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Wilson's Phalarope in the Central Andes and its Interaction with the Chilean Flamingo *

Pollito de mar tricolor en los Andes Centrales y su interacción con el flamenco chileno

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ABSTRACT

More than 500,000 Wilson's phalaropes (*Phalaropus tricolor*) have been observed during the austral summer on shallow, saline lakes of the Bolivian puna. This region, with adjacent parts of Chile and Argentina, thus appears to be the major wintering grounds of the species. The lakes on which it is found in greatest numbers are simultaneously inhabited by large numbers of the Chilean flamingo (*Phoenicopterus chilensis*) and populations of a few invertebrates on which both birds feed: brine shrimp (*Artemia salina*), copepods (*Boeckella poopoensis*), chironomid midges (*Paratrichocladius* sp.), and brine flies (Ephydridae). As *P. chilensis* feed, *P. tricolor* individuals sometimes swim rapidly around them and feed on invertebrates that these larger companions stir up from the lake bottom. *P. tricolor* ignores the other two flamingo species (*Phoenicoparrus andinus, P. jamesi*) present on the lakes; these feed on diatoms and move about less rapidly than does *P. chilensis.*

Keywords: altiplano, saline lakes, zooplankton, Bolivia, Chile.

RESUMEN

Más de 500.000 Pollitos de mar tricolor (*Phalaropus tricolor*) han sido observados durante el verano austral en las someras lagunas salinas de la puna boliviana. Al parecer, esta región, en conjunto con regiones adyacentes de Chile y Argentina, constituye el área principal de invernación para la especie. Las lagunas donde esta ave se encuentra con mayor abundancia están pobladas también por grandes números del Flamenco chileno (*Phoenicopterus chilensis*) y por densas poblaciones de unos pocos invertebrados utilizados por las dos aves como alimento: branquiópodos (*Artemia salina*), copépodos (*Boeckella poopoensis*), quironómidos (*Paratrichocladius* sp.), y moscas de playa (Ephydridae). Cuando los individuos de *P. chilensis* están alimentándose activamente, a veces unos ejemplares de *P. tricolor* nadan rápidamente alrededor de ellos y aprovechan los invertebrados que los primeros revuelven desde el fondo de la laguna. *P. tricolor* ignora las otras dos especies de flamenco (*Phoenicoparrus andinus, P. jamesi*) que se hallan en las lagunas; estas especies se alimentan de diatomeas y se mueven de un sitio a otro más lentamente que *P. chilensis.*

Palabras claves: altiplano, lagos salinos, zooplancton, Bolivia, Chile.

"The mystery which surrounds the winter quarters of the Phalarope has always been an interesting study..."

MEINERTZHAGEN (1925)

INTRODUCTION

Wilson's phalarope or the Pollito de Mar Tricolor (*Phalaropus tricolor*) (Viellot) is an unusual member of the family Scolopacidae. We here report observations indicating that it is one of the most abundant birds in the Central Andes, though there are very few published records of its presence there. We also describe its close association with the Chilean flamingo (*Phoenicopterus chilensis* Molina) in this region.

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P. tricolor typically nests in herbaceous vegetation around lakes and marshes in southern Canada and northwestern United States (Bent 1927, Palmer 1967). It has long been suspected to overwinter in South America and, indeed, there are numerous records of its occurrence there during the austral summer (records summarized by J. Jehl, in manuscript). However, there are no published records of the species having been seen there in large numbers. The largest flock seen by Wetmore (1926) consisted of 40 individuals (Lago Epiquen, Argentina). For Buenos Aires Province, Olrog (1967) reported flocks of up to 28 individuals and Myers and Myers (1979) likewise noted that "Flock sizes were generally small, but ranged to > 50 birds". But in the Argentine interior, 30,000 - 50,000 or more individuals have been observed on both Laguna Pozuelos (22°00' S, 66°00' W; ca. 3500 m) and Mar Chiquita (30°40' S, 62°30' W) (C. Olrog, pers. comm.), and "hundreds" were observed in February 1972 on "a small lake about 10 km north of Abra Pampa", just south of Laguna Pozuelos (M.P. Kahl, pers. comm.). The largest flock recorded for Chile was 20 birds (Johnson 1965), but M. Sallaberry (pers. comm.) has recently observed more than 200 at Lago Chungara (18°15' S, 69°09' W; 4520 m). For coastal lagoons and pools of southern Peru, *P. tricolor* has been reported as "common on passage with some remaining in the district throughout the austral midsummer months" (Hughes 1970). In the Peruvian Andes, "hundreds of thousands" of phalaropes were observed on Lago Junin (11°00' S, 76°20', W; 4080 m) in early October 1977 (J. Fjeldså, pers. comm.) and on Laguna Las Salinas (16°22' S, 71°09' W; 4295 m) in mid-April 1973 (M.P. Kahl, pers. comm.); and there have been several sightings of small numbers of phalaropes on lakes to the north and west of Lago Titicaca, as well as on Lago Titicaca itself (J. Fjeldså, pers. comm., Holmes 1939). A strong tendency to co-occur has been observed for *P. tricolor* and *P. chilensis* on these lakes (Fjeldså 1981). All other records for South America are for small (< 30) or unstated numbers of individuals. Since the number of Wilson's Phalaropes migrating southward from North America at the end of each breeding season is on the order of 1,000,000 - 3,000,000 (J. Jehl, pers. comm.) it is apparent that the species main wintering areas have gone undetected or at least unreported.

