DISTRIBUTION AND SPATIAL PATTERNING OF FLAMINGOS IN THE ANDEAN ALTIPLANO

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ABSTRACT.—A census of three flamingo species (Phoenicoparrus jamesi, P. andinus, Phoenicopterus chilensis) on 28 high-elevation lakes (2,300–4,500 m) in the central Andes (17°–27°S) was conducted during November and December 1975. Phoenicoparrus jamesi was observed at Salar de Pedernales, Chile (26°22'S), and, on a later expedition, at Laguna Parinacochas, Peru (15°18'S). These observations extend the known distribution of P. jamesi along the Andes by about 530 km. An additional nesting locality of this species is reported: Salar de Chalviri, Bolivia (22°31'S). All flamingos were absent from deep lakes and lakes with indurated sediments. The majority of lakes possessed all three species. Average densities (total birds/total lake area) were 0.24/ha for P. chilensis, 0.45/ha for P. andinus, and 3.1/ha for P. jamesi. Phoenicoparrus jamesi was the species most uniformly distributed over the lake area available, and P. andinus was the most patchily distributed. Between-lake distributional overlap was greatest between P. chilensis and P. andinus and least between P. chilensis and P. jamesi. Within-lake distributional overlap probably was greatest for P. andinus and P. jamesi. The absolute degree of interspecific crowding was least for P. chilensis on P. jamesi (0.2/ha) and greatest for P. jamesi on P. andinus (4.7/ha). Received 9 May 1978, accepted 4 January 1979.

THREE species of flamingos (Phoenicopterus chilensis, Phoenicoparrus andinus, and Phoenicoparrus jamesi) are found in the Andean altiplano of South America. This extensive region of internal drainage and high elevation (mostly 3,600–4,500 m above sea level) is located between the eastern and western ranges into which the central Andes are split. Lakes are numerous in the altiplano, and most serve as feeding grounds for one or more of these flamingo species. Two of the flamingos (P. andinus, P. jamesi) are only rarely found outside the altiplano, while the third (P. chilensis) ranges widely over southern South America (Allen 1956, Johnson 1967, Kahl 1975).

In this article we report census data for flamingo flocks on 28 bodies of water in the altiplano region of northeastern Chile and southwestern Bolivia and examine certain statistical properties of the flamingos' distributions. These data were gathered between 22 November and 21 December 1975. This period corresponds to early summer, the beginning of the rainy season and the onset of flamingo breeding, which in this region usually begins in late November or early December.

THE LAKES

The 28 waterbodies censused represent only a sampling of the many dozens of lakes and ponds present and presumably utilized by flamingos in the southern altiplano, i.e. the altiplano south of Salar de Uyuni, Bolivia. No lakes of the Argentinian portion, which comprises more than 50% of the southern altiplano, were censused. Nevertheless, our sampling included a variety of lake types distributed over more than 5° of latitude (Fig. 1). Information on flamingo distribution in this region has been provided by Cordier (1968), Johnson et al. (1958), Kahl (1975), McFarlane (1975), Morrison (1968, 1974) and Peña (1961, 1962) but is scant.

The lakes censused are listed in Table 1 together with their locations, surface areas, and the flamingo census data. With two exceptions they are distributed along the westernmost edge of the altiplano among the 5,000–6,000-m high peaks that form the western range or Cordillera Occidental of the Andes. One exception is Salar de Atacama, the largest salar (3,170 km², Stoertz and Ericksen 1974) in Chile, which

Fig. 1.   Location of salars and lakes visited in the southern altiplano. Lakes, mudflats and dry salar surfaces are shaded without differentiation; only a tiny fraction of the shaded area represents lakes. Laguna Colorada, of which 60% is open water and 40% mudflats, is the largest lake in the region shown. Completely dry, low elevation salars near the Pacific coast are not figured.

is located just to the west of and at a lower elevation than the altiplano and occupies its own rather unique basin of internal drainage (Fig. 1). The second exception is Laguna Huairapata, a lake near a village of the same name in the eastern altiplano north of Oruro, Bolivia.

Most of the lakes are small, and all are shallow, only a few having maximum depths greater than 1 m, namely Laguna Fulica, Laguna Verde I, La Ola Reservoir, Laguna Verde II, and Laguna Totoral. All lakes were entered in hip boots for the purpose of taking water, sediment, and plankton samples (which will be reported in later articles), and this experience together with observations of water height on the legs of grazing flamingos provided our principal information on lake depth. Estimates of surface areas were made from topographic maps, supplemented by field observations.

Most of the lakes are saline, though to widely varying degrees. As indicated in Table 1, many are located in shallow depressions within salars; these often salt-encrusted plains or flats are the remnants of large, deep, less saline lakes that existed during the Pleistocene. The geology of these salars, in particular the Chilean ones, has been discussed by Stoertz and Ericksen (1974) and Vila (1975).

