SEASONAL ACTIVITY PATTERNS AND ABUNDANCE OF ANDEAN FLAMINGO (PHOENICOPARRUS ANDINUS) AT TWO CONTRASTING WETLANDS IN ARGENTINA

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Resumen. – Patrones de actividad y abundancias estacionales del Flamenco Andino (Phoenicoparrus andinus) en dos humedales contrastantes en Argentina. – El Flamenco Andino utiliza de forma complementaria y alternativa humedales altoandinos de Argentina, Bolivia, Chile y Perú, además de humedales en las tierras bajas de Argentina. Estudios previos se enfocaron en su comportamiento en sitios andinos, pero no existen al momento estudios de este tipo en sitios de tierras bajas. Debido a esto, el objetivo del estudio fue analizar los patrones de actividad, de despliegues de cortejo y abundancias de esta especie de flamenco en dos humedales contrastantes. Los sitios de estudio fueron: la Laguna de Vilama, en el noroeste de Argentina, a 4500 m s.n.m., la cual es utilizada en el verano durante el período reproductivo, y la Laguna Melincué, en la planicie del centro-este de Argentina y a 84 m s.n.m., que es utilizada durante el período no reproductivo invernal. Entre sitios y entre años hubo marcadas diferencias en la abundancia y en los patrones de actividad. En la Laguna de Vilama, los flamencos se alimentaron durante la mayor parte del tiempo (95%), mientras que en la Laguna Melincué, los flamencos mostraron un rango más amplio de comportamientos, destacando sólo el 60% del tiempo a alimentarse. No registramos despliegues nupciales (marchas) en la Laguna de Vilama, mientras que en la Laguna Melincué sí registramos marchas, las cuales fueron más frecuentes y de mayor duración en aquellos años con mayores abundancias de flamencos. Las diferencias en actividades entre los sitios estarían asociadas a la calidad y disponibilidad de recursos y al momento del ciclo reproductivo, donde los sitios de tierras bajas proveen hábitats críticos para las actividades de cortejo que finalmente influyen el éxito reproductivo en los humedales de los Altos Andes.
Abstract. – The Andean Flamingo (Phoenicoparrus andinus), one of three flamingo species in southern South America makes complementary and alternative use of high Andean wetlands in Argentina, Bolivia, Chile and Peru, and lowland wetlands in Argentina over its life cycle. Previous studies have focused on its behavior in Andean sites, but there are no such studies in lowland sites. Therefore, we analyzed the activity patterns, courtship displays, and individual abundance of this flamingo species at two contrasting wetland sites, Laguna de Vilama, located at 4500 m a.s.l. in northwestern Argentina and used in summer during the breeding season, and Laguna Melincué, a lowland wetland located at 84 m a.s.l. in the plains of central east Argentina and used in winter during the non-breeding season. There were marked differences in flamingo abundance and activity patterns between sites and years. In Laguna de Vilama, flamingos were feeding most of the time (95%), whereas at Laguna Melincué, flamingos showed a broader range of behaviors, with only a 60% of time spent feeding. We did not record marching displays at Laguna de Vilama, whereas at Laguna Melincué we recorded marching events in each of the three study years, being more frequent and lasting longer in the year with higher flamingo abundance. The differences in behaviors at these sites are associated with resource quality and availability and with timing of the reproductive cycle, with lowland wetlands providing critical habitats for courtship displays that influence reproductive success of this species breeding colonies in high Andean wetlands. Accepted 1 October 2014.

Key words: Phoenicoparrus andinus, abundance, activity patterns, Andes, Argentina, conservation, courtship, marching display, Pampas, wetlands.

INTRODUCTION


Flamingos show a wide array of behaviors (Hurfbert et al. 1984, Arengo & Baldassarre 1995, Khaleghizadeh 2010, Bouchard & Anderson 2011), which are affected by several factors such as flock size (Pickering et al. 1992, Beauchamp & McNeil 2004, Boukhriss et al. 2007), weather conditions (Bouchard & Anderson 2011, Barisón 2012), time of the year (Espino-Barros & Baldassarre 1989), and habitat conditions and productivity (Arengo & Baldassarre 1995, Mawhinney 2008). Most behavioral studies of flamingos have been done on Caribbean Flamingos (Phoenicopterus ruber ruber), Lesser Flamingos (Phoeniconaias minor), and Greater Flamingos (Phoenicopterus ruber), while fewer studies focused on South American flamingos, Andean Flamingo (Phoenicoparrus andinus), Puna Flamingo (Phoenicoparrus jamesi), and Chilean Flamingo (Phoenicopterus chilensis) (Hurfbert 1982, Hurfbert et al. 1984, Lindgren & Pickering 1997, Mascitti & Castanera 2006).