METHODS

Our observations of Wilson's phalaropes have been made during a number of expeditions to the Central Andes since 1971. The primary purpose of these expeditions has been a comparative study of altiplano lakes and the three flamingo species (*Phoenicopterus chilensis, Phoenicoparrus andinus* (Philippi), *Phoenicoparrus jamesi* (Sclater) inhabiting them (Hurlbert 1978, 1981, 1982, Hurlbert and Chang 1983, Hurlbert and Keith 1979; Hurlbert, Lopez and Stein, unpub. data) and analysis of the structure and origin of massive blocks of ancient freshwater ice present in a few of the highest salt lakes in the region (Hurlbert and Chang, unpub. data). On every expedition since 1974 we have made a detailed census of the flamingos present on each lake visited. For other bird species, such as *P. tricolor,* we have kept less systematic records and usually have estimated numbers only when these were great or when detailed behavioral observations were made. Censuses have been made using 10X binoculars and 15-60X zoom spotting scopes.

Quantitative zooplankton samples have been collected from all lakes visited. The sampling procedure consisted of walking out into the lake with a 3.5 liter saucepan (cacerola) and plunging in into the always shallow water 5-20 times, each time pouring the collected water through a zooplankton net with 50-60 μm mesh apertures. Samples were preserved in 5-10% formaldehyde.

RESULTS

Phalarope Abundance and Distribution

Our first observations of *P. tricolor* in the altiplano were made in Salar de Carcote (21°20' S, 68°21' W), Chile, during visits in December 1971 and March and December 1972. In the numerous, small (< 0.5 km^2) saline ponds around the margin of this salar, we observed *P. tricolor* in numbers ranging from 1 to 14 per pond. Larger flocks of *P. tricolor* were not observed until we began study of lakes of the Bolivian puna (Fig. 1) in 1975. In Table 1 we list all of our records for

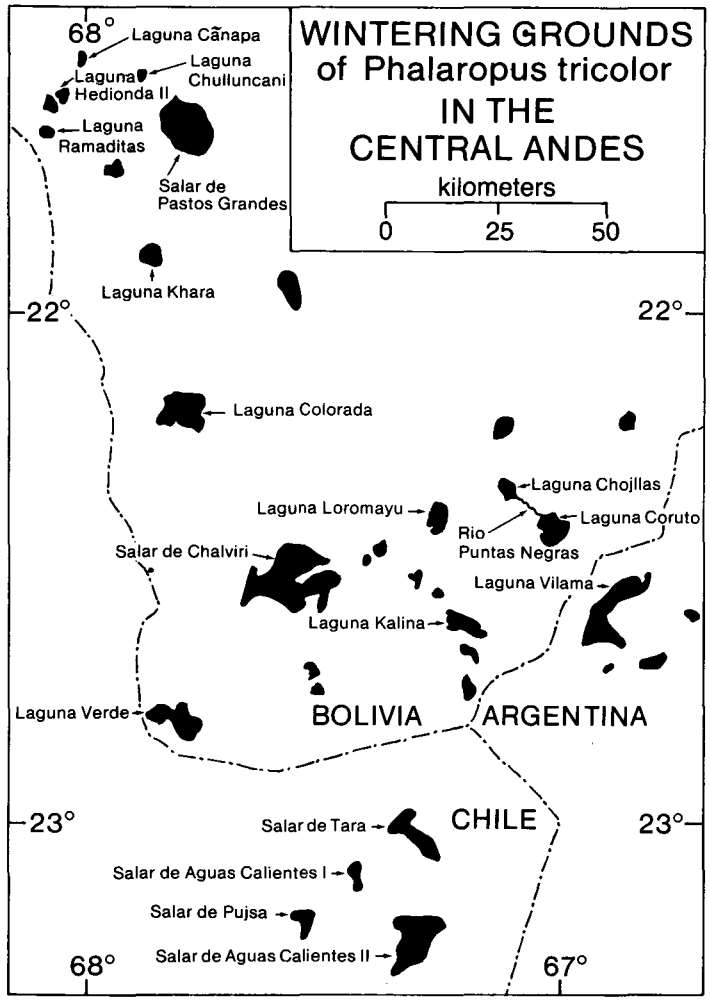

Fig. 1: Location of lakes in the Central Andes where large numbers of Wilson's phalarope occur during the austral summer.