The names of lakes and salars require comment. To distinguish between lakes and salars having the same name, we have employed Roman numerals, which in the case of Chile follow the numbering system of Vila (1975). For many lakes we had to coin a name, as none was given on the appropriate 1:50,000 topographic map; sometimes even the lake itself was not indicated. Laguna Santa Rosa was not a single lake at the time of our visit but consisted of eastern, western, and southern ponds of very different characteristics, which we named Fulica, Parina, and Escondida, respectively. Laguna Blanca is not shown on maps but is a narrow lake (ca. 0.1 × 1.0 km) lying at the very margin of the northeasternmost part of Salar de Maricunga. Laguna Zlosilo we have named after Don Danko Zlosilo, a miner who has worked in this region for 54 yr and who aided us in our exploration of it; this is the only lake in Salar de Aguas Calientes III. Laguna Salada is in Salar de Atacama just west of Peine and is shown and named on the topographic map ("Peine," 1:50,000); Laguna Saladita is not shown but is located about 1 km northwest of Laguna Salada. Laguna Polques, in Salar de Chalviri, is designated as Laguna Salada on one map ("Volcan Juriques," 1:250,000) but is known locally as "Polques," and we prefer this more distinctive name.

DISTRIBUTIONAL EXTENSION FOR *P. JAMESI*

On the morning of 25 November we observed 14 individuals of *P. jamesi* and like numbers of *P. chilensis* and *P. andinus* grazing in narrow (<20-m-wide), grass-bordered channels of very shallow (mostly <4 cm), fresh water along the western margin of Salar de Pedernales in northern Chile. This represents a southward extension of the known distribution of *P. jamesi* in the Andes mountains, the previous southernmost record (Johnson 1967) being for Salar de Atacama, approximately 280 km to the north. *Phoenicoparrus jamesi* also may have been present in Salar de Maricunga, which lies about 60 km due south of Salar de Pedernales. No flamingos were present at Laguna Blanca at the margin of Salar de Maricunga, but unidentified flamingos were glimpsed on bodies of water in the interior of the southern portion of the salar. The only record of *P. jamesi* south of Salar de Pedernales is the extraordinary observation of 2 individuals on a lake at 750 m in the Andean foothills of western Chubut Province, Argentina, more than 1,700 km to the south of this salar (Muñoz and Muñoz 1975).

A northwestward extension of the known range of *P. jamesi* resulted from observations made during a later survey (Hurlbert, unpub. data) and is worth noting here. On 28 June 1976, about 80 *P. jamesi,* 1,600 *P. chilensis,* and 3,000 flamingos too distant to be identified were observed on Laguna Parinacochas, Peru (15°18'S, 73°40'W). This lake lies about 250 km northwest of Laguna Salinas (above Arequipa) and 450 km west of Lago Titicaca, the previously known northwestern limits of the distribution of *P. jamesi* (Kahl 1975, Hellmayr 1932). It is a large (64 km²), brackish (total filtrable residues = 5.6 g/L) lake of high elevation (3,100 m) in an isolated closed basin less than 100 km from the Pacific coast. The lake is known for its beauty and the diversity of its birdlife, and *P. chilensis* and *P. andinus* have been

TABLE 1. Results of census of flamingos on 28 bodies of water in the Chilean and Bolivian altiplano, November–December 1975.