The Andean Flamingo (Phoenicoparrus andinus Philippi, 1854) is the least abundant flamingo in the world (Rose & Scott 1994). It is considered Vulnerable by the IUCN
Species Survival Commission (IUCN 2013), is included in Appendix I of Convention of Migratory Species (CMS 2013), and is listed in the US Endangered Species Act (2014). Throughout its annual cycle, the Andean Flamingo alternatively uses high-altitude wetlands in the Andes in Argentina, Bolivia, Chile, and Peru during the breeding season (summer: October–March) and lowland wetlands in the central plains of Argentina during the non-breeding season (winter: May–October), particularly when some of the high-altitude wetlands freeze over (Romano et al. 2006, Caziani et al. 2007, Romano et al. 2008, 2009, Marconi et al. 2011).

Previous studies on Andean Flamingos in South America have focused on spatial distribution, population size, reproduction, habitat characterization, and conservation aspects (Derlindati 1998, Caziani & Derlindati 2000, Caziani et al. 2001, 2007, Romano et al. 2006, Marconi et al. 2011). Only a few studies have analyzed their behavior, and to our knowledge, these were only carried out at high-altitude sites (Hurlbert 1982, Hurlbert et al. 1984, Mascitti & Castañera 2006), and no such studies have been done for this species at lowland sites. Moreover, there is only one published study on courtship displays of this species in captivity (Lindgren & Pickering 1997).

The objective of this study was to evaluate activity patterns, courtship displays, and abundances of Andean Flamingos at two contrasting wetland sites, one high-altitude wetland in the Andes, and one in lowland plains in Argentina, to help determine how different sites provide complimentary resources that are critical for flamingos over their annual cycle.

METHODS

Study area. The study was conducted in two wetland sites, both saline endorheic basins, located at opposite extremes of the Andean Flamingo distribution in Argentina (Fig. 1). Laguna de Vilama, Jujuy Province, is a high-altitude wetland in northwest Argentina (22°36'S, 66°55'W; 4500 m a.s.l.). The climate is cold and dry, with high solar radiation, wide daily temperature range between -5°C to 30°C in summer, and -20°C to 0°C in winter, strong winds, and low annual precipitation (200 to 300 mm) (Bianchi & Yáñez 1992, Hong & Seggiaro 2001). Vegetation is dominated by grass steppes of Festuca orthophylla (Cabrera & Willink 1973), with a high proportion of bare soil (95%). The study site is almost inaccessible and human activities are restricted to herding llama (Lama glama), and mineral prospecting. This wetland attracts over 30% of global Andean and Puna Flamingo populations (Caziani et al. 2007, Marconi et al. 2011) during the breeding season (December–March), and high numbers of Chilean Flamingos throughout the year (Caziani & Derlindati 2000). The nesting period of Andean Flamingos begins in November/December and lasts until March/April. Even though, there are no records of breeding colonies at this high-altitude wetland, we know from satellite tracking data that flamingos nesting in nearby wetlands in Bolivia, Chile, and Argentina move to Laguna de Vilama to feed throughout the breeding season (FA unpub. data). In contrast, Laguna Melincué, Santa Fe Province, is a lowland wetland in the plains (Pampas) of central-east Argentina (33°43', 61°28'; 84 m a.s.l.). The climate is temperate and wet (Pasotti et al. 1984), with mean annual temperature around 16°C, and mean annual precipitation around 917 mm, concentrated in December-April (summer-autumn) (Biasatti et al. 1999). In some years, this wetland attracts up to 30% of the Andean Flamingo population in the non-breeding season (July–October; Romano et al. 2002, 2006, 2008, 2009), and in recent years, we have recorded Puna Flamingos for the first time (Cruz et al. 2013). Chilean Flamingos use
Laguna Melincué throughout the year (Romano et al. 2005). The site is located within the main agricultural area of Argentina, with soybean, wheat, and maize cultivation and cattle ranching dominating land use. Native vegetation is composed of grasslands dominated by *Distichlis spicata* and *Paspalum vaginatum* (Romano et al. 2006).