Ubicación de los lagos en los Andes centrales donde se encuentran grandes números de *P. tricolor* durante el verano austral.

P. tricolor flocks exceeding 100 birds. Smaller flocks have been observed during the austral summer in Bolivia on Laguna Totoral (22°32' S, 67°17' W) and in Salar de Chalviri (Laguna Polques, Laguna Norte, Laguna Puripica Chica, Laguna Herrera - see Hurlbert and Chang 1983, for exact locations; 22°33' S, 67°33' W), in Chile on Laguna Lejia (23°30' S, 60° 42' W) and in Laguna Salada (23°41' S, 68°08' W, Salar de Atacama), and in Peru (November 1976) on Laguna Chaccas (15°25' S, 70°12' W) and Lago Titicaca (Puno Bay, 15°45' S, 69°50' W). We also have seen *P. tricolor* in small numbers on several other lakes in the Bolivian puna but did not keep written records of the observations.

Our estimates of the sizes of the larger *P. tricolor* flocks (Table 1) are very approximate, are given verbatim from our field notes, and may in some cases be in error by 50 percent or more. For small birds in large flocks on large and briefly visited lakes, more accurate estimates are not possible. Our census data for the much larger flamingos are more reliable and rarely would be in error by more than 10-20 percent.

The number of *P. tricolor* that overwinter in the southwestern tip of Bolivia is best indicated by our observations in

TABLE 1

Records of Wilson's phalarope on Bolivian lakes, with data on flamingo numbers and other features of the lakes

Registros de *P. tricolor* en lagos bolivianos, con datos sobre números de flamencos y otras características de los lagos.

Lake (latitude S longitude W)	Elevation above sea level (m)	Water surface (km^2)	Salinity[a] (‰)	Date	No. of birds on lake				
					P. chilensis	*P. andinus*	*P. jamesi*	Unidentified flamingos	*P. tricolor*
Laguna Cañapa (21°30', 68°01')	4140	0.4	69-80	14 Feb. 1979	55	2	4	0	"at least 500"
				23 Feb. 1979	29	1	6	0	"400"
Laguna Chulluncani (21°32', 67°52')	4450	0.8	19-69	12 Dec. 1976	354	47	320	0	(no data)
		2.0		22 Feb. 1979	1161	56	86	0	"possibly 25,000"
Laguna Ramaditas (21°38', 68°05')	4117	1.0	28-38	17 Dec. 1975	0	15	10	0	"about 150"
				12 Dec. 1976	67	29	0	0	"thousands"
Laguna Khar Kkota (21°35', 68°04')	4112	2.0	104-180	17 Dec. 1975	20	102	15	0	"about 100"
Laguna Hedionda II (21°34', 68°03')	4121	3.0	66-80	12 Feb. 1979	4154	404	45	0	"about 100,000"
Laguna Colorada (22°10', 67°47')	4278	30	60-292	16 Dec. 1975	46	2	5965	8987	"100+"[d]
				24 Jan. 1979	634[b]	228[b]	7648[b]	900[b]	"4000-5000"
Laguna Loromayu (22°18', 67°13')	4650	7.5	94	18 Feb. 1979	1450	50	0	700	"many hundreds of thousands"
Rio Puntas Negras (22°23', 67°04')	4550	0.02	14[e]	18 Feb. 1979	14	1	0	0	"hundreds"
Laguna Kalina (22°32', 67°11')	4530	16	43-65	1 Feb. 1979	3302	1675	958	6934	"a few hundred thousand"
Laguna Verde[c] (22°48', 67°48')	4315	10	49-55	13 Dec. 1975	588	12	0	300	"3000-5000"
				11 Dec. 1976	734	35	6	0	"thousands"
				20 Jan. 1983	92	119	4	150	"thousands"

a. Determined with an American Optical hand refractometer (Model 10419). Ranges are for samples taken in different locations and/or different years.
b. These data obtained on January 21.
c. Data (including area) are for eastern part of lake only.
d. Only the northwestern most corner of the lake was censused for *P. tricolor*.
e. Value given is actually for Laguna Chojllas from which this river flows.

the first half of February 1979 (Table 1). At that time three lakes –Hedionda II, Loromayu and Kalina– were each estimated to have 100,000 or more *P. tricolor* on them. The total number present on the lakes examined at this time was on the order of 500,000 to 1,000,000, reasonably assuming that we were not simply censusing a single mobile flock moving from lake to lake. Whether large numbers of *P. tricolor* were present at this time at any of the unvisited lakes in this region or in other parts of the altiplano is not known.

