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Relative abundance of aquatic birds and their use of wetlands in the Patagonia of southern Chile

Abundancia relativa de aves acuáticas y su uso de áreas acuáticas en la Patagonia del sur de Chile

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ABSTRACT

The aquatic birds on 16 wetlands in Torres del Paine National Park, Chile, were surveyed monthly from July 1985 to June 1988. Seasonal patterns varied for each species, but average monthly numbers increased from 464 in August to a high of 911 in January, with migration from the park occurring from March to May. Average December density and diversity had significant negative linear regression relationships with pond or lake size. Absolute numbers were not related to size of wetland area. The Upland Goose (*Chloephaga picta*) and the Redgartered Coot (*Fulica armillata*) were the most abundant species and the ones found on the greates number of ponds and lakes.

Key words: Aquatic birds, Chile, density, diversity.

RESUMEN

Las aves acuáticas de 16 áreas acuáticas en el Parque Nacional Torres del Paine, Chile, fueron muestreadas mensualmente de julio de 1985 a junio de 1988. Los patrones estacionales variaron para cada especie, pero el número promedio de cada mes aumentó de 464 en agosto hasta un máximo de 911 en enero, la emigración desde el parque ocurrió entre marzo y mayo. La densidad y diversidad promedio de diciembre presentó una significativa regresión lineal negativa con relación a la superficie del área acuática. El número absoluto no presentó relación con el tamaño del área acuática. El Caiquén (*Chloephaga picta*) y la Tagua (*Fulica armillata*) fueron las especies más abundantes y las que se encontraron en mayor número en las áreas acuáticas.

Palabras claves: Aves acuáticas, Chile, densidad, diversidad.

INTRODUCTION

The Patagonia of South America is an arid region dominated by desert, grassland, steppe, and shrubland (Edit 1968). On the southwestern edge of the Patagonia at the base of the Andean mountains and foothills there are numerous wetland areas –marshes, ponds, and lakes suitable for summertime use by aquatic birds. The few previous studies on the wetland birds in this region have focused on the local presence of aquatic species (Jory *et al.*, 1974; Guzman *et al.*, 1985), summer densities of Sheldgeese (*Chloephaga sp.*) (Siegfried *et al.*, 1988), and winter abundance of the Chilean Flamingo (*Phoenicopterus chilensis*), Coscoroba Swan (*Coscoroba coscoroba*), and Black-necked Swan (*Cygnus melancoryphus*) (Markham 1971). Data on seasonal and yearly changes in aquatic bird abundance and their migration patterns are especially lacking.

The primary objectives of this study were: 1) to determine the composition and density of aquatic birds on certain principal ponds and small lakes in a portion of Torres del Paine National Park on the western edge of the Patagonia, 2) to monitor monthly changes in abundance over a

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three-year period, and 3) to determine habitat preferences of these aquatic species. Specifically we tested the hypotheses that lake size was correlated with absolute numbers, density and diversity of waterfowl, and that diversity was correlated with density.

MATERIAL AND METHODS

Study area

Torres del Paine National Park is located in southern Chile in the Ultima Esperanza Province (51°3'S, 72°55'). Created in 1959, the park is an International Man and Biosphere Reserve with a large variety of wildlife and habitat. The 22 km² study area lies between lakes Nordenskjold to the north and Sarmiento to the south and extends from Lake Pehoe to the west and the park boundary to the east (Fig. 1). Scattered throughout the area are a variety of wetlands, ranging from ephemeral ponds with or without emergent vegetation to semipermanent and permanent ponds and lakes with different vegetation to semipermanent and permanent ponds and lakes with different degrees of vegetative cover (for definitions see Stewart & Kantrud 1971). These wetlands have been identified as important summer habitat for waterbirds (Scott & Carbonell 1986).

Upland vegetation is classified as a xeric pre-Andean shrub association ("asociación matorral xerófito preandino") with areas of transition to Patagonian steppe (Pisano 1974). Although annual rainfall at Estación Pudeto (now Guardería Pehoe), on the west end of the study area, averages 546 mm (Pisano 1974), there is a precipitations gradient across the study area decreasing from west to east. High-speed winds (often gusting to 80 km/h) from the 3,000 m Andean rain barrier and continental ice fields to the immediate west dominate the area in the summer. These high winds cause rapid evaporation, creating xeric conditions despite relatively high rainfall and making spring and summer water levels highly dependent on winter snowfall and the subsequent spring runoff. Wetland water levels thus may vary considerabley from year to year. Levels on some of the ponds and lakes decreased over the three years of the study, due in part to a decrease in precipitation rates. Precipitation at the park headquarters from July 1985 to June 1986 totaled 865.4 mm, but decreased to 544 and 554 mm during the following two years. Amounts in the actual study was probably lower due to local differences in precipitation patterns (Pisano 1974).

Winter, from June through August, is relatively cold (mean daily July temperature from 1985 to 1988 was 2.9°C) and dry. Depending upon the winter, many smaller wetlands freeze for two to three months. Summer, from December through February, is relatively warm (January mean daily temperature was 12.2°C), windy, and rainy (temperatures from records obtained from June 1985 to July 1988 at park headquarters). Spring and fall are intermediate, with more variable weather patterns.