*Activity patterns, marching displays, and abundance estimation. We conducted four behavioral sampling sessions, two during the breeding season at Laguna de Vilama and two during the non-breeding season at Laguna Melincué. At Laguna de Vilama, we conducted observations between 10:00–17:00 h during 12 days, from 2 to 12 February and from 11 to 12 March in 2007, and 10 days from 7 to 17 February in 2008, for a total of 154 hours. At Laguna Melincué we conducted observations between 10:00–16:00 h during 4 days from 31 August to 4 September 2007, and on 15 days from 13 to 29 July 2011, for a total of 100
Mean temperatures were lower in August 2007 (8.7°C) than in July 2011 (10.3°C). In fact, mean temperatures in winter 2007 were lower than the average winter temperature over the last two decades (A. Coronel pers. comm.). Annual precipitation was higher in 2007 than in 2011 (1062 mm vs. 834 mm), however during the study period there were more sunny days in 2007 and more rainy and windy days in 2011.

We recorded activity patterns of flamingos by randomly selecting a focal individual within a flock and recording time spent doing each of 11 behaviors: stamp-feeding, walk-feeding, resting, grooming, walking, flying, alert, aggression, swimming, drinking, and stretching (Ogilvie & Ogilvie 1986) for three minutes. These observations excluded flocks that were courting. We recorded activity patterns of 433 Andean Flamingos at both sites (Laguna de Vilama: 44 in 2007, 85 in 2008; Laguna Melincué: 110 in 2007, 194 in 2011).

As in other flamingo species, the courtship display of Andean Flamingos is highly complex including ritualized head displays, ritualized wing displays, marching displays, and aggressive displays (Brown & Root 1971, Ogilvie & Ogilvie 1986, Lindgren & Pickering 1997). In our study, we observed only marching, a locomotory display where three or more flamingos gathered together walking forward in a tight group often touching one another (Lindgren & Pickering 1997). In addition to the focal observations, we recorded all marching events, counted the number of individuals involved (i.e., flock size), and the time spent on the marching display. We also counted total number of Andean Flamingos in the wetland. We conducted another separate sampling session for marching displays at Laguna Melincué during 12 days from 20–26 July and 21–27 August, 2010.

Statistical analyses. We performed a Principal Component Analysis (PCA) on the focal individual observations to evaluate the variation in activity patterns of Andean Flamingos between sites and between years. As these proportional data add up to 180 sec for each individual, one of the eigenvalues of the covariance matrix must be zero. In order to solve this problem, we transformed the data using the following equation (Aitchison 1983, cited by Khattree & Naiki 2000):

\[
v_j = \log(x_j + 1) - \frac{1}{p} \sum_{i=1}^{p} \log(x_i + 1), \quad j = 1, \ldots, p
\]

where \(x\) are the measurements on the \(p\) behavioral variables, and carried out the principal component analysis based on the simple-covariance matrix of the \(p\) log-contrasts of the original variables (Khattree & Naiki 2000).

We also used MultiResponse Permutation Tests (MRPP program, PC-ORD ver. 6.0, McCune & Mefford 2010) to analyze whether there were differences in the activity patterns of Andean Flamingos between sites and between years. For this nonparametric method for testing multivariate differences among pre-defined groups, we constructed a primary matrix of 433 individuals × 11 activities, and a secondary matrix identifying the study site where the individuals were located and the sampling year. We estimated the test statistic \(T\), which is \(T = (d - m_d)/s_d = (\text{observed} - \text{expected})/\text{standard deviation of expected}\), where \(d\) is the weighted mean within-group distance, \(m_d\) and \(s_d\) are the mean and standard deviation of \(d\) under the null hypothesis. The \(P\) value associated with \(T\) was determined by numerical integration of the Pearson type III distribution. Both analyses were carried out with PC-ORD software using the Euclidean distance (McCune & Mefford 2010).

We analyzed whether time spent in marching displays was correlated with flock size using Spearman rank-order correlation. We also evaluated whether there were differences
in flock size and time spent in courtship displays in different years using Kruskal-Wallis rank sum tests. These non-parametric analyses were performed in R (R Development Core Team 2009).

RESULTS

We found significant differences in Andean Flamingo activity patterns between Laguna de Vilama and Laguna Melincué and between years ($T = -116.2, A = 0.25, P < 0.00001$; all pairwise comparisons $P < 0.00001$; Fig. 2). At Laguna de Vilama, flamingos mainly foraged by walk-feeding, whereas at Laguna Melincué, time spent stamp-feeding was higher in 2007 or similar to walk-feeding in 2011 (Fig. 2). There were also differences in activity patterns between years at both sites. At Laguna de Vilama, flamingos spent less time foraging in 2007 than in 2008, and more time grooming in 2007 compared to 2008, whereas at Laguna Melincué, flamingos spent more time foraging and less time resting in 2007 than in 2011 (Fig. 2).