Laguna Kalina was where we first saw *P. tricolor* in tremendous numbers. In our field notes we recorded that "phalaropes are everywhere in flocks of thousands and tens of thousand" bobbing in the open lake and resting on mudflats and along the shoreline. At one point along the western shoreline we observed one mudflat that was dark gray, unlike the whitish calcium carbonate mudflats seen elsewhere in the lake. A moment later this darker "mudflat" self-levitated and dispersed over the lake: it was a single flock of roughly 30,000 *P. tricolor.*

The physical characteristics of the lakes hosting large numbers of *P. tricolor* are extreme. The lakes occur at very high elevations, are very saline and very shallow (Table 1). Except possibly for Laguna Verde and Laguna Loromayu, the deeper parts of which we have not inspected, all the lakes have mean depths of less than 0.3 m. Their ionic compositions are, in all cases, of the sodium sulfato-chloride type (unpubl. data).

During the summer the lakes contain dense populations of invertebrates. This food source is undoubtedly the principal feature attracting phalaropes to these lakes. Summer zooplankton abundance has been determined at one time or another for all lakes, though not always at the same time or year that we recorded phalarope numbers (Table 2). In such shallow lakes, the distinction between zooplankton and benthos is somewhat artificial; during the afternoon, when there is almost always a strong wind, crustacean zooplankters are often observed resting on or holding onto the lake bottom. On the other hand, typically benthic organisms such as chironomid larvae and microscopic nematodes frequently are found in the upper part of the water column, leading, at least temporarily, a planktonic existence.

The zooplankton data illustrate very clearly that only a few taxa are present in any one lake,· a condition typical of salt lakes. As each sample represents a single location in the lake, the calculated absolute abundances (Table 2) should be regarded as only roughly indicative of true lake-wide densities.

At all lakes where *P. tricolor* has been observed in large numbers the zooplankton is strongly dominated either by calanoid copepods (*Boeckella poopoensis* Marsh) or by brine shrimp (*Artemia salina* Leach) (Table 2). The greatest numbers of *P. tricolor* were recorded for lakes with *Artemia* –Laguna Hedionda II, Laguna Loromayu and Laguna Kalina. No lake in the set has both *Boeckella* and *Artemia.* Salinity is a fairly good predictor of which will be present, *Artemia* occurring at the higher salinities.

After *Artemia* and *Boeckella,* the most important prey for the *P. tricolor* in this region may be midges (Chironomidae) and brine flies (Ephydridae). During the austral summer chironomids of the genus *Paratrichocladius* are found in great numbers at two lakes –Laguna Verde and Laguna Loromayu. Our plankton data probably underrepresent the real abundance of their larvae. The adult chironomids swarm abundantly around the margins of these same lakes and, when the wind comes up in the afternoon, seek shelter under rocks on the shoreline and vegetation-free pampa surrounding the lakes. However, both adults and pupae may be most available to phalaropes at the water surface on days of mass emergence (J. Fjeldså, pers. comm.). Phalarope excrement on the shoreline of Laguna Verde on December 13, 1975 contained remains of both adult and immature chironomids in abundance, as well as lesser quantities of copepod remains.

Larvae and pupae of ephydrids have never been found in our plankton samples and only occasionally in qualitative samples of the benthos. However, large swarms of adults have been observed at most of the salt lakes of the region, so the rarity of the aquatic stages is probably only apparent, a reflection of patchy within-lake distributions and a preference for firm substrates, which we did not sample. Larvae, pupae and adults of ephydrids

TABLE 2

Zooplankton abundance in lakes hosting large numbers of Wilson's phalarope in the austral summer

Abundancia de zooplanctontes en lagunas con grandes números de *P. tricolor* durante el verano austral

Lake and Date	Number per liter			
	Boeckella poopoensis copepodids	*Boeckella poopoensis* nauplii	*Artemia salina*	Other invertebrates
Laguna Cañapa				
23 Feb. 1979	0	0	45	–
Laguna Chulluncani				
12 Dec. 1976	269	0	0	–
23 Feb. 1979	16.5	6.2	0	*Branchinecta* sp. (2.2)[a]
Laguna Ramaditas				
12 Dec. 1976	36	3	0	–
23 Feb. 1979	202	0	0	nematodes (1.8), harpacticoid copepods (1.8)
Laguna Khar Kkota				
17 Dec. 1975	0	0	0	chironomid larvae ("common")
Laguna Hedionda II				
23 Feb. 1979	0	0	0.9	nematodes (24), harpacticoids (0.9)
Laguna Colorada				
27 Nov. 1977	0	0	1.3	–
Laguna Loromayu				
1 Dec. 1977	0	0	21.4	chironomid larvae (3.1)
18 Feb. 1979	0	0	30.7	–
Río Puntas Negras[b]				
18 Feb. 1979	"abundant"		0	–
Laguna Kalina				
2 Dec. 1977	0	0	124	nematodes (6.2)
3 Feb. 1979	0	0	10.9	nematodes (21.6)
Laguna Verde				
11 Dec. 1976	46	0	0	cyclopoid copepods (27), nematodes (48), chironomids (1.1)
3 Dec. 1977	62.4	22.3	0	–

a. Possibly *Branchinecta palustris* Biraben 1946 (R. Hartland-Rowe, pers. comm.).
b. Quantitative sample was not taken.

have been found in abundance in *P. tricolor* stomachs elsewhere (Bent 1927; J. Jehl, pers. comm.).