Methods

Sixteen of 64 seasonal, semi-permanent, and permanent ponds and lakes in the study area were chosen on the basis of preliminary observations of their importance to waterfowl and their accessibility (Table 1). Bodies of water 10 ha and larger were arbitrarily called lakes, and those less than 10 ha were called ponds. Locally the lakes and ponds surveyed were called "lagunas", or lagoons. These wetlands were placed in two categories of cover following the Stewart & Kantrud (1971) classification system. Cover Type 4 included wetland areas with open water or bare soil covering more than 95% of the area and included small ponds and lakes with marginal bands of emergent cover less than six feet in average width. Cover Type 3 represented wetlands areas with central expanses of open water or bare soil of more than 5% of the wetland area and with peripheral bands of emergent cover averaging six feet or more in width. Surface area of each lake was determined by using aerial photos (1:150,000). With the excep-

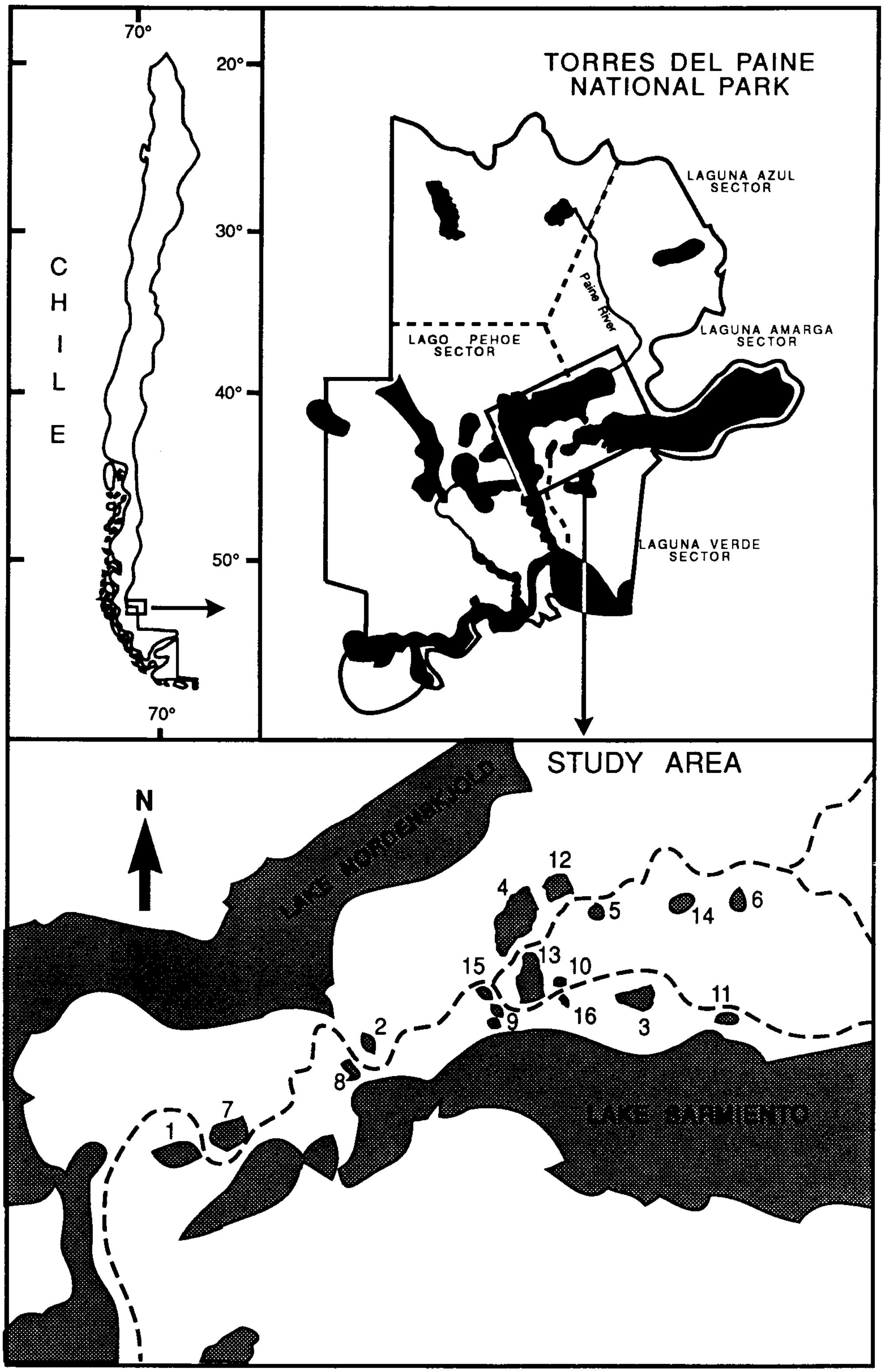

Fig. 1: Location of the 16 ponds and lakes in the study area in Torres del Paine National Park, Chile. The numbers refer to the areas listed in Table 1.

Ubicación de las 16 áreas acuáticas en el área de estudio en el Parque Nacional Torres del Paine, Chile. Los números corresponden a las áreas acuáticas indicadas en Tabla 1.

TABLE 1

Size (ha), mean number of aquatic birds, mean density of birds (N°/ha), and mean index of diversity (Shannon & Weaver 1949) in December for 16 wetland areas in Torres del Paine National Park, Chile from 1985 to 1988. Wetland numbers refer to their location on Fig. 1.

