

Influence of long-term climatic changes on breeding of the Chilean flamingo in Mar Chiquita, Córdoba, Argentina

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Abstract We report a comparative analysis of the environmental conditions prevailing at each successful breeding event of the Chilean flamingo (*Phoenicopterus chilensis*) during the 1969–2010 period in Mar Chiquita, a large salt lake near Córdoba, Argentina. Breeding was monitored annually by air. The following parameters were measured: rainfall, water level, water salinity, availability of shoreline and offshore (islands) mudflats, presence of brine shrimp (*Artemia franciscana*), and presence of the Argentine silverside fish (*Odonthotestes bonariensis*). During the study period, Mar Chiquita underwent great variations in level, reaching the highest level in its geological history. Salinity ranged from 274 down to 22 g l⁻¹. *Artemia* was present during the high-salinity periods and was absent when salinity dropped below 55 g l⁻¹, and the lake was invaded by the silverside. Flamingos bred irregularly during both high- and low-salinity periods (11 successful attempts in 42 years). Comparison of breeding and non-breeding years showed that the only environmental factor always associated with breeding events was availability of mudflats, mostly

bordering islands. Water level increases over 0.90 m during the breeding season may flood the nesting areas and affect breeding success. Rapid decreases in lake level may also affect breeding by favoring predation or via nutrient availability. Other factors (water level, water salinity, local rainfall, and presence of *Artemia* and silverside) were within similar ranges in breeding and non-breeding years. Our surveys provided indirect evidence suggesting that food availability may influence flamingo breeding in Mar Chiquita. Management implications of our study include: (a) habitat suitability analysis of wetlands like Mar Chiquita should consider that availability of offshore mudflats free of vertebrate predators is an essential requirement for flamingo conservation and (b) drastic and rapid increases or decreases in water level due to human control of river inflows may affect chances of successful flamingo breeding and therefore should be evaluated carefully.

Keywords Climate change · Salt lake dynamics · Brine shrimp · Silverside fish

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Introduction

In waterbirds, the onset of breeding is closely associated with the hydrological and limnological factors that control both breeding habitat and food availability. With regard to flamingos, most of our present understanding of the interaction between

environmental factors and flamingo breeding comes from long-term studies of the Greater flamingo in the Camargue (delta of the Rhone River, southern France), both in natural (Johnson & Cézilly, 2007) and anthropogenic habitats (commercial salt pans) (Cézilly et al., 1995; Johnson & Cézilly, 2007; Bechet & Johnson, 2008; Bechet et al., 2009). These studies have shown that the initiation of breeding is a complex phenomenon driven mostly by climate and water regime through interactions that show significant temporal and spatial variations. However, further research is needed to elucidate the key factors involved in the onset of flamingo breeding activity (Johnson & Cézilly, 2007).

Information on the breeding ecology of other flamingo species is very limited, particularly for the Neotropical Chilean (*Phoenicopterus chilensis*), Andean (*Phoenicoparrus andinus*), and Puna (*Phoenicoparrus jamesi*) flamingos. More specifically, there is a lack of long-term records to explore the relationship between environmental factors and breeding events, with the exception of the long-term breeding survey of the Chilean flamingo in Mar Chiquita started in 1969 (Bucher et al., 2000).

Chilean flamingo breeding records available from Mar Chiquita include a very contrasting period during which the lake showed substantial variation in water level and area, as a result of an exceptional, long-term rainfall increase in the catchment basin of the lake. In fact, the water level reached during this period was the highest since the lake originated about 50,000 years ago. As a result, the ecological conditions of the lake changed substantially in recent decades, particularly salinity, distributions of islands and mudflats, and abundances of fish and invertebrates (Reati et al., 1997; Bucher & Bucher, 2006).

Such a wide range of environmental conditions provides a unique opportunity for assessing the influence of environmental factors on the breeding behavior of the Chilean flamingo. Moreover, understanding the functional interactions between flamingo breeding biology and environmental factors may also contribute to our understanding of the potential effects of climate change on wildlife (IPCC, 2001). Here we report a comparative analysis of the environmental conditions prevailing during 42 nesting seasons in Mar Chiquita, with the aim of identifying those factors associated with successful breeding of the Chilean flamingo.