The first three axes of the PCA explained 78.3% of the data. The first axis (43.5%) segregates those flamingos that spent most of their time feeding, whereas at Laguna Melincué, in addition to feeding they spent time in other activities, mainly resting and grooming (Fig. 2). At Laguna de Vilama, flamingos mainly foraged by walk-feeding, whereas at Laguna Melincué, time spent stamp-feeding was higher in 2007 or similar to walk-feeding in 2011 (Fig. 2). There were also differences in activity patterns between years at both sites. At Laguna de Vilama, flamingos spent less time foraging in 2007 than in 2008, and more time grooming in 2007 compared to 2008, whereas at Laguna Melincué, flamingos spent more time foraging and less time resting in 2007 than in 2011 (Fig. 2).

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spent most of their time walk-feeding (Laguna de Vilama in 2007, 2008), whereas the second axis (18.1%) segregates flamingos grooming from those resting (Fig. 3a). The third axis (16.5%) segregates to the negative side those flamingos that spent most of their time foraging by stand-feeding (Laguna Melincué 2007) (Fig. 3b).

There were marked differences in flamingo abundance between sites and years. At Laguna de Vilama, we recorded 1022 flamingos in 2007 and 4510 flamingos in 2008, and

FIG. 3. PCA biplots showing the distribution of flamingos at Laguna de Vilama and Laguna Melincué, Argentina, in different years (centroids ± 99% confidence interval) according to different activities (arrows). A) PCA Axes 1 and 2, B) PCA Axes 1 and 3.
at Laguna Melincué, we recorded 3254 flamingos in 2007, 450 flamingos in 2010, and 275 flamingos in 2011.

We did not observe marching displays at Laguna de Vilama during the breeding season in any year, while in Laguna Melincué, we observed Andean Flamingos forming marching flocks during our three sampling sessions (Fig. 4). However, there were differences among years. In 2007, for each sampling day there were more marching events, more flamingos marching, and more time spent marching (Fig. 4).

Time spent marching was not associated with flock size ($r_s = -0.06; P = 0.718$). Even though there were no differences in the number of flamingos involved in each marching event between years ($K = 0.174; P = 0.9166$; Fig. 5a), there were differences in the duration of each marching event ($K = 21.91; P = 1.744e-05$), with marching events in 2007 lasting markedly longer than those in 2010 and 2011 (55 min vs. fewer than 5 min; Fig. 5b). We did not record any copulation after these marching events.

**DISCUSSION**

In our study, numbers of flamingos using Andean and lowland wetlands were markedly different between years, and dominant behaviors were different between sites and between years, potentially reflecting a wide range of resource availability and environmental conditions (Hurlbert 1982), including weather (Barisón 2012), and energetic constraints related to their life history. However, we did observe some broad patterns. At Laguna de Vilama, the high-altitude wetland used primarily during the breeding season, flamingos spend 80% of their time feeding. Similar patterns have been recorded for Caribbean Flamingos and Greater Flamingos in coastal wetlands (Espinò-Barros & Baldassarre 1989, Bildstein et al. 1991, Arengo & Baldassarre 2002, Khaleghizadeh 2010). At Laguna Melincué, in contrast, where time spent for feeding was lower, there was a broader repertoire of behaviors, including courtship, and there were differences between years in the dominant behaviors. Feeding was higher in 2007, while resting and grooming was higher in 2011. Foraging behavior could be affected by several factors (e.g., prey availability, weather conditions; Kumssa & Bekele 2014). We have no information about differences in prey availability between years, but it is likely, that these differences in activity patterns could be associated with marked differences in weather conditions among sampling periods, since we recorded colder temperatures and more sunny days in 2007 and more rain and higher winds in 2011. On the other hand, it should be taken into account that we did not record nocturnal activities (Beauchamp & McNeil 2003), even though we observed signs of foraging activity at night (Barisón 2012).