Tamaño (ha), número promedio de aves acuáticas, densidad promedio de aves (número/ha), e índice promedio de diversidad (Shannon & Weaver 1949) en diciembre para 16 áreas acuáticas en el Parque Nacional Torres del Paine, Chile, desde 1985 a 1988. Los números de las áreas acuáticas se refieren a sus ubicaciones en Fig. 1.

Wetland	Size	Number (± SE)	Density (± SE)	Diversity (± SE)
Permanent Lakes and Ponds (Cover Type 4[a])				
1. West Twin Lake	17.6	8 ± 4	0.4 ± 0.2	0.44 ± 0.38
2. Earthwatch Lake	13.5	7 ± 1	0.5 ± 0.1	0.60 ± 0.56
3. Guanaco Lake	10.2	68 ± 16	6.7 ± 1.6	1.57 ± 0.95
4. Larga Lake	24.9	81 ± 27	3.3 ± 1.1	0.29 ± 0.35
5. Isla Pond	0.7	32 ± 20	45.2 ± 28.4	1.59 ± 0.18
6. Blanquillo Lake	17.7	102 ± 73	5.8 ± 4.1	1.64 ± 0.44
Permanent Lakes and Ponds (Cover Type 3[b])				
7. East Twin Lake	14.5	52 ± 34	3.6 ± 2.3	1.31 ± 0.22
8. Paso Pond	3.6	61 ± 18	16.9 ± 5.1	1.68 ± 0.44
9. Calafate Pond	5.3	34 ± 11	6.4 ± 2.1	1.45 ± 0.07
10. Espejo Pond	0.9	25 ± 10	27.8 ± 10.7	1.40 ± 0.33
11. Pato Rana Pond	2.3	31 ± 12	13.3 ± 5.2	1.37 ± 0.30
12. Cuadrada Pond	8.4	51 ± 35	6.0 ± 4.1	1.74 ± 0.16
Semi-permanent Lakes and Ponds (Cover Type 4)				
13. Cisnes Pond	9.3	164 ± 87	17.1 ± 9.4	1.68 ± 0.12
14. Flamencos Pond[a]	8.6	166 ± 66	19.3 ± 7.7	1.80 ± 0.18
Semi-permanent Lakes and Ponds (Cover Type 3)				
15. Chingue Pond	1.2	12 ± 4	10.3 ± 2.9	1.46 ± 0.16
16. Zorra Pond	1.0	12 ± 6	11.7 ± 6.1	1.25 ± 0.24

[a] Not surveyed in December 1988 because it was dry.

tion of four months in 1985-86, the ponds and lakes were surveyed once a month from July 1985 to June 1988 from high vantage overlooks, always in the same order. All waterbirds on or within 10 m of the lake edge were counted. Surveys were made on calm days, because the birds would often refuge in thick vegetation on windy days, reducing their visibility. The major potential source of error was in the identification of the Chilean Teal (*Anas flavirostris*) and the Brown Pintail (*A. georgica*), which were difficult to distinguish when in large groups. When it was impossible to distinguish between these two species, for the purpose of our calculations, we assumed they were present in equal numbers. Surveys taken from July to June were used when comparing yearly differences in aquatic bird desnities.

We sampled waterbirds from the families Anatidae, Podicipedidae, Phoenicopteridae, and Rallidae and classified them as either a year-round resident (nesting birds present in > 80% of the surveys), common summer residents (present in 20-80% of the surveys), or occasional (present in < 20% of the surveys). Species classified as occasional were not included in subsequent analyses. The Buff-necked Ibis (*Theristicus* *caudatus*), Southern Lapwing (*Vanellus chilensis*), and Magellanic Oystercatcher (*Haematopus leucopodus*) were commonly observed around the wetland areas but were not sampled either because they left the wetland areas during the survey hours, or were difficult to accurately census.

Absolute numbers of waterbirds were calculated monthly for each pond or lake, and monthly totals of all areas were combined to determine abundance patterns. Aquatic bird density was calculated monthly for each wetland area by dividing the number of birds surveyed by the surface area of water. To determine if yearly densities changed significantly, December densities of each pond or lake were compared by single-classification ANOVA (Sokal & Rohlf 1981). December was chosen for comparisons because it was near the peak waterfowl abundance, and the number of birds was less likely to be influenced by ponds drying out or by large flocks of migrating birds.

Species richness was measured monthly for each lake as the number of species present. Diversity (H) was calculated in December of each year for each lake with the Shannon-Weaver index (Shannon & Weaver 1949). December averages were compared to determine the relationships between diversity, lake size, density and absolute numbers. Simple linear regression and Pearson's correlation coefficient were used to determine if diversity was correlated to density, and to relate lake size with absolute numbers of waterfowl, density and diversity, and a t-test was used to determine the significance of the correlation coefficient. The different waterfowl species were compared by their December average abundance, the month of average maximum abundance, and by the average percentage of the ponds and lakes each species occupied during December. Student t-tests were used to compare average December densities of each species between lakes and ponds, semi-permanent and permanent wetlands, and wetlands of cover types 3 and 4.

Scientific names and common names in English and Spanish follow Araya & Millie (1989).