Salar or lake	Date censused	S latitude, W longitude	Elevation above sea level (m)	Lake surface area (km²)	Number of flamingos[a]				Density (number/ha)[a]		
					Total	ch	and	jam	ch	and	jam
CHILE											
Laguna Santa Rosa											
Laguna Fulica	Nov. 22	27°05', 69°10'	3,760	0.2	1	1	0	0	0.05	0	0
Laguna Parina	Nov. 22	27°05', 69°10'	3,760	0.4	120	68	43	0	1.8	1.2	0
Laguna Escondida	Nov. 22	27°05', 69°10'	3,760	0.1	18	11	2	0	1.5	0.3	0
Salar de Maricunga											
Laguna Blanca	Nov. 21	26°52', 69°03'	3,749	0.1	0	0	0	0	0	0	0
Laguna Verde I	Nov. 23	26°53', 68°27'	4,281	20	0	0	0	0	0	0	0
Reservoir La Ola[b]	Nov. 24	26°31', 69°04'	3,615	0.1	3	3	0	0	0.3	0	0
Salar de Pedernales											
Channels along western margin	Nov. 25	26°22', 69°12'	3,500	0.1	38	12	12	14	1.2	1.3	1.4
Salar de Aguas Calientes III											
Laguna Zlosilo	Nov. 29	25°00', 68°38'	3,670	6.0	915	146	763	6	0.24	13	0.01
Salar de Atacama											
Laguna Salada	Dec. 5	23°41', 68°08'	2,300	0.3	540	13	125	1	1.7	16	0.13
Laguna Saladita	Dec. 7	23°40', 68°09'	2,300	0.2	234	77	145	12	3.8	7.2	0.6
Laguna Lejia	Dec. 10	23°30', 67°42'	4,325	2.1	649	6	614	29	0.029	2.9	0.14
Salar de Aguas Calientes II											
Laguna Aguas Calientes[b]	Dec. 11	23°31', 67°34'	4,195	5.0	300	—	—	—	—	—	—
BOLIVIA											
Laguna Verde II											
Eastern half	Dec. 13	22°48', 67°48'	4,315	10	900	588	12	0	0.88	0.018	0
Salar de Chalviri											
Laguna Puripica Chico	Dec. 14	22°31', 67°30'	4,393	1.0	3,000	106	640	1,456	1.4	8.7	20
Ponds west of Puripica Chico[b]	Dec. 14	22°31', 67°30'	4,393	?	2,000	—	—	—	—	—	—
Laguna Polques (Lag. Salada)	Dec. 15	22°32', 67°37'	4,393	12	865	218	347	0	0.28	0.44	0
Channel, north side of salar	Dec. 15	22°28', 67°32'	4,388	0.3	49	9	21	19	0.3	0.7	0.63
Laguna Kollpa	Dec. 14	22°28', 67°25'	4,515	1.0	370	3	24	343	0.03	0.24	3.43
Laguna Hedionda I	Dec. 14	22°27', 67°23'	4,538	2.8	13	6	0	7	0.021	0	0.025
Laguna Totoral	Dec. 14	22°32', 67°17'	4,555	1.0	0	0	0	0	0	0	0
Laguna Colorada	Dec. 16	22°10', 67°47'	4,278	50	25,000	46	2	5,965	0.063	0.0027	8.27
Laguna Cachi	Dec. 16	21°44', 67°57'	4,490	1.4	1,437	54	66	1,317	0.39	0.47	9.4
Laguna Ramaditas	Dec. 17	21°38', 68°05'	4,117	1.0	25	0	15	10	0	0.15	0.10
Laguna Honda	Dec. 17	21°37', 68°03'	4,110	0.5	80	4	60	16	0.08	1.2	0.32
Laguna Khar Kkota	Dec. 17	21°35', 68°04'	4,112	2.0	137	20	102	15	0.10	0.51	0.075
Laguna Hedionda II	Dec. 17	21°34', 68°03'	4,121	3.0	1,687	236	389	1,062	0.79	1.3	3.5
Laguna Cañapa	Dec. 17	21°30', 68°01'	4,140	0.4	225	0	125	100	0	3.1	2.5
Laguna Huairapata[b]	Dec. 21	17°50', 67°15'	ca. 3,750	0.1	54	54	0	0	5.4	0	0

[a] ch = *Phoenicopterus chilensis*, and = *Phoenicoparrus andinus*, jam = *Phoenicoparrus jamesi*.
[b] Census data for these lakes were not used in calculating the statistics reported in Tables 2, 3, and 5 (see text).

observed on it previously (Koepcke and Koepcke 1952). The lake seemed very different from any other lake on which we have seen *P. jamesi*. The flamingos were distributed almost continuously along the margins of the lake and, at least along the northeastern portion of the shoreline, were interspersed in suprisingly intimate fashion with groups of cattle. The latter were grazing on aquatic vegetation, mostly *Potamogeton* or *Ruppia,* with some *Enteromorpha* sp. Plants uprooted or broken off by the cattle formed loose floating mats in many places. It was clear that the cattle were responsible for the very thinned condition of the shallow-water (<½ m) vegetation, a condition that may have facilitated the peripatetic filter-feeding of the flamingos. Invertebrates such as copepods, cladocerans, corixids, and amphipods were present in high densities, reflecting a bovigenic acceleration and re-routing of nutrient cycles.

We also report a new nesting locality for *P. jamesi*. On 14 December 1975, we observed exceptionally high densities of all three flamingos in Laguna Puripica Chico, which is located in the easternmost portion of Salar de Chalviri (Table 1). Within a hundred meters of the eastern shore there were several small, low-lying islets of mud and sand. On three of these islets was a total of 25 active nests occupied by *P. jamesi*; these birds were either sitting quietly or adding more sediment to the nest walls. We glimpsed eggs in four of these nests. Neither of the other flamingo species gave any evidence of nesting in this lake. Our Quechua guide, who lives in the area, told us that flamingos did not nest here every year and never nested elsewhere in Salar de Chalviri, even though this large (>100 km²) salar contains several other small lakes and two large ones.

A notable feature of this colony is that it is completely without protection from terrestrial predators such as foxes (*Dusicyon* spp.). Unlike the nesting islands of *P. jamesi* at Laguna Colorada (45 km to the northwest), which are surrounded by and indeed composed of soft, miry clay sediments, those in Laguna Puripica Chico are separated from the salar margin by firm sediments and very shallow (<10 cm) water. Foxes could reach the nests with ease. But perhaps the desertic nature of the countryside in the vicinity of Salar de Chalviri does not provide a sufficient abundance of alternative prey (e.g. rodents) for foxes to hunt and reside successfully in the area.

Very few nesting localities are known for *P. jamesi,* the world's rarest flamingo. The main colony is probably at Laguna Colorada, but there is circumstantial evidence that they breed in Salar de Surire, in the Andes above Arica, Chile (McFarlane 1975). Cordier (1968, in Kahl 1975) states that in Bolivia they also nest along the northeastern side of the gigantic (9,000 km²) Salar de Uyuni and at the southern end of Lago Poopo, and that in Argentina they nest in Laguna Vilama, just a few km from the Bolivian border.