A higher feeding effort in Laguna de Vilama during the breeding season could be associated with a higher energy demand in some adult flamingos during chick rearing since birds breeding in colonies in Bolivia and Chile are known to feed in these nearby wetlands (Rocha 1997, Caziani et al. 2007, Rocha et al. 2009, Derlindati et al. 2010). Lowland wetlands, such as Laguna Melincué, are highly productive habitats (Drago & Quirós 1996, Boveri & Quirós 2007), and it is likely that even in winter (the non-breeding season) they have higher or similar availability of food than high altitude wetlands in summer (the breeding season) (T. Uraoka & M. Contreras pers. comm.). Therefore, flamingos at lowland wetlands during non-breeding season may not have to spend as much time feeding as they do during the breeding season. The availability of food at this time of the reproductive cycle would mean flamingos have the energy to be used in courtship and other social behaviors.
Feeding activities include different foraging modes like stand-feeding and walk-feeding. At Laguna de Vilama, walk-feeding was more frequent than stand-feeding. This pattern matches some observations on the feeding modes of three flamingo species (Andean, Puna, and Chilean Flamingo) at upland wetlands in Chile, Bolivia and Peru, where all species get their food by walking (Hurlbert 1982). At Laguna Melincué, in contrast, stand-feed-
ing was more common than walk-feeding in 2007, but similar in 2011. It is likely that difference in foraging modes between sites and years could be associated with differences in weather conditions or food availability, and food type.

Andean Flamingos showed seasonal patterns in their marching displays. We did not observe any marching in Laguna de Vilama during the breeding season, nor have previous studies carried out at this site during breeding season (Caziani & Derlindati 2000), whereas in Laguna Melincué we recorded marching flocks in the three non-breeding season sampling periods of this study, as well as in other years in Melincué and nearby lowland wetlands (MCR, CB, & IMB pers. observ.). This contrasting seasonal pattern is similar to other flamingo species (e.g., Caribbean Flamingo), which can engage in courtship displays throughout the year, but show a peak in frequency and intensity prior to the breeding season (Espino-Barros & Baldassarre 1989). Likewise, differences in marching activities between breeding and non-breeding sites have been recorded for these species in Chile.

FIG. 5. Flock size and time spent in courtship display for Andean Flamingos for each marching event at Laguna Melincué, Argentina in the non-breeding seasons in 2007 (n = 20 marching events), 2010 (n = 13) and 2011 (n = 4). In each boxplot, the lower and upper boundaries of the box indicate the 25th and 75th percentiles, the line within the box marks the median, and whiskers indicate the 10th and 90th percentiles of distributions.
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(Parada 1987) and in other flamingo species. For instance, the main regular display grounds for Lesser Flamingo and Greater Flamingo breeding in Lake Natron, Tanzania, are well away from the colonies (Brown & Root 1971).

Interestingly, Andean Flamingos showed marked differences in the number of marching events between years, being higher and lasting longer in those years with high flamingo abundance. Similar patterns have been recorded in the wild for Lesser and Greater Flamingos in Africa (Brown & Root 1971), and in captivity for Chilean and Caribbean Flamingos (Stevens 1991, Pickering et al. 1992, Stevens & Pickett 1994, Farrell et al. 2000). Group displays and marching events may play a role in ensuring synchronous nesting and/or facilitating pair formation (Pickering & Duverge 1992).

There is a lack of information on the timing of copulations of flamingos (Johnson & Cézilly 2007). We did not observe any copulation near courtship-displaying flocks at Laguna Melincué, as recorded for Lesser and Greater Flamingos in Africa (Brown & Root 1971). However, as flamingos are opportunistic breeders, copulation may take place just before arriving at the breeding sites, as has been observed for Greater Flamingo, whose group displays are observed months before breeding (Rendón et al. 2011).

**Conservation implications.** Our data on flamingo behavior provided an initial description of the activity patterns of the most threatened flamingo species in the world at two contrasting sites. Our study shows that there were differences in number of flamingos using these wetlands and in activity patterns between sites and years. Energetic constraints of individuals across the annual cycle (incubation, chick rearing, wintering) may condition the behavior of flamingos, and therefore, the observed differences between localities may be due at least in part to differences in flamingo phenology (breeding vs. wintering). On the other hand, inter-annual variations in flamingo behavior within each locality may be a response to environmental variability. We did find differences in time spent for feeding and resting, and courtship marching displays. The quantity and quality of food that flamingos find at these wetlands may condition the reproductive success of the Andean Flamingo, as has been shown for other bird species (Chávez-Ramírez & Webjie 2012, Stirnemann et al. 2012, Li et al. 2013). It is important to note that during our study there was virtually no human disturbance affecting flamingo behavior. The effects of human activities on these activity patterns are little known but could potentially adversely affect flamingos by decreasing time spent feeding or courting and affecting fitness. While this study provides preliminary information on the dynamics and use of different wetlands used by flamingos, there is a need for further research on feeding ecology and reproductive physiology of the Andean Flamingo, as well as detailed studies of wetland hydrology and food availability. Continued studies monitoring flamingo abundances and recording behaviors and activity patterns at different sites throughout the year are necessary to fully understand the conditions that ensure the persistence of Andean Flamingo populations.

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