Materials and methods

Study area and species

Mar Chiquita, located in the central plains of Argentina (30°30'S, 62°30'W) at an elevation of about 70 m above sea level, is a large salt lake with an area that ranges between 2,000 and 6,000 km² according to water level (Fig. 1). Because of its rich biodiversity, the area is a provincial reserve and a Ramsar convention site, officially known as “Bañados del Rio Dulce y Laguna Mar Chiquita.” Local climate is subtropical, semi-arid. Mean annual temperature ranges from 23°C in the northern part of its catchment to 17°C in the southern portion. Mean annual rainfall ranges from 1,000 mm on the eastern portion part of the catchment to 700 mm in the western end. Rainfall is concentrated in summer months (October–April) (Bucher, 2006b).

Mar Chiquita is the terminal collector of a vast (92,280 km²) river basin that covers a significant portion of northwestern and central Argentina. It is fed by three inflows, the Dulce, Segundo, and Primero Rivers (Fig. 1) with catchment basins of 89,950, 1,350, and 980 km², respectively. Mar Chiquita hydrology is, to a large extent, controlled by local rainfall and the inflow from these rivers. Annual inflow from rivers ranges from 11 to 36 hm³. Detailed mathematical modeling indicates that the lake's water balance is primarily controlled by variations in the Rio Dulce flows (Rodríguez et al., 2006; Troin et al., 2010).

During the study period (1969–2010), Mar Chiquita underwent considerable hydrological change. Starting in the late 1970s, rainfall in the Rio Dulce river basin increased markedly, causing a 9-m rise in the lake level and a ~80–90% decrease in salinity. This situation lasted, with some oscillations, until 2003, when water level started to decrease slightly but steadily, a trend that has continued until present (2010). During this period, lake area ranged from 2,500 to 6,000 km², and salinity varied accordingly, ranging from 297 down to 25 g l⁻¹ (Bucher & Bucher, 2006).

Drastic variations in salinity resulted in important changes in the biota of the lake. Of particular interest was the disappearance of the brine shrimp *Artemia* (*Artemia franciscana*) and the subsequent invasion by a single fish species (the Argentine silverside,

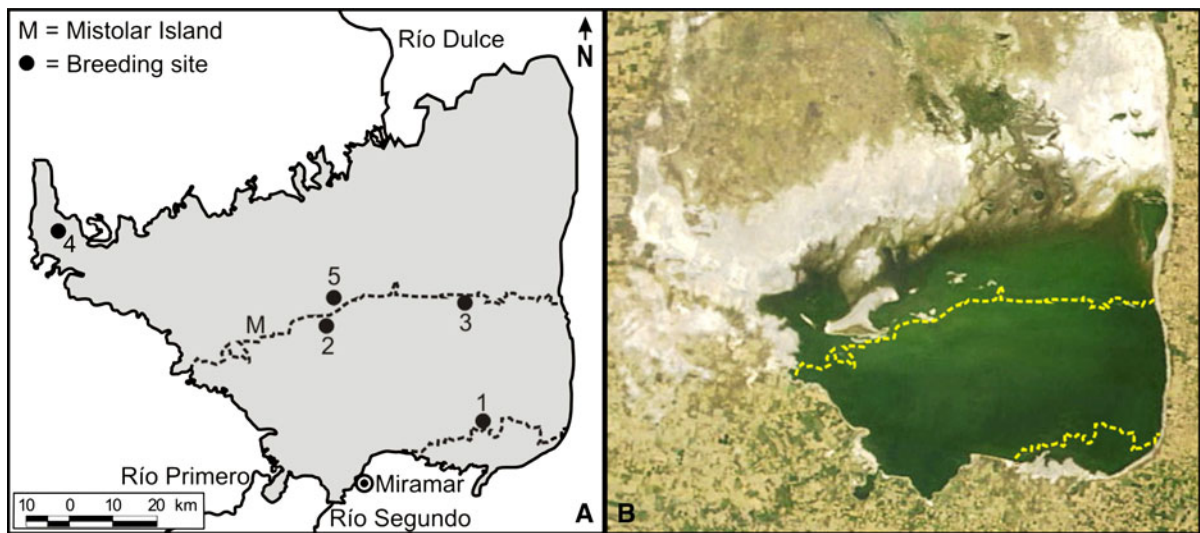


Fig. 1 Mar Chiquita, Córdoba, Argentina. **A** Breeding sites and major tributaries. *Dotted line* corresponds to original northern shoreline prior to the rise in water level that began in the late

1970s. **B** Satellite image of the lake (October 11, 2010). *Dotted line*, same as in **A**

Odonthestes bonariensis) once salinity fell below 55 g l^{-1} (Bucher & Etchegoin, 2006). This transformation was reversed in 2009, when salinity returned to values $>55 \text{ g l}^{-1}$, silverside disappeared and *Artemia* became abundant again.