At the time of our visit to Laguna Colorada, nesting undoubtedly had begun. Although we could not see the centrally located nesting mudflats clearly, thousands of flamingos were thickly concentrated in the area, and the constant activity there was indicative of early reproductive behavior. On the morning of 16 December, we observed a group of 17 persons enter the lake from the eastern shoreline and slog for about 3 h across water and mud in the direction of the nesting flats. Eventually we lost sight of them, but they were surely a flamingo egg-gathering expedition from the small villages lying more than 50 km to the east of the lake. These egg-gathering activities have been commented on by several visitors to the lake (Walcott 1925, Johnson et al. 1958, Conway 1960, Cordier 1968, Morrison 1975).

Behavior of Other Flamingos

We saw no active nests of *P. chilensis* or *P. andinus*. It was reported to us that natives collected flamingo eggs on Salar de Atacama on 8 December 1975. Nests there probably would have been of *P. andinus* and *P. chilensis*.

Agonistic and reproductive behavior were seen in *P. andinus* on most lakes where they were present. In *P. jamesi*, fighting was seen on Lagunas Saladita and Puripica Chico, and fighting and copulation were observed at Laguna Colorada. Intense reproductive behavior was seen in *P. chilensis* on Lagunas Polques and Huairapata. Fighting among *P. chilensis* was seen on several of the other lakes. The only interspecific agonistic behavior observed was several brief attacks by *P. andinus* against *P. jamesi*.

Flamingo-free Lakes

Only three of the lakes visited lacked flamingos completely (Table 1). In each case the explanation seemed apparent. At the time of our visit, the surface of Laguna Verde I was rough, with waves having trough-to-crest amplitudes of perhaps 0.5 m. Given the exposed location, large surface area, and relatively great depth (maximum depth at least several meters), such conditions may exist much of the time and would batter any flamingo that tried to feed. Additionally, the shallow-water sediments consist of boulders and slabs of clastic materials cemented together in a gypsum matrix, and any bird attempting to feed at the sediment-water interface, which is where all three species usually feed, would abrade its beak seriously.

The absence of flamingos on Laguna Blanca (a name of our own coinage) at the northern tip of Salar de Maricunga was also associated with indurated sediments, in this case a thin (1–5 cm) crust of essentially pure halite that covers the bottom of the western half of this shallow (<20 cm) lake. Fresh water seeps into the lake along its eastern margin and apparently is responsible for preventing such a crust from developing in the eastern half of the lake, where the surface sediments are reddish brown clay.

In an earlier report (Hurlbert et al. 1976), we described two small lakes in Salar de Carcote that have bottoms consisting of indurated gypsum slabs and other formations. We have visited these lakes on several occasions and never seen flamingos, although they are usually present on many other water bodies in Salar de Carcote.

Indurated sediments consisting, in all the above cases, of precipitated salts are a reflection of water chemistry, and perhaps a negative effect of water chemistry *per se* on the aquatic biota is partly responsible for the unattractiveness of these lakes to flamingos. For example, zooplankton and other invertebrates are very sparse or absent from these lakes, and these are the principal items in the diet of *P. chilensis*.

Absence of flamingos on Laguna Totoral was probably due to the steepness of the lake's shoreline and the consequently reduced area where flamingos could reach bottom sediments. The gravelly nature of the sediments also may have been a factor.

Spatial Distribution of Individual Species

In later reports, we will analyze further the relations between flamingo distributions and the biotic, chemical, and bathymetric properties of the individual lakes. These reports will be prepared when analysis of our samples of biota and water for these and several dozen additional altiplano lakes is completed. In the remainder of

TABLE 2. Summary of distributional data for individual flamingo species on 24 lakes. Numbers in parentheses are standard deviations.

Species	Mean elevation (m)[a]	Number of lakes occupied	Overall density (number/ha)[b]	Intraspecific crowding (number/ha)[c]	Patchiness[d]
P. chilensis	4,141 (486)	19/24	0.24	0.83 (.71)	3.51
P. andinus	3,955 (689)	19/24	0.45	4.8 (5.1)	10.8
P. jamesi	4,295 (84)	16/24	3.10	8.8 (3.2)	2.84

[a] Individuals weighted equally.
[b] Total individuals on all lakes divided by total area of all lakes.
[c] Mean density of conspecifics encountered, on average, by an individual (see text).
[d] Ratio of intraspecific crowding to overall density (see text).

this report, we neglect the characteristics of individual lakes and attempt to answer statistical questions such as: what is the mean density of a flamingo species in the region? How evenly is it distributed over the available lakes? How much do the distributions of the three species overlap? The answers obtained will depend, of course, as much on the natures of the lakes censused as on the biology of the flamingos themselves.

Certain features of the census data should be pointed out. For some salars (Maricunga, Pedernales, Atacama) the waterbodies censused were not the major waterbodies in the salar. Waterbodies near salar margins, being more accessible, are somewhat over-represented in our sample at the expense of interior ones.

At many lakes some flamingos were too distant to be identified to species; consequently, in Table 1 the counts for the individual species do not always add up to the total count. In calculating species densities (last three columns of Table 1) however, we have apportioned the unidentified individuals among the species in accordance with the relative abundances of the species among the identified individuals. Where flamingos numbered in the thousands, our estimates sometimes may be in error by as much as 20–30%.