Branchiopods in the genus *Branchinecta* have been associated with large numbers of *P. tricolor* only once –in Laguna Chulluncani at a time when its salinity was only 19°/∞ (22 Feb. 1979; Table 2). However, *Branchinecta* spp. are often the dominant form present in the small temporary rainwater pools that form in January or February and last for a few weeks to a few months in wet years. We observed many such pools only in January and February 1979 but saw no *P. tricolor* on them. These rainwater pools develop more abundantly in the rainier central and northern portions of the altiplano.

The abundance of nematodes in many of the *P. tricolor* lakes was striking (Table 2), as this group is rarely seen in the plankton. They may represent benthic forms swept up into the water column by turbulence. The observed nematodes were very small (mostly 200-2000 μm long by 10-40 μm in diameter) and it is unlikely that *P. tricolor* fed on them.

Phalarope-Flamingo Relations

P. tricolor is strongly associated with the Chilean flamingo (*P. chilensis*) during the austral summer both distributionally and behaviorally. In the puna region (roughly the Andes between 21° and 27°) of Bolivia and Chile, the two species occur predominantly on the same lakes, as is also the case in the Peruvian altiplano (Fjeldsa 1981). The three lakes –Hedionda II, Loromayu and Kalina– where *P. trico-*

lor has been recorded in greatest abundance are the same three lakes where we have recorded *P. chilensis* in greatest numbers in the puna, though we have censused flamingos 2-6 times not only for the lakes listed in Table 1 but also for about 60 other lakes in this region (Hurlbert 1978, 1981, and unpubl. data; Hurlbert and Keith 1979). Laguna Chulluncani and Laguna Colorada also commonly have large numbers of both *P. tricolor* and *P. chilensis* present. The rich food supply of invertebrates that makes the lakes of Table 1 favorable wintering grouns for *P. tricolor* also makes them favorable nesting sites for *P. chilensis,* which feeds on the same aquatic insects and crustaceans (Allen 1956, Rooth 1965, Hurlbert, Lopez, and Stein, unpub. data). We have observed *P. chilensis* nesting at Laguna Colorada, Laguna Loromayu, and Laguna Kalina, though most of the eggs laid are harvested by the local inhabitants (Hurlbert and Keith, unpubl. data). *P. chilensis* nested at Laguna Verde in the past and occasionally still attempts to do so, but always unsuccessfully due to visits of the eggers.

P. tricolor abundance shows weak or no correlation with the abundances of the other two flamingos, *P. andinus* and *P. jamesi,* on the puna lakes. Though *P. andinus* and *P. tricolor* sometimes abundantly co-occur on some lakes (e.g. Hedionda II, Kalina: Table 1), *P. andinus* has been observed in large numbers on many puna lakes where *P. tricolor* was uncommon or absent (e.g. in Bolivia, Laguna Polques, Laguna Puripica Chica, Salar de Pastos Grandes, and, in Chile, Laguna Lejia: Hurlbert 1981). Both *P. andinus* and *P. jamesi* feed primarily on diatoms (Hurlbert, Lopez and Stein, unpubl. data).

A more intimate association between *P. tricolor* and *P. chilensis* was observed on Laguna Lejia in December 1975 and on several of the smaller Bolivian lakes in February 1979. At Laguna Lejia we observed phalaropes following Chilean flamingos, apparently picking up organisms stirred up by them. At Laguna Herrera on February 5 we noted *P. tricolor* individuals (numbers unrecorded) clustering around actively feeding *P. chilensis* and pecking at the water surface, presumably feeding on copepods brought to the surface by the rapid stomping or treading motion of the feet of *P. chilensis.* The *P. tricolor* did not associate at all with the 104 *P. andinus* or 54 *P. jamesi* which were present along with the 197 *P. chilensis.*

The numerous *P. tricolor* on Laguna Hedionda on February 12 were feeding in close association with the *P. chilensis* there, ignoring the *P. andinus* and *P. jamesi* present (Table 1). At Laguna Cañapa on February 14 we began observing the small *P. chilensis* flock (Table 1) starting early in the morning while they were still resting, mostly on one leg with heads crooked or tucked under wings, in a group in the center of the lake. At 0610 hours (air temperature = −3°C; sun hit lake at 0655 hours), we observed that "about 60 phalaropes have flown in and swin around flamingos as if waiting for them to wake up and feed"; later interactions were not recorded.