RESULTS AND DISCUSSION

Fifteen species of aquatic birds were categorized as common in the study area and three were categorized occasional (Table 2). Six species, the Whitetufted Grebe (*Podiceps rolland*), Silvery Grebe (*P. occipitalis*), Great Grebe (*P. major*), Upland Goose (*Chloephaga picta*), Red-gartered Coot (*Fulica armillata*), and Ruddy Duck (*Oxyura jamaicensis*) were present almost all year (except when the lakes were frozen) and were considered to be year-round residents. The Chilean Flamingo also was present throughout most the year, depending upon the water level of the lakes, but did not nest in the park. The Ashy-headed goose (*Chloephaga poliocephala*), although found only occasionally in our study area, is found almost year-round in other sections of the park, often in groups of Upland Geese.

Overall abundance patterns were reflected by the average number of aquatic birds and number of species surveyed each month (Fig. 3). Migrating birds began to arrive in August, when an average of 70 ± 10% of the species classified as common were in the study area. The average population of wetland birds on the 16 lakes in August was 464 and increased to the greatest numbers from December to February (Fig. 3). Migration from the study area occured from March to May and by June nearly all aquatic birds had disappeared from the ponds and lakes, which often were frozen during June and July.

The Upland Goose was the most common waterbird in the study area, being found in greatest numbers in December. It inhabited a large percentage of the wetlands during the summer (87 ± 4%, Table 3). Due to its habits of nesting in upland areas, of using riversides, and of grazing on forbs and grasses away from wetland areas (Weller 1972), the Upland Goose was even more prevalent than our data indicate. The Upland Goose generally nested in November and began to decrease in abundance around the wetlands in January and February. Although the Upland Goose was not found on the ponds

TABLE 2

Waterfowl species surveyed in 16 wetland areas in Torres del Paine National Park, Chile, from July 1985 to June 1988. Species classified as year-round residents were present in more than 80% of the monthly surveys, common were present 20 to 80%, and occassional were present in less than 20%

Especies de aves acuáticas muestreadas en 16 áreas acuáticas en el Parque Nacional Torres del Paine, Chile, desde julio de 1985 a junio de 1988. Las especies clasificadas como residentes permanentes estaban presente en más de 80% de las muestras mensuales, las comunes entre 20 y 80% y las ocasionales en menos de 20%

Scientific	Spanish	English
YEAR-ROUND RESIDENTS		
Podiceps rolland	Pimpollo	White-tufted Grebe
Podiceps occipitalis	Blanquillo	Silvery Grebe
Podiceps major	Huala grande	Great Grebe
Chloephaga picta	Caiquén	Upland Goose
Fulica armillata	Tagua	Red-gartered Coot
Oxyura jamaicensis	Pato rana de pico ancho	Ruddy Duck
COMMON SUMMER RESIDENTS		
Phoenicopterus chilensis	Flamenco chileno	Chilean Flamingo
Coscoroba coscoroba	Cisne coscoroba	Coscoroba Swan
Cygnus melancoryphus	Cisne de cuello negro	Black-necked Swan
Lophonetta specularioides	Pato juarjual	Crested Duck
Thachyeres patachonicus	Quetru volador	Flying Steamer Duck
Anas sibilatrix	Pato real	Chiloe Wigeon
Anas flavirostris	Pato jergón chico	Chilean Teal
Anas georgica	Pato jergón grande	Brown Pintail
Anas platalea	Pato cuchara	Red Shoveler
OCCASSIONAL (not included in analysis)		
Chloephaga poliocephala	Canquén	Ashy-headed Goose
Anas specularis	Pato anteojillo	Bronze-winged Duck
Anas versicolor	Pato capuchino	Silver Teal

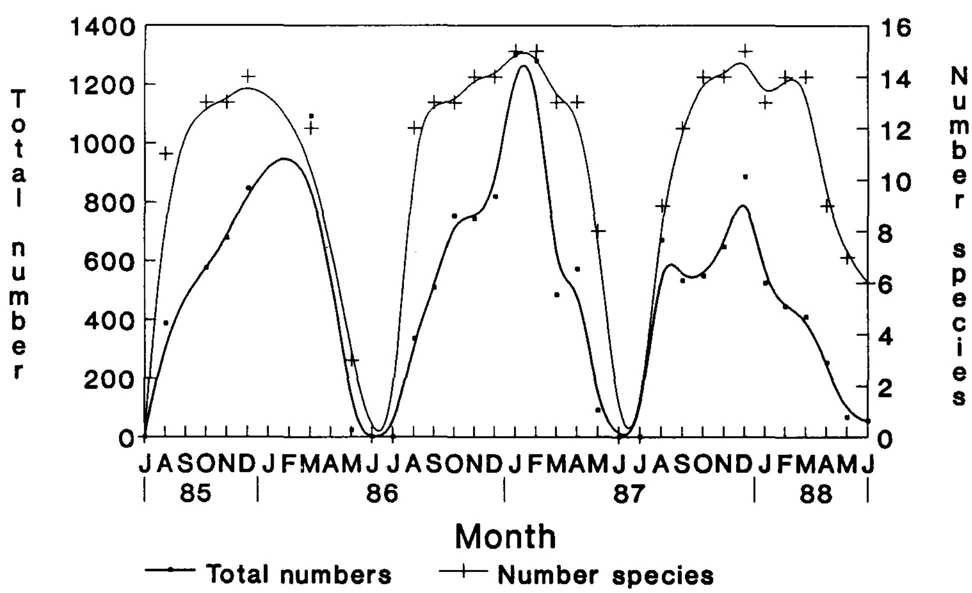

Fig. 2: Number of waterbirds and number of species surveyed from June 1985 to July 1988 in Torres del Paine National Park, Chile.