Our statistical analyses are based on only 24 of the 28 waterbodies censused. The other four are excluded because they were artificial (Reservoir La Ola), because all flamingos were too distant to be identified (Salar de Aguas Calientes II, ponds west of Laguna Puripica Chico), or because they lay well north of the southern altiplano (Laguna Huairapata).

Distributional characteristics of the separate species are summarized in Table 2. As indicated by overall density, *P. jamesi* is by far the most abundant species in the region. This is not a surprising finding considering that their principal known breeding ground, Laguna Colorada, is included in our sample, while those of the other two species are not.

Our estimate of flamingo abundance on Laguna Colorada is two to four times greater than any previous estimates for the lake (Kahl 1975, Morrison 1975). It must be emphasized that flamingos were extremely abundant at the time of our visit. We counted 5,516 flamingos in the southwestern corner which represented only about one-fourth of the lake area densely occupied by flamingos. Birds were especially dense and abundant in the area of the breeding colony. The lake is large and difficult to census, but the total number present was clearly four to five times greater than the number counted.

Recently Kahl (1975) estimated total population size to be 50,000 for *P. jamesi*, 150,000 for *P. andinus*, and 500,000 for *P. chilensis*. On our 24 lakes, we saw an

estimated 29,739 *P. jamesi,* 4,301 *P. andinus* and 2,263 *P. chilensis.* Thus, the following analyses are based on a large fraction of *P. jamesi's* total numbers but on a small fraction of the other two species' total numbers.

The three species differed in the evenness with which they were distributed over the total surface area of the lakes studied, that is in the patchiness of their distributions (Table 2). We define patchiness as the degree to which the frequency of intraspecific encounter is greater or less than the frequency that would be experienced by the average individual if individuals were distributed uniformly in space or, in our case, over the lakes. We calculate it as:

$$G = \frac{A}{X(X - n)} \sum \frac{x_i(x_i - 1)}{a_i}, \tag{1}$$

where x_i = number of individuals of species X on the ith lake
$X = \sum x_i$
a_i = area of ith lake
$A = \sum a_i$
n = number of lakes censused (24).

This represents a generalization of Lloyd's (1967) patchiness index for quadrat data to the case where the units censused vary in size. It assumes that encounters can occur only between birds on the same lake and that frequency of encounter is a function solely of density. It represents the ratio of intraspecific crowding, i.e.

$$C_i = \frac{1}{X} \sum \frac{x_i(x_i - 1)}{a_i}, \tag{2}$$

to $[(X - n)/A]$, this latter quantity being the magnitude of intraspecific crowding expected under conditions of uniform distribution. For our data, the magnitude of intraspecific crowding is effectively equal to overall density (X/A). These indices are developed and discussed in Hurlbert (1978).

The patchiness values (Table 2) are easily interpreted. On the lakes studied, the average individual of *P. andinus* confronted a density of *P. andinus* that was 10.8 times greater than the density the individual would have confronted if the *P. andinus* population had been uniformly distributed over the total water surface available. This high value is due in large measure to the almost complete non-utilization of the largest lake censused (Laguna Colorada) by *P. andinus* and to their presence at very high densities on two other lakes (Laguna Salada, Laguna Puripica Chico). The lower patchiness values for the other two flamingos indicate that they are distributed more uniformly over the available water surfaces than is *P. andinus*. Numerous factors relating to sociality, reproductive state, diet, and physiological tolerances may account for the differences. Especially when lake size is highly variable, as in the present case, patchiness values are largely a function of abundances on the largest lakes and will be explained only when we know the particular features of those lakes that attract or repel the flamingos.

The differences between species in mean elevation of occurrence (Table 2) in this region are not great; each species occurred over the entire 2,300–4,500-m elevational range sampled. The differences could well be attributable to the combined effects of patchiness and chance. We suspect the difference (300–400 m) between *P. andinus*

and *P. jamesi,* however, to be a fairly accurate reflection of the elevational difference between these species over their whole range at this time of year; during the winter, i.e. May through August, the difference may be negligible. The mean elevation for *P. chilensis* over its whole range, which includes large areas of the lowlands of southern South America, is naturally much lower than that reported in Table 2. Taking into account all information available to us, we estimate that over their entire ranges the flamingos occur in December at mean elevations of approximately 1,800 m (*P. chilensis*), 3,700 m (*P. andinus*), and 4,000 m (*P. jamesi*). It remains to be determined what atmospheric, climatological, or limnological correlate of elevation is the proximate cause of these elevational separations.

DISTRIBUTIONAL OVERLAP OF SPECIES

To analyze the statistical relationships that the species distributions bear to each other, we have adopted a novel but straightforward approach. As an index of distributional overlap, we employ

$$L = \frac{A}{XY} \sum \left(\frac{x_i y_i}{a_i} \right) \tag{3}$$

(where y_i = the number of individuals of species Y on the ith lake and $Y = \sum y_i$), which measures the degree to which the frequency of interspecific encounter is higher or lower than it would be if both species were distributed uniformly over the total lake area (Hurlbert 1978). This index represents a generalization of Lloyd's (1967) "interspecies patchiness" index to the case where the units censused vary in size.