Our most detailed observations on the association were made at Laguna Chulluncani on February 22 (Table 1). All three flamingo species were present, but again *P. tricolor* associated only with actively feeding *P. chilensis.* In the morning, almost every *P. chilensis* individual was closely accompanied by 1-3 *P. tricolor* (Table 3), rapidly swimming between and around the flamingo's legs. *P. chilensis* individuals which were resting or standing still lacked these little companions. In the afternoon, the association broke down somewhat (Table 3). The light southwest wind, which began about 1030 hours, may have stirred the water column sufficiently that *P. tricolor* did not have to depend so much on the movements of *P. chilensis* for raising the *Boeckella* and/or *Branchinecta* to the surface.

Only on one occasion was *P. tricolor* observed to associate with one of the other flamingo species. At Laguna Puripica Chica on February 17 at 1920 hours there were 12 *P. chilensis,* 10 *P. jamesi,* and 1005 *P. andinus* present and we recorded "many phalaropes (number unrecorded) feeding along with the *P. andinus* –but not in as frenzied fashion as when with *P. chilensis*". This lake is only slightly saline (13‰) and contains corixids and amphipods as well as copepods.

The preferential association of *P. tricolor* with *P. chilensis* is almost certainly due to the fact that this flamingo walks much more rapidly and, consequently, stirs up the water and lake bottom more

than do *P. andinus* and *P. jamesi*. We had noted and quantified this difference several years before observing its consequences for *P. tricolor* (Table 4). Typically, *P. chilensis* walks steadily along, *P. andinus* meanders, stopping occasionally, and *P. jamesi* walks very slowly, often spending many seconds working the sediments at one spot. In certain situations *P. chilensis* will remain in one place and furiously stomp the lake botton at a rate of more than 200 "stomps" per minute. The behavioral differences among the species are correlated with the escape ability of their respective prey (Hurlbert, López and Stein, unpubl. data).

TABLE 3

Association of Wilson's phalarope with flamingos on Laguna Chulluncani. 22 February 1979

La asociación de *P. tricolor* con los flamencos en Laguna Chulluncani. 22 febrero 1979

Flamingo species	Activity	Number of phalaropes in attendance per flamingo (k)								
		0	1	2	3	4	5	6	7	
		Number of flamingos attended by k phalaropes								*Total number of flamingos observed*
Morning (0920 hours)										
P. jamesi	feeding	40	0	0	0	0	0	0	0	40
P. andinus	feeding	23	0	0	0	0	0	0	0	23
P. chilensis	feeding	5	36	14	7	2	1	0	1	66
P. chilensis	resting	10	0	0	0	0	0	0	0	10
Afternoon (1320 hours)										
P. chilensis	feeding	128	41	6	2	0	0	0	0	177

TABLE 4

Rates of walking of the three flamingo species during continuous feeding

Velocidad de caminar de las tres especies de flamenco durante alimentación continua

Place, date and species	Walking rate (steps/minute)			
	mean (x)	no. birds. observed (n)	standard deviation (s)	range
Salar de Pedernales, Chile, 25 Nov. 1975 (26°22' S, 69°12' W)				
P. jamesi	8.7	7	3.9	4–16
P. andinus	29.2	6	13.4	5–40
P. chilensis	43.1	7	14.6	23–68
Salar de Aguas Calientes III, Chile. 29 Nov. 1975 (25°00' S, 68°38' W)				
P. jamesi	8.5	4	4.7	5–15
P. andinus	18.4	10	5.6	10–31
P. chilensis	37.3	9	10.5	23–55
Laguna Chulluncani, Bolivia, 12 Dec. 1976				
P. jamesi	17.0	10	7.2	2–26
P. andinus	25.8	9	9.0	12–36
P. chilensis	54.3	7	4.7	50–64

DISCUSSION

Abundance. The salt lakes of southern Bolivia clearly constitute one of the major, if not *the* major, wintering grounds for *P. tricolor.* It also seems likely that during the austral summer this species is the most abundant bird in the entire Andean altiplano. Yet there are no previous published records of its presence in the Bolivian altiplano and very few for elsewhere in the Central Andes –Cumbres Calchaquies, to the east of Tucuman, Argentina (Dabbene 1920). Lago Titicaca and a few other localities in Peru (Morrison 1939, Holmes 1939), and Lago (Embalse de) Caritaya, Chile (Johnson 1965).

