occur in the same area. However, during the winter, these species are gregarious. In contrast, the Mute Swan, another northern species, may defend a territory year-round with intensive aggression or, in climates where the water freezes during the winter, it defends territories only during the breeding season (Kear 1972). In the Southern Hemisphere, the Black Swan breeds in large colonies in situations where food is abundant and water levels are

unstable, but is territorial around the breeding season when it occurs in water bodies with constant water levels and limited food (Kear 1972, Williams 1981). The stability of water levels at the nesting places might be the main factor influencing the length of time that Coscoroba Swan pairs defend a territory. Some pairs defended a territory year round, although these pairs abandoned their territories when the nesting places were no longer available because of high water levels. However, other pairs defended a territory only during the nesting season because the salt marsh dried up after this period.

*Conservation implications.* Coscoroba Swans are not globally threatened, but populations have been reported to be declining. In Chile in the 1970s, the total population was estimated at fewer than 1000 birds (Carboneras 1992). The main threat to Coscoroba Swans seems to be the loss of temperate marsh habitats, as there is little evidence of extensive exploitation and hunting pressure does not appear intense (Todd 1996). Unfortunately, the El Yali wetland is only partially protected, and all pairs observed during this study were nesting in lakes within private lands, outside the boundaries of the reserve. Furthermore, at most of the lakes in the El Yali wetland, recreational activities, such as off-road motorized vehicle use in the surroundings, disturb birds and destroy sand-nesting habitats. We observed illegal hunting several times and intensive cattle grazing within the National Reserve on the marsh at Laguna Costera at the mouth of the El Yali River. Although cattle might not be a direct threat to Coscoroba Swans, they are notorious for destroying the marsh habitat on the shoreline, a potential breeding habitat, and hunting, although seemingly not directed towards swans, might be a strong disturbance factor. Although no pairs were observed nesting in Laguna Costera, possibly because of the high level of disturbance, most young swans

and nonbreeding pairs stayed there during the winter. In addition, local landowners use water for agriculture and, in the saltmarsh, they draw off the water for salt extraction. This evidently affected the pairs nesting at the saltmarsh, because five pairs abandoned their nests before brood hatching, apparently due to the decrease in the water levels. Also, when the marsh finally dried up, the rest of the pairs nesting in this area, along with their flightless cygnets, moved through extended open areas on dry land to a different water body. This increased their exposure to predators and the risk of aggression from other pairs already present in the new sites, which might increase cygnet stress or mortality.

Another potential threat to this species is urbanization. If development in the surrounding areas increases as planned, it may lead to a change in use of the agricultural land, which will increase recreational and tourist pressures. Therefore, urbanization planners urgently need to consult wildlife biologists, and to follow the environmental impact assessment regulations in Chile. We recommend further protection within the National Reserve and better communication and revision of the agreements between private landowners and the government land manager, to efficiently conserve this area declared to be of international habitat for Coscoroba Swans and other wetland species.

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