Thus, the distributions of *P. chilensis* and *P. andinus* are such that the two species are likely to encounter each other 3.4 times (or 240%) more often than they would if each were distributed uniformly over the available lake area (Table 3). *Phoenicopterus chilensis* and *P. jamesi,* on the other hand, show a slight segregation or negative overlap and are likely to encounter each other 17% less often than they would if both were distributed uniformly. One should note that while an overlap value of 1.0 would be obtained for two species both of which were distributed uniformly, it does not follow that a value of 1.0 is necessarily indicative of uniformity: two species, both of which had very patchy distributions, could also yield an overlap value of 1.0.

The same approach outlined above may be used to measure distributional overlap *within* lakes. We can do this by dividing a lake into zones, censusing each zone separately, and making our calculations on the assumption that an encounter or crowding is possible only between individuals in the same zone. A significant practical difficulty to this approach is that the values of overlap and other indices will depend in part on the number of zones into which a lake is divided and on the

TABLE 3. Analysis of distributional overlap and related measures for the three flamingo species.

Species pair	Distributional overlap (equation 3)	Rank correlation[a] of densities (Spearman's r_s)	Similarity (equation 4)
chilensis-andinus	3.4	0.55*	0.45
chilensis-jamesi	0.83	0.15[ns]	0.21
andinus-jamesi	1.5	0.52*	0.13

[a] Asterisk (*) indicates $P \leqslant 0.01$; ns indicates $P > 0.05$.

TABLE 4. An example demonstrating the effect on overlap and similarity values of partitioning a lake into zones. Data are from Laguna Hedionda II (Fig. 1).

Zone	Area (ha)	Number of birds (x_i)			Percentage[a] (x_i/X)		
		chilensis	*andinus*	*jamesi*	*chilensis*	*andinus*	*jamesi*
1	140	230	0	0	0.1016	0	0
2	60	0	0	0	0	0	0
3	20	0	229	60	0	0.0532	0.0020
4	70	6	26	948	0.0027	0.0060	0.0319
5	10	0	134	54	0	0.0312	0.0045
Totals	300	236	389	1,062	0.1043	0.0904	0.0357

	Species pair		
	chilensis-andinus	*chilensis-jamesi*	*andinus-jamesi*
Contribution to overlap (L)			
Lake treated as a unit	0.302	0.034	0.103
Lake partitioned into zones	0.00219	0.0115	0.132
Percent change	−99	−66	+28
Within-lake overlap	0.073	0.338	1.28
Contribution to similarity (C)			
Lake treated as a unit	0.0904	0.0357	0.0357
Lake divided into zones	0.0027	0.0027	0.0125
Percent change	−97	−92	−65
Within-lake similarity	0.025	0.025	0.174

[a] Percentages are calculated using total numbers observed on the 24 lakes as the bases, i.e. 29,739 *P. jamesi*, 4,301 *P. andinus*, and 2,263 *P. chilensis*.

locations of the zone boundaries (Colwell and Futuyma 1971), and these must be arbitrary to a large extent.

To demonstrate the effect of taking the heterogeneity of within-lake distribution into account, we will use the data for Laguna Hedionda II in Bolivia (Fig. 1). At the time of our visit, the flamingos at this lake were segregated spatially into four partially distinct groups, providing us with a way of delineating five zones in a manner that was not completely arbitrary.

The results of treating the five zones of Laguna Hedionda II just as if they were five separate lakes were striking (Table 4). For all species pairs involving *P. chilensis,* the lake's contribution to overlap was greatly reduced, as this species occurred almost entirely by itself, in the center of the lake. For *P. jamesi* and *P. andinus,* the lake's contribution to overlap actually increased slightly, as these species were both restricted to the same one-third of the lake's area. Values for within-lake overlap (Table 4), which can be calculated as the ratio of the two contributions (e.g. .00219/.302 = .073 for *P. chilensis* and *P. andinus*), contrast markedly with those for between-lake overlap (Table 3).

What biological conclusions are warranted by these statistics? First, the overlap values in Table 3 indicate that *P. andinus* is positively associated with each of the other species but that there may be a slight segregation or negative association between *P. chilensis* and *P. jamesi.* To some extent these values are the result of our sample, including lakes such as Laguna Verde I that are markedly unsuitable for all flamingos. If we exclude from our analysis the three lakes on which no flamingos of any kind were found, each overlap value in Table 3 is reduced by 22%.

The data for Laguna Hedionda II (Table 4) suggest that when heterogeneity of within-lake distribution is taken into account, the overlap of *P. chilensis* with the

other two species is greatly reduced, while that between *P. andinus* and *P. jamesi* increases. Most other lakes were not censused on a zonal basis, and within-lake overlap values cannot be calculated for them. We did census the northern and southern halves of Laguna Puripica Chico separately, however. Within-lake overlap values based on this partitioning were 0.96 for *chilensis-andinus*, 0.91 for *chilensis-jamesi*, and 1.14 for *andinus-jamesi*. These values parallel those for Laguna Hedionda II in three ways: they are mostly lower than the between-lake overlap values (Table 3); they indicate a segregation ($L < 1.0$), albeit slight, of *P. chilensis* from the other two species; and they indicate a slight positive association ($L > 1.0$) between *P. andinus* and *P. jamesi*. We should not try to extract too much from these statistics, as they are derived from a single census of very mobile populations in a limited region. They do suggest, however, that the species tend to use the same types of lakes, and that spatial segregation, when it exists, is a result primarily of differential distributions within lakes.