Número de aves acuáticas y de especies muestreadas de junio desde 1985 a julio de 1988 en el Parque Nacional Torres del Paine, Chile.

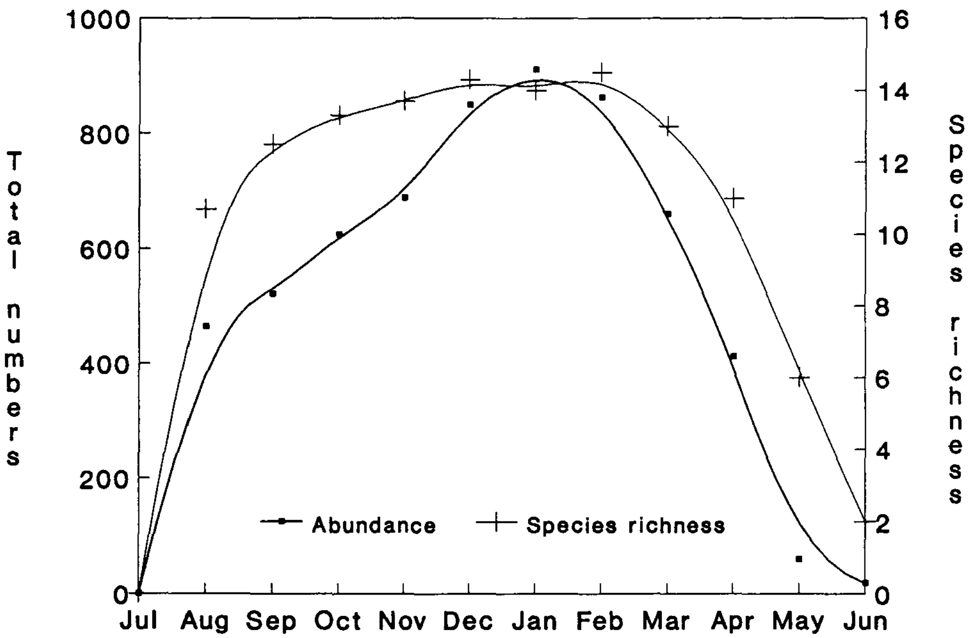

Fig. 3: Mean number of waterbirds and numbers of species surveyed each month on 16 wetlands from Junes 1985 to July 1988 in Torres del Paine National Park, Chile.

Número promedio de aves acuáticas y de especies muestreadas cada mes en 16 áreas acuáticas, desde junio de 1985 a julio de 1988, en el Parque Nacional Torres del Paine, Chile.

TABLE 3

Mean December abundance, month of maximum numbers, number in that month, and mean percentage of the wetland areas on which the species was present in December for 15 aquatic birds from 1985 to 1988 in Torres del Paine National Park, Chile.

Promedio de abundancia en diciembre, mes de números máximos, número en ese mes, y porcentaje de las áreas acuáticas en que la especie estuvo presente en el mes de diciembre para 15 aves acuáticas, desde 1985 a 1988, en el Parque Nacional Torres del Paine, Chile

	Average Abundance (± SE)		Percent Lakes
Species	December	Maximum (month)	% ± SE
White-tufted Grebe	28 ± 5.0	40 ± 7.0 (Feb.)	53 ± 0
Silvery Grebe	80 ± 8.3	143 ± 8.5 (Feb.)	47 ± 11
Great Grebe	12 ± 4.3	14 ± 5.5 (Jan.)	27 ± 4
Upland Goose	237 ±44.2	237 ± 44.2 (Dec.)	87 ± 4
Red-gartered Coot	98 ±19.3	110 ± 7.4 (Aug. & Feb.)	93 ± 4
Chilean Flamingo	8 ± 7.0	16 ± 15.5 (Feb.)	7 ± 4
Coscoroba Swan	12 ± 5.7	13 ± 0.8 (Nov.)	13 ± 7
Black-necked Swan	57 ±40.7	57 ± 40.7 (Dec.)	20 ± 15
Crested Duck	54 ±51.9	54 ± 51.9 (Dec.)	20 ± 10
Flying Steamer Duck	6 ± 3.7	11 ± 5.3 (Aug.)	20 ± 14
Chiloe Wigeon	8 ± 5.9	20 ± 1.2 (Mar.)	13 ± 11
Chilean Teal	46 ±25.0	110 ± 61.0 (Jan.)	27 ± 14
Brown Pintail	33 ±15.8	110 ± 75.0 (Jan.)	27 ± 4
Red Shoveler	13 ± 5.7	54 ± 76.4 (Nov.)	13 ± 0
Ruddy Duck	33 ± 5.4	45 ± 5.4 (Nov.)	60 ± 7

and lakes during June and July, it was the only waterfowl species to remain in the region in great numbers during the winter, forming large flocks of 20 to 300 birds, usually in meadows free of snow. Perhaps because of its abundance and use of upland as well as wetland areas, this goose is one of the most frequent avian prey of local predators. For example, it was the most common bird species in the diet of the Patagonia puma (*Felis concolor*), making up 5% of the vertebrate items in the puma's diet (Iriarte 1989; Iriarte *et al.* 1991a and 1991b). It also was preyed on by the gray fox (*Pseudalopex griseus*) culpeo fox (*P. culpaeus*), and the Geoffroy's cat (*Felis geoffroyi*) (Johnson and Franklin 1991). Nest predation by the two fox species and by the Patagonia hog-nosed skunk (*Conepatus humboldti*) also may be important sources of mortality (Fuller *et al.* 1987, Johnson *et al.* 1988).