The Chilean flamingo is the commonest flamingo species in Argentina, and Mar Chiquita is one of the species' main breeding areas. Two other flamingo species, Andean and Puna, also occur in Mar Chiquita, mostly as winter visitors. The Chilean flamingo is present in the area all year round. Numbers change over the years but rarely drop below 10,000 birds. The breeding cycle usually starts in November, when birds concentrate in large numbers in traditional sites, usually islands with wide mudflat beaches. Adult numbers in the colony peak in January–February. Nestlings abandon the islands and start to congregate in crèches in early March, reaching peak numbers from April to mid-May. In April, adults start to leave the colony (Bucher, 2006a).

Methods

We surveyed breeding colonies annually, using single-engine, high-wing aircraft, between 1969 and 2010, except in 1971, 1972, 1986, 1988, 1989, and 1990. Flights were conducted from late March to early May.

During this period, juveniles are already in crèches where they can be easily recognized and photographed from the air. We also used the aerial surveys to search for flamingo feeding areas.

Breeding colonies were detected by systematic flights that covered the entire lake shoreline and existing islands. Flight level was the lowest possible without disturbing the birds, about 400 m above ground. After detecting a colony, we counted juveniles standing in crèches in the water using color photographs. All colonies detected comprised over 1,000 young. We assumed that all juvenile flamingos seen were Chilean, because the other flamingo species present on the lake have never been observed to breed there (Bucher et al., 2000). As the occurrence of breeding is based on a single flight during the period of fledging, it is possible that unsuccessful breeding attempts were missed, given that breeding interruption after a few weeks of incubation is common in flamingos. Therefore, in this article, the term breeding event refers only to successful breeding events.

The following environmental variables were measured in the lake throughout the study period: water level at the beginning (October) and end (April) of the flamingo breeding season, salinity, annual rainfall in the vicinity of the lake, presence of suitable breeding habitat (mudflats) along the shore (shoreline mudflats) or bordering islands (offshore mudflats), and presence

Fig. 2 Photo taken on May 5, 2010, of an island, 2.6 km long, in central Mar Chiquita lake (30°35'S, 62°43'W, in between points 2 and 5 in Fig. 1B). This was created in the late 1970s when a rising lake level inundated the low-lying scrublands up to the vegetation line shown in the photograph, making a topographic high spot an island. Since 2003, the steadily receding water level has exposed extensive mudflats, optimal flamingo breeding habitat



of *Artemia* and silverside. Water level data were obtained from monthly records provided by the Córdoba's provincial water resources agency. Starting in 2008, a complementary automatic recorder was installed by us. Change in water level between October and April was considered of interest, given the possibility of significant increases or decreases in water level affecting the nesting colonies. For example, flooding of nests might result from a sudden increase in lake level, or receding waters might negatively impact flightless juveniles by increasing the distance between nests and water.

Water salinity was assessed using non-systematic records obtained from published and unpublished reports, as well as our own measurements. Missing data were extrapolated from a regression function between water level and salinity variables (Bucher & Bucher, 2006). Available information indicates that salinity values are similar in the entire lake, except near the mouths of rivers, where salinity gradients exist. Annual rainfall near the breeding sites was estimated based on averaged data from four meteorological stations located within a radius of 70 km of them. Availability of suitable breeding habitat (shoreline and offshore mudflats) was assessed based on previous observations on nesting habitat selection by Chilean flamingos in Mar Chiquita (Bucher et al., 2000), which indicated that shoreline mudflats are usually less preferred by flamingos, probably because they allow access to nests of terrestrial predators such

as the puma (*Puma concolor*), pampas fox (*Lycalopes gymnocercus*), Geoffroy's cat (*Leopardus geoffroyi*), tayra (*Eira barbara*), and lesser grison (*Galictis cuja*). Availability of shoreline mudflats was assessed by checking the presence of mudflats at least 10 m wide along the whole lake perimeter. Availability of offshore mudflats was estimated by checking the presence of islands surrounded by mudflats over 10 m wide. In both cases, we used satellite images and aerial photographs as the primary source of information (Figs. 1, 2).

The presence of silverside was determined from fishing records until 2008, when fishing was prohibited because of a rapid silverside decline due to increased salinity. After 2008, we used sonar transects. The presence of *Artemia* was assessed by periodic sampling of Mar Chiquita nearshore waters in spring and summer each year.

Water pollution in Mar Chiquita, another environmental factor potentially influencing flamingo breeding behavior, was not considered because of difficulties associated with in situ measurements in remote places. However, available information suggests that at present this is not an important factor.