Our suggestion that it may be the most abundant bird in the altiplano is based on the size of flocks we observed and our extensive inspection, flamingo censusing, and invertebrate sampling of Central Andean lakes between the latitudes of Cuzco, Peru (14° S) and Copiapo, Chile (27° S) (Hurlbert 1978, 1981, unpubl. data; Hurlbert and Keith 1979). Using abundance of aquatic invertebrates and *P. chilensis* as a criterion, we predict that large numbers (> 1000 individuals) of *P. tricolor* should sometimes be found in the following additional lakes: in Bolivia, at Laguna Khara (Fig. 1), Lago Soledad (17°44' S, 67°22' W), Lago Uru-Uru, Lago Poopo; in Chile, at Salar de Pujsa and Salar de Aguas Calientes I and II (Fig. 1); and in Peru, at Lago Parinacochas (15°17' S, 73°42' W) and Lago Salinas (14°59' S, 70°07' W). Other waterbodies not visited by us, such as Laguna Vilama, Argentina (Fig. 1) and the temporary rainwater pools of the central and northern altiplano possibly serve as winter feeding grounds, too.

The second most abundant bird in the Andean altiplano probably is *P. chilensis,* of which there are estimated to be about 350,000 individuals (Kahl 1980). However a significant but unknown fraction of these occurs in lowland areas of Chile and Argentina.

Though there are numerous published records of *P. tricolor* for lowland areas of Argentina (summarized in J. Jehl, in manuscript), none of them report large numbers. Nevertheless we believe this may reflect only insufficient inspection of the most suitable regions and lakes and that, as has been long suspected and as suggested by the earlier-mentioned observations at Mar Chiquita (C. Olrog, pers. comm.), lowland Argentina serves as wintering grounds for a large fraction of this species. It is likely that lowland Argentina served as wintering ground for greater numbers of *P. tricolor* in the past than at present. Expansion of the human population, agriculture, fish introductions and other habitat-modifying activities of man probably have destroyed the suitability of many areas for *P. tricolor,* just as it has rendered them unsuitable as nesting areas for *P. chilensis* (Johnson 1965). Of course many other birds are likely to have been affected similarly by such change.

Salinity. Because *P. tricolor* overwinters mostly in inland areas, it has been assumed to be less associated with saline waters than are the other two phalaropes, which are oceanic except during the breeding season. Murphy (1936) stated that *P. tricolor* "is found inland to a greater extent than on salt water", failing to recognize that the saltiest waters in the world are inland lakes. Palmer (1967) refers to it as "A fresh-water bird, with rudimentary salt gland (rather than large gland as in the marine phalaropes)". Our data (Table 1) show that on its wintering grounds in Bolivia *P. tricolor* confronts much higher salinities than do the ocean-going phalaropes (ocean salinity is about 35‰). Moreover, at the beginning of its southward migration *P. tricolor* assembles in large numbers and feeds at a few large, highly saline lakes in northern United States (J. Jehl, pers. comm.): Mono Lake, California (80-90‰), Great Salt Lake, Utah (110-270‰), and Lake Abert, Oregon (35-105‰). In these respects, it is one of the most "salt water" birds in the world. However, at all of these lakes, freshwater springs, seeps and/or streams are present at the lake margins and so the birds never need to go for long periods without drinking freshwater. That undoubtedly accounts for the small size of their salt gland, which, in any case, is capable of rapid enlargement (J. Jehl, pers. comm.).

Interaction with P. chilensis. The advantage to *P. tricolor* of consorting with *P. chilensis* is clear. *P. tricolor* in some situations will submerge head and neck while feeding (Bent, 1927), but even where water is only 10 cm deep, they cannot feed on inverte-

brates that remain at the bottom of the water column or on the sediment surface. The vigorous movements of feeding *P. chilensis* bring invertebrates within the smaller bird's reach.

P. tricolor has been observed to cluster about feeding American avocets (*Recurvirostra americana Gmelin)* in exactly the manner they do with *P. chilensis* (Williams 1953). Perhaps they sometines associate with the Andean avocet (*Recurvirostra andina* Philippi & Landbeck) several dozen of which are often present on individual altiplano lakes, but we have not observed this. The ocean-going phalaropes, *Phalaropus lobatus* (Linnaeus) and *P. fulicarius* (Linnaeus), occasionally dine in the commotion of even more distant relatives, feeding on invertebrates chased to the surface by schools of fish or carried there by the turbulent wake of swimming whales (Bent 1927).

P. chilensis is very tolerant of *P. tricolor* despite the insolence with which the latter dodges about the flamingo's legs. We have never observed any hostile reaction of the flamingos to the phalaropes. Yet when present in large numbers *P. tricolor* must markedly reduce food availability to *P. chilensis,* and vice versa. They are clearly competitors.