The grebes were one of the most abundant families of waterbirds in the area. All three species were year-round residents and commonly nested. The White-tufted and Silvery Grebes had two peaks in their average monthly abundance patterns, first in October and then in February (Fig. 4). This could be due to the formation of flocks on the lakes just before and after migration by portions of the population, or because of increased visibility during these months. During the intervening months they were more dispersed on smaller bodies of water or, because of their nesting activities, were harder to see and count. The White-tufted and the Silvery Grebes were found in nearly significant greater densities on ponds or lakes with emergent vegetation (0.8 and 1.6 birds/ha for Type 3 wetland versus 0.2 and 0.5 birds/ha for Type 4 wetlands; $t = 1.89$, $df = 14$, $P = 0.08$). In contrast, the Great Grebe inhabited only permanent ponds and lakes.

The final waterbirds classified as a year-round residents were the Red-gartered Coot and the Ruddy Duck. The Red-gartered Coot was found, on average, on the greatest percentage of wetlands in December (93 ± 4%), but in significantly greater densities on ponds compared with lakes (7.17 compared with 1.39 birds/ha; $t = 6.33$, $df = 12$,

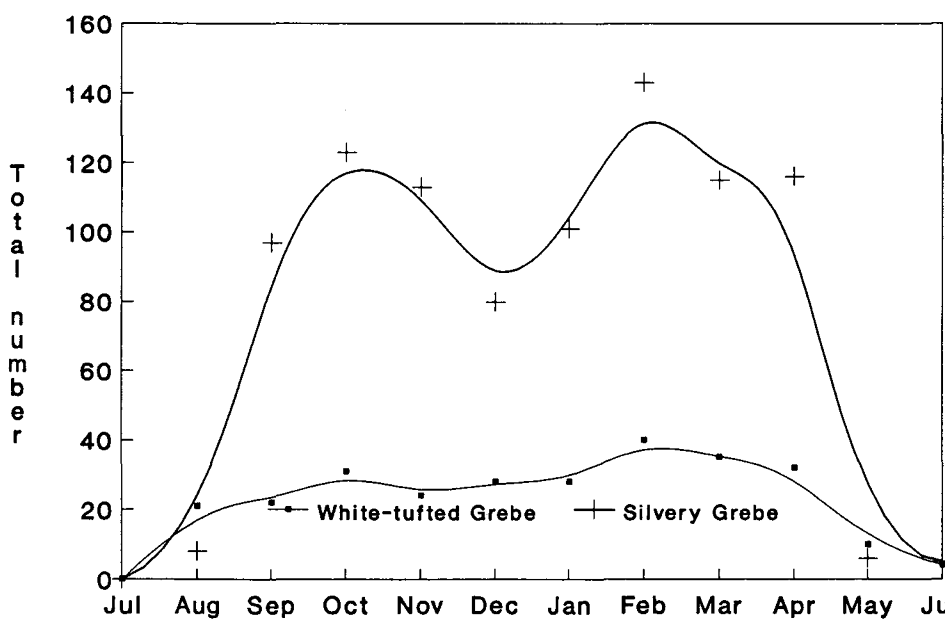

Fig. 4: Mean number of White tufted grebes (*Podiceps rolland*) and Silvery Grebes (*P. occipitalis*) surveyed each month on 16 wetlands from June 1985 to July 1988 in Torres del Paine National Park, Chile.

Número promedio de Pimpollos (*Pociceps rolland*) y de Blanquillos (*P. occipitalis*) muestreados cada mes en 16 áreas acuáticas, de junio desde 1985 a julio de 1988, en el Parque Nacional Torres del Paine, Chile.

$P < 0.001$). The Ruddy Duck was most common in November (45 ± 5.4), and was found in significantly greater densities on ponds and lakes with central expanses of open water (4.25 birds/ha for Type 3 wetland versus 0.27 for Type 4 wetlands: $t = 3.22$, $df = 7$, $P = 0{,}01$.

The Chilean Flamingo, which did not nest in the study area, had the most unpredictable migration pattern. Groups of 3 to 160 flamingos were found during different months of the year with no consistent pattern. Because the nearest Chilean Flamingo nesting areas are in the Andes of northern Chile and the province of Chubut, Argentina (Venegas 1986), flamingos counted in the study area during the summer were probably juveniles or nonbreeding adults. The Chilean Flamingo was the most specialized of the waterbirds studied, using only Cisnes and Flamencos Ponds, both very shallow (1-2 m), alkaline, semipermanent ponds with muddy bottoms and without emergent vegetation.

The family Anatidae had the most species of waterbirds in the study area. Two of these, the Coscoroba and Black-necked Swans, have a protected status in Chile (Glade 1988). The Coscoroba Swan, classified as endangered in Chile, was present in small numbers. One or two pairs nested each year in dense fringe vegetation on different ponds and lakes, especially those which were remote and less disturbed. Average numbers peaked at 13 ± 0.8 birds in November, with most leaving by January or February (Fig. 5). The Black-necked Swan, classified as vulnerable in Chile, was more common, averaging 57 ± 47 birds on the 16 ponds and lakes in December. Like the numbers of Coscoroba, numbers of Black-necked swans dropped sharply between December and January, with only a few swans remaining by March. Both swan species congregated on Cisnes and Flamencos Ponds when these ponds had sufficient water, but also periodically used other wetland areas.