Feeding areas were assessed during the survey flights around the lake. We estimated the number of flamingos feeding in the following sectors (as well as in breeding colonies): north coast, west coast, south coast, and east coast. Special consideration was given to the Rio Dulce delta on the north coast and the

mouths of Primero and Segundo rivers on the southern coast. These estimates were subject to considerable error. The great size of the sampled area affected visibility toward the edges of the flying paths, and particular weather conditions, especially strong winds, can cause large changes in the location of flamingos between consecutive days. Even if our data do not allow reliable comparisons among years, they do provide useful information on the relative use of different feeding areas within years.

Results

Historical summary of recorded events

During the study period, Mar Chiquita underwent great variations in level. Despite the fact that in 2003 the lake reached the highest level in its geological history, the observed changes suggest a long-term cycle, rather than a secular trend to new, permanent conditions. For recent decades, at least four distinctive periods are clearly recognizable (Table 1; Fig. 3): (1) low level; (2) rapid rise, (3) high level, and (4) steady decline.

Low level (1969–1972)

The water level during this short period was probably one of the lowest during the twentieth century (Bucher & Bucher, 2006; Piovano et al., 2006). This exceptional situation was the result of a combination of both low rainfall and, more importantly, the filling of the Rio Hondo reservoir in the upper Rio Dulce (Bucher & Bucher, 2006). Shoreline mudflats were very wide, but no islands were available. Salinity was $>250 \text{ g l}^{-1}$. *Artemia* was present, but fish were not.

During this period, the Chilean flamingo bred only once (1969). The colony was located on the shoreline, at the end tip of a long (4 km), narrow (0.5 km) spit on the southern coast of the lake (Fig. 1, site 1). During this period, one breeding episode was detected (Table 1).

Rapid rise (1973–1988)

During this 15-year period, a rapid increase in the lake level followed exceptionally high rainfall in the catchment. Accordingly, salinity decreased

substantially, reaching 55 g l^{-1} in 1979. Shortly thereafter *Artemia* disappeared, and silverside invaded the lake from the rivers (Bucher & Bucher, 2006).

Early in this period, the Chilean flamingo bred in three consecutive years, when the water level remained temporarily stable and salinities high, before continuing its rapid rise (see Fig. 1). Colonies were located on two islands $\sim 3\text{--}5 \text{ km}$ long and 0.5 km wide that soon were covered by water (Fig. 1, sites 2 and 3).

By 1979, mudflats had disappeared, and the lake margin had reached areas with permanent vegetation (Fig. 2B). After that, breeding ceased for more than a decade until 1991 (Table 1). Although no surveys were conducted in some years during this period (Fig. 2), we assume that no breeding events were missed because the shoreline was inside dead woody vegetation, an unsuitable habitat for flamingo nesting.

High level (1988–2003)

During this period, lake level fluctuated mostly between 69 and 71 m a.s.l. and salinity remained low (Table 1; Fig. 1). As a result *Artemia* was absent, and the silverside population increased markedly, leading to the development of a significant commercial fishery industry (Bucher & Etchegoin, 2006).

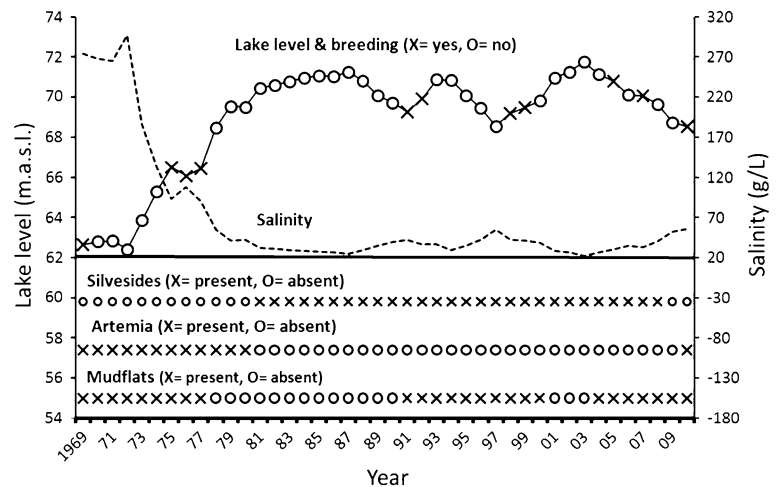
Initially there was a slight decline in level until 1991. This again exposed mudflats along the shoreline and also on the margins of newly emerged islands (Figs. 1, 2). Coincidentally, flamingos bred again in 1991 on a new island area located on the recently expanded northwestern portion of the lake (Fig. 1, site 4). This nesting area consisted of an archipelago of three islands covering an area $\sim 0.8 \text{ km}$ long by 0.3 km wide. A total of four successful breeding attempts were recorded.