CORRELATION AND SIMILARITY

Values of two other indices have been calculated for comparison with overlap values (Table 3). The three indices cannot be used interchangeably and, in general, cannot be expected to yield concordant results, as they measure different aspects of joint distributions. For this reason, when examined in concert the indices may add to our insight and help us avoid superficial interpretation.

Spearman's rank correlation coefficient was calculated for each species pair using the density data in Table 1. A significant feature of this coefficient is that all lakes are given equal weight in its calculation: the five least populated lakes, for example, have as much influence on the value of the coefficient as do the five most heavily populated ones. Consequently, the magnitude and statistical significance of this coefficient do not necessarily indicate anything about how the major portions of the two species are distributed relative to each other. It tells us only whether the lakes rank in attractiveness to one species in approximately the same order they rank in attractiveness to the second species.

The similarity coefficient we have employed,

$$C = \sum \min\left(\frac{x_i}{X}, \frac{y_i}{Y}\right), \tag{4}$$

has been used for various purposes, including the measurement of niche overlap (cf. discussion in Hurlbert 1978). Its values, which can range from 0 to 1, are determined principally by those few lakes where flamingos are very *abundant*. As the measure does not take flamingo *densities* into account, however, it is unsuitable as an index of overlap, at least if we desire such an index to reflect the degree to which two species might impinge on each other in some way.

Correlation and similarity are, like overlap, greatest for *P. chilensis* and *P. andinus*, indicating that these two species are indeed more positively associated in various ways than either is with *P. jamesi*. It must be noted, however, that for all three measures (though less for correlation than for the others) the ranking of species pairs is strongly influenced by the largest lake, Laguna Colorada, the surface area of which represents 31% of the total surface area of the 24 waterbodies. *Phoenicopterus chilensis* and *P. andinus* both occurred on this lake at very low densities, *P. jamesi* at a very high density. Consequently, if we were to exclude this one lake

from our analysis, overlap, correlation, and similarity would, for species pairs involving *P. jamesi,* increase markedly and be greatest for *P. jamesi* and *P. andinus.* It may make us uneasy that one lake can have such a large influence, but this is a consequence of the great variability in lake size and in flamingo densities and can be counteracted only by increasing the number of lakes censused.

The fact that the same species-pair was ranked highest by all three measures and the agreement of the overlap and correlation rankings (Table 3) represent fortuitous coincidences. To demonstrate how distinct the three measures really are, we may consider the *P. chilensis-P. andinus* species pair and determine, for each measure, which lakes contribute most to its value. The contribution of a given lake to each index is as follows:

$$\text{overlap:} \quad A x_i y_i / a_i X Y$$
$$\text{correlation:} \quad (1/n) - [6 d_i^2 / n^2 (n - 1)]$$
$$\text{similarity:} \quad \min(x_i/X, \ y_i/Y),$$

where d_i is the difference between ranks.

When the individual contributions have been calculated, we find that different measures are most influenced by different lakes. For *P. chilensis-P. andinus,* the two lakes making the greatest contributions to overlap were Laguna Puripica Chico and Laguna Salada, which accounted for 59% of total overlap (i.e. of 3.4); their influence was a result of flamingos being both numerous and very dense on these lakes. The lakes making the greatest contributions to correlation were those where both species had the same position in their respective density rankings: these lakes were Laguna Verde I, Laguna Blanca, and Laguna Totoral, all of which were completely unoccupied by flamingos! Together these three lakes account for 23% of the rank correlation value. Finally, the two lakes contributing most (47%) to similarity were Laguna Polques and Laguna Hedionda II; their influence derived from each lake having on it a moderately large fraction of each species' total population, though densities were only about average.

A notable mathematical difference between overlap and similarity is illustrated in Table 4. Note that for *P. andinus-P. jamesi* the zonal approach resulted in an *increased* overlap value but a *decreased* similarity value. A finer partitioning of space can only reduce similarity values but may either reduce *or* increase overlap values. Of course, if individuals are distributed completely uniformly over space, finer partitioning will have no effect on either overlap or similarity.

We conclude that overlap, being expressed in units relating directly to probability of encounter, is the most useful indicator of spatial relationships between the species. Correlation and similarity yield dimensionless values that are difficult to relate, even in an abstract way, to biological events and that consequently are very susceptible to erroneous interpretations.

INTERSPECIFIC CROWDING

We refer to the absolute density of one species experienced by another as *interspecific crowding* (Hurlbert 1978) and calculate it as

$$Z_{x(y)} = \sum \left(\frac{x_i}{X} \cdot \frac{y_i}{a_i} \right), \tag{5}$$

TABLE 5. Analysis of interspecific and intraspecific crowding for the three flamingo species. Numbers in parentheses are standard deviations.