The remaining Anatidae, the Flying Steamer Duck (*Tachyeres patachonicus*), Chiloe Wigeon (*Anas sibilatrix*), Chilean Teal (*A. flavirostris*), Brown Pintail (*A. georgica*), and Red Shoveler (*A. platalea*) had less regular migration patterns. With the exception of the Flying Steamer Duck, which was only seen in pairs, all were

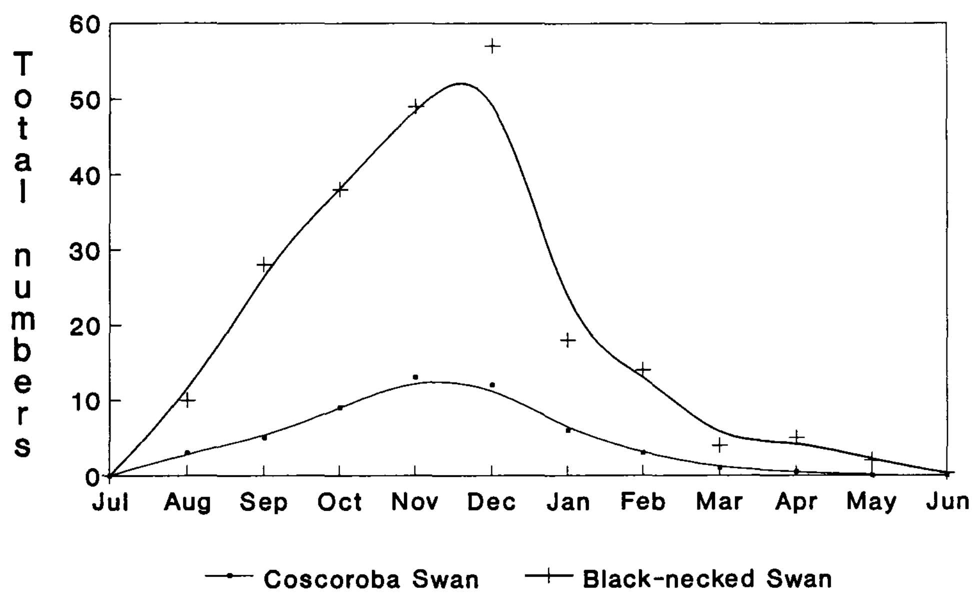

Fig. 5: Mean number of Coscoroba Swans (*Coscoroba coscoroba*) and Black-necked Swans (*Cygnus melancoryphus*) surveyed each month on 16 lakes from June 1985 to July 1988 in Torres del Paine National Park, Chile.

Número promedio de Cisnes Coscorobas (*Coscoroba coscoroba*) y de Cisnes de Cuello Negro (*Cygnus melancoryphus*) muestreados cada mes en 16 áreas acuáticas, desde junio de 1985 a julio de 1988, en el Parque Nacional Torres del Paine, Chile.

regularly found in groups. Although a portion of the population of each of these species nested in the study area, the Red Shoveler and the Flying Steamer Duck did so only occacionally.

Average December densities of waterbirds ranged from 0.4 to 45.2 / ha. There was no significant difference in average density of aquatic birds between the three years ($F = 0.24$, $df = 2$, $P = 0.80$), but overall numbers appeared to be decreasing (Fig. 2), probably related to the decreased water levels of many of the ponds and lakes, especially the drying out of Cisnes and Flamencos Ponds. Density of waterbirds had a significant negative relation with lake or pond size ($r = -0.63$, $t = 3.01$, $df = 14$, $P = 0.009$), but the absolute number of wetland birds did not ($r = 0.28$, $t = 1.078$, $df = 14$, $P = 0.30$).

During the months of greatest aquatic bird densities, a large percentage of the birds were concentrated on a few ponds and lakes. For example in March, 1986, 75% of the birds surveyed were found on three wetland areas, Flamencos and Cisnes Ponds and Blanquillo Lake.

Average December aquatic-bird diversity varied widely for each wetland area, but had significant negative relation with lake or pond size ($r = -0.60$, $t = 2.77$, $df = 14$, $P = 0.02$). Average December aquatic-bird diversity was not correlated with average density, although there was a nearly significant trend for diversity to increase with density ($r = 0.47$, $t = 1.993$, $df = 14$, $P = 0.07$).

Smaller ponds and lakes thus had greater densities and diversities of waterfowl species than larger ones, indicating they had qualities that were important to more waterbirds. Species diversity is usually directly related to a heterogeneous environment (Ricklefs 1987). This seems to be true in Torres del Paine because wetlands with high diversity indexes had a mixture of open water, vegetative cover (predominantly *Junco* sp.), and at least a portion of its shallow bottom covered by rooted vegetation. The only two exceptions were Lakes Flamencos and Cisnes, which did not have bottom or emergent vegetation, but were large and shallow and attracted a diverse array of waterfowl to feed on the fauna and flora of their muddy bottoms.