Even by itself *P. chilensis* can rapidly deplete the invertebrate populations of a shallow lake (Rooth 1965). At Laguna Herrera (area = 1 km^2), Bolivia on December 25, 1976 the density of copepods (*Boeckella poopoensis* copepodids) was 382/liter. Fourty-three days later (February 6, 1979) the copepod density was 11/liter. Nauplius larvae declined correspondingly. The evidence is only circumstantial, but it seems highly probable that this reduction was the result of predation by the approximately 150 pairs of *P. chilensis* that were nesting at this lake. Some *P. tricolor* (numbers unrecorded) were feeding in close association with the *P. chilensis* on February 6, and may have contributed to the copepod decline. There is evidence that predation by the Red Phalarope (*P. fulicarius*) may have a significant impact on the zooplankton of shallow ponds in the Arctic tundra (Dobson and Egger 1980).

By its effects on prey abundance, *P. chilensis* may influence *P. tricolor* in several ways. It could affect the number of *P. tricolor* that overwinter in the region, their distribution and movement among lakes in the region, and their physiological conditlon (and hence chances for survival) at the start of their migration back to North America. Whether man, by intensively harvesting the eggs of *P. chilensis* and thereby reducing its numbers, has indirectly increased the abundance of aquatic invertebrates in altiplano lakes and thus made them more favorable as wintering grounds for *P. tricolor* is open to speculation. It is clear, however, that intensive harvesting is occurring (Hurlbert and Keith, unpubl. data) and it probably has been going on since man arrived in South America. The small colony observed at Laguna Herrera in 1978-79 was the only *P. chilensis* colony (of the several we have observed in the altiplano) that escaped the attention of the egg harvesters and produced flamingo chicks. However, we do not have direct evidence that egg harvesting has reduced the numbers of *P. chilensis* or even that *P. chilensis* has declined in abundance.

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LITERATURE CITED

BENT AC (1927) Life histories of North American Shorebirds, Part 1. U. S. National Museum, Bulletin 142: 1-359.

DABBENE R (1920) Notas sobre los chorlos de Norte América que inviernan en la República Argentina. El Hornero 2: 99-128.

DODSON SI & DL EGGER (1980) Selective feeding of Red Phalaropes on zooplankton of Arctic ponds. Ecology 61: 755-763.

FJELDSA J (1981) A comparison of bird communities in temperate and subarctic wetlands in northern Europe and the Andes. Proceedings of the Second Nordic Congress of Ornithology, 1979: 101-108. Norwegian Ornithological Society.

HOLMES PF (1939) Some oceanic records and notes on the winter distribution of phalaropes. Ibis 81: 329-342.

HURLBERT SH (1978) Results of five flamingo censuses conducted between November 1975 and December 1977. Andean Lake and Flamingo Investigations, Technical Report No. 1, 16 pp. San Diego State University, San Diego, California.

HURLBERT SH (1981) Results of three flamingo censuses conducted between December 1978 and July 1980. Andean Lake and Flamingo Investigations, Technical Report No. 2, 9 pp. San Diego State University, San Diego, California.

HURLBERT SH (1982) Limnological studies of flamingo diets and distributions. National Geographic Research Reports 14: 351-356.

HURLBERT SH & CCY CHANG (1983) Ornitholimnology: effects of grazing by the Andean flamingo *(Phoenicoparrus andinus).* Proceedings of the U. S. National Academy of Sciences 80: 4766-4769.

HURLBERT SH & JO KEITH (1979) Distribution and spatial patterning of flamingos in the Andean altiplano. Auk 96; 328-342.

JOHNSON AW (1965) The birds of Chile and adjacent regions of Argentina, Bolivia and Peru. 2 vols. Platt Establecimientos Gráficos, Buenos Aires.

KAHL MP (1980) Population ecology of the flamingos of the world. National Geographic Society Research Reports 12: 407-415.

MEINERTZHAGEN DSO (1925) The distribution of the phalaropes. Ibis 1925: 325-345.

MORRISON A (1939) The birds of the Department of Huancavelica, Peru. Ibis 3: 453-486.

MURPHY RC (1936) Oceanic birds of South America, Vol. II. American Museum of Natural History, New York.

MYERS JP & LP MYERS (1979) Shorebirds of coastal Buenos Aires Province, Argentina. Ibis 121: 186-199.

OLROG CC (1967) Observaciones sobre aves migratorias del hemisferio norte. El Hornero 10: 292-298.

PALMER RS (1967) Species accounts. In: Stout, GD ed., The shorebirds of North America. Viking Press, New York. 143-267.

ROOTH J (1965) The flamingos on Bonaire. Publications of the Foundation for Scientific Research in Surinam and the Netherlands Antilles, No. 41, 151 pp. Utrecht, Netherlands.

WETMORE A (1926) Observations on the birds of Argentina, Paraguay, Uruguay and Chile. U. S. National Museum, Bulletin 133: 1-448.

WILLIAMS GG (1953) Wilson phalaropes as commensals. Condor 53: 158.