Encoun-tering species	Mean density (number/ha) encountered of				
	chilensis	andinus	jamesi	Total	PIE[a]
chilensis	0.83 (0.71)	1.52 (3.2)	2.59 (5.2)	4.94	0.83
andinus	0.80 (0.85)	4.78 (5.1)	4.66 (7.8)	10.24	0.53
jamesi	0.20 (0.37)	0.67 (2.2)	8.81 (3.2)	9.68	0.08

[a] PIE = probability of interspecific encounter, i.e. proportion of encounters that are with individuals of other species rather than with conspecifics.

which is the density of species Y encountered, on the average, by individuals of species X. Interspecific crowding values are presented for all species combinations in Table 5. (Note that the values along one diagonal of this table are actually values for *intraspecific* crowding, which are presented in Table 2 also.) For every species pair, we thus calculate a single overlap value (Table 3) and two interspecific crowd-ing values to complement it. The latter not only indicate the intensity of crowding, which is a function of mean density and overlap, but also indicate the degree to which the crowding is reciprocal or not. For example, in Table 5 we find that the average *P. chilensis* confronted 2.6 *P. jamesi*/ha, while the average *P. jamesi* experienced only 0.2 *P. chilensis*/ha. Both of these values are 17% lower than they would be if both species were uniformly distributed over the lake, i.e. overlap is 0.83 (Table 3).

Each species and species pair experienced a unique set of conditions with respect to crowding. The greatest degree of reciprocity in crowding was shown by *P. chi-lensis* and *P. andinus,* the least by *P. chilensis* and *P. jamesi*. The average *P. chilensis* experienced a total flamingo density about half (4.9) that experienced by individuals in the other two species, and most of the individuals it encountered (83%) were of other species. The crowding of *P. andinus* by *P. jamesi* was the highest degree (4.7) of interspecific crowding observed in the study. The very patchy distribution of *P. andinus* (Table 2) resulted in that species experiencing a high degree of intraspecific crowding, too. As a result, roughly half of the encounters of the average *P. andinus* were intraspecific, half interspecific. *Phoenicoparrus jamesi* individuals confronted, on the average, very low densities of the other species but showed the highest degree of intraspecific crowding.

CONCLUSION

The data presented here refer to the spatial distributions of three flamingo species at regional, interlacustrine, and intralacustrine scales. The limited extent of our census does not allow much generalization about the distributional characteristics of the species, let alone the factors that determine them. This report is mainly a demonstration of possibilities, and in that regard we make two observations.

First, the three flamingos in the altiplano are ideal subjects for a comparative study of factors determining distribution at all spatial scales, from the microhabitat to the continental. They are conspicuous, large birds readily identifiable to species, and they remain constantly in the open, are almost never obscured by vegetation of any sort, and hence can be censused more easily than most other vertebrates. Also, the total numbers of *P. jamesi* and *P. andinus* are sufficiently small and geograph-ically concentrated so that it is feasible to observe and study a large fraction of the individuals in each species.

Second, the essentially two-dimensional structure of their environment facilitates quantitative analysis of flamingo distributional properties such as dispersion, crowding, and overlap. Some may feel that this type of analysis is too abstract to be of much use. Certainly the biological interpretability of such indices can be improved by basing calculations only on the shallow-water (depth < 1 m) area of a lake and by taking more explicitly into account the intralacustrine distributional patterns of the birds. We are adopting this approach. But the indices themselves really are no more abstract than is mean density, and they represent perhaps the simplest way of summarizing distributional relationships. Approaches similar to ours have rarely been applied to the study of bird distributions, because for most species, it is difficult to obtain accurate census data for entire, discrete, naturally bounded patches of habitat. When that constraint is not operative, novel statistical approaches may prove the most informative.

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ANNOUNCEMENT AND CALL FOR PAPERS

The **Third Annual Meeting of the Colonial Waterbird Group** will be held 25–28 October 1979 at the University of Southwestern Louisiana, Lafayette. Field trips to the Gulf coast are planned, and a **Proceedings** will be published as in 1978 and 1979. For information on contributing papers, please contact P. A. Buckley, North Atlantic Regional Office, National Park Service, 15 State Street, Boston, Massachusetts U.S.A. 02109. **Abstracts must be received by 1 September.** For information on registration, please contact D. McCrimmon, Laboratory of Ornithology, Cornell University, Ithaca, New York, U.S.A. 14853.

An international **symposium on the Physiology of the Avian Egg** will be presented under the auspices of the American Society of Zoologists at their annual meeting, 27–30 December 1979, in Tampa, Florida. Sixteen papers will be presented on topics that concern the interrelationships of conductance of eggshells to respiratory gases, metabolism, incubation periods, shell formation, and ecological and evolutionary aspects of avian reproduction. The symposium is organized by Cynthia Carey, Department of EPO Biology, University of Colorado, Boulder, Colorado 80309. Information on registration and housing can be obtained from the ASZ Business Office, Box 2739, California Lutheran College, Thousand Oaks, California 91360.