Two lakes, due to their special history, provided a natural experiment, and demonstrated the relationship between habitat and waterbird diversity. When the main park road was built, it divided a lake into two similarly sized and shaped lakes, now called the Twin Lakes (Lagunas Mellizas). East Twin Lake, which had emergent vegetation (primarily rushes, *Junco* spp.) along one side and was partly covered with vegetative growth along its bottom, had significantly greater average monthly densities than West Twin Lake ($t = 5.88$, $df = 30$, $P < 0.001$) and a much larger average December diversity index than its twin, which was without either submerged or emergent vegetation and appeared to be much deeper. Another notable difference between the two lakes was that West Twin Lake was much more exposed to the wind, suggesting that wind proteccion also may be a factor in determining waterfowl density and diversity.

From the lack of systematic studies on both local and regional waterbird populations in the southern cone of South America, it is apparent that making conclusions about their status and vulnerability is difficult. Most of the management problems such as habitat loss and the lack of good data discussed by Weller (1969) are still unresolved. This study, however, demonstrated the importance of protecting certain wetland areas which could have a major impact on waterbird populations. Smaller ponds and lakes in Torres del Paine were used extensively by waterbirds. Shallow, semipermanent ponds were especially important, being used by the greatest variety and numbers of birds. Because these small lakes and ponds drain easily and degrade quickly with trampling from sheep and cattle, they are vulnerable to human and agricultural activity.

Further studies are needed to determine population characteristics and migration patterns of Patagonian waterbird species and to determine the factors influencing their local distributions. Efforts are especially needed to determine critical habitat for less common waterfowl species before their numbers are even further reduced.

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LITERATURE CITED

ARAYA B & G MILLIE (1989) Guía de campo de las aves de Chile. Editorial Universitaria, Santiago, 405 pp.

EIDT R (1968) Climatology of South America. Monographiae Biologicae 18: 54-80.

FULLER TK, WE JOHNSON, WL FRANKLIN & KA JOHNSON (1987) Notes on the Patagonian hog-nosed skunk (*Conepatus humboldti*) in southern Chile. Journal of Mammalogy 68: 864-867.

GLADE A, (ed) (1988) Red list of Chilean terrestrial vertebrates. Proceedings of the symposium "Conservation status of Chilean terrestrial vertebrate fauna". Corporación Nacional Forestal. Santiago, Chile, 67 pp.

GUZMAN L, A ATALAH & C VENEGAS (1985) Composición específica y estructura de la comunidad de aves de verano en el complejo de la tundra magallánica. Anales del Instituto de la Patagonia (Chile) 16: 75-86.

IRIARTE JA (1989) Feeding ecology of the Patagonia puma (*Felis concolor patagonica*) in Torres del Paine National Park, Chile. M.A. Thesis, University of Florida, Gainesville, 79 pp.

IRIARTE JA, WL FRANKLIN, WE JOHNSON & KH REDFORD (1991a) Biogeographic variation of food habits and body size of the American puma (*Felis concolor*). Oecologia 85: 185-190.

IRIARTE JA, WE JOHNSON, and WL FRANKLIN (1991b) Feeding ecology of the Patagonia puma in southernmost Chile. Revista Chilena de Historia Natural 64: 145-156.

JOHNSON WE, TK FULLER, G ARRIBILLAGA, WL FRANKLIN & KA JOHNSON (1988) Seasonal changes in activity patterns of the Patagonian hog-nosed skunk (*Conepatus humboldti*) in Torres del Paine National Park, Chile. Revista Chilena de Historia Natural 61: 217-221.

JORY JE, C VENEGAS & WA TEXERA (1974) La avifauna del Parque Nacional Laguna de los Cisnes, Tierra del Fuego, Chile. Anales del Instituto de la Patagonia (Chile) 5: 131-154.

MARKHAM BJ (1971) Censo invernal de cisnes y flamencos en Magallanes. Anales del Instituto de la Patagonia (Chile) 2: 146-157.

PISANO E (1974) Estudio ecológico de la región continental sur del área andinopatagónica. II: Contribución a la fitogeografía de la zona del Parque Nacional "Torres del Paine". Anales del Instituto de la Patagonia (Chile) 5: 59-104.

RICKLEFS RE (1987) Community diversity: relative roles of local and regional processes. Science 235: 167-171.

SCOTT DA & M CARBONELL, compilers (1986) A directory of Neotropical wetlands. IUCN Cambridge and IWRB Slimbridge, 684 pp.

SIEGFRIED WR, PAR HOCKEY, PG RYAN & AL BOSMAN (1988) Sex and plumage-type ratios of the Lesser Magellan Goose in southern Chile. Wildfowl 39: 15-21.

SHANNON CE & W WEAVER (1949) The mathematical theory of communication. University Illinois Press, Urbana.

SOKAL RR & FJ ROHLF (1981) Biometry. W.H. Freeman and Company, New York, 859 pp.

STEWART RC & HA KANTRUD (1971) Classification of natural ponds and lakes in the glaciated prairie region. U.S. Fish and Wildlife Service Resource Publication 92: 1-57.

VENEGAS C (1986) Aves de Patagonia y Tierra del Fuego chileno-argentino. Ediciones de la Universidad de Magallanes, Punta Arenas, Chile, 79 pp.

WELLER MW (1969) Comments on waterfowl habitat and management problems in Argentina. Wildfowl 20: 126-130.

WELLER MW (1972) Ecological studies of Falkland Islands' waterfowl. Wildfowl 23: 25-44.