During this period, extensive offshore mudflats became available on a large island, named “Mistolar,” $>20 \text{ km}$ long and 3 km wide (Fig. 1) that was created when the neck of a peninsula was flooded during the previous period of rapid rise in lake level. These shoreline mudflats were not occupied by flamingo colonies, probably because Mistolar has extensive woody shrub vegetation and mammalian predators, including puma, pampas fox, Geoffroy’s cat, tayra, and lesser grison. These predators have survived following separation from the mainland thanks to the availability of fresh water from abandoned, man-

Table 1 Occurrence of flamingo breeding events, lake level (July), water salinity, variation in water level from beginning (October) to end (April) of the breeding season, availability of mudflats, and occurrence of silverside fish (*Odonthotestes bonariensis*) and *Artemia* (*Artemia franciscana*) in Mar Chiquita during the study period

| Year | Breeding | Lake level (m a.s.l.) | Salinity (g l ⁻¹) | Level change (m) | Presence of: | | |
|------|----------|--------------------------|----------------------------------|---------------------|--------------|------|----------------|
| | | | | | Mudflats | Fish | <i>Artemia</i> |
| 1969 | Yes | 62.65 | 274 | 0.87 | Yes | No | Yes |
| 1970 | No | 62.79 | 268 | 0.19 | Yes | No | Yes |
| 1971 | No | 62.83 | 265 | 0.06 | Yes | No | Yes |
| 1972 | No | 62.41 | 297 | -0.33 | Yes | No | Yes |
| 1973 | No | 63.85 | 186 | 1.38 | Yes | No | Yes |
| 1974 | No | 65.30 | 133 | 0.70 | Yes | No | Yes |
| 1975 | Yes | 66.50 | 93 | 0.70 | Yes | No | Yes |
| 1976 | Yes | 66.06 | 108 | -0.37 | Yes | No | Yes |
| 1977 | Yes | 66.44 | 90 | -0.39 | Yes | No | Yes |
| 1978 | No | 68.46 | 55 | 1.26 | No | No | Yes |
| 1979 | No | 69.54 | 41 | 0.39 | No | No | Yes |
| 1980 | No | 69.50 | 42 | -0.01 | No | No | Yes |
| 1981 | No | 70.45 | 32 | 0.03 | No | Yes | No |
| 1982 | No | 70.58 | 31 | 0.01 | No | Yes | No |
| 1983 | No | 70.78 | 29 | 0.31 | No | Yes | No |
| 1984 | No | 70.94 | 28 | 0.23 | No | Yes | No |
| 1985 | No | 71.07 | 27 | -0.08 | No | Yes | No |
| 1986 | No | 71.02 | 26 | 0.16 | No | Yes | No |
| 1987 | No | 71.26 | 25 | 0.07 | No | Yes | No |
| 1988 | No | 70.80 | 29 | -0.08 | No | Yes | No |
| 1989 | No | 70.07 | 35 | -0.21 | No | Yes | No |
| 1990 | No | 69.72 | 39 | 0.14 | No | Yes | No |
| 1991 | No | 69.26 | 42 | -0.09 | Yes | Yes | No |
| 1992 | Yes | 69.92 | 36 | 0.51 | Yes | Yes | No |
| 1993 | No | 70.87 | 36 | 0.73 | Yes | Yes | No |
| 1994 | No | 70.83 | 29 | -0.26 | Yes | Yes | No |
| 1995 | No | 70.08 | 35 | -0.52 | Yes | Yes | No |
| 1996 | No | 69.44 | 42 | -0.44 | Yes | Yes | No |
| 1997 | Yes | 68.56 | 55 | 0.32 | Yes | Yes | No |
| 1998 | Yes | 69.18 | 42 | -0.22 | Yes | Yes | No |
| 1999 | Yes | 69.47 | 41 | 0.28 | Yes | Yes | No |
| 2000 | No | 69.81 | 38 | 0.43 | Yes | Yes | No |
| 2001 | No | 70.95 | 28 | 1.05 | No | Yes | No |
| 2002 | No | 71.25 | 26 | 0.05 | No | Yes | No |
| 2003 | No | 71.75 | 22 | 0.35 | No | Yes | No |
| 2004 | No | 71.15 | 26 | -0.47 | Yes | Yes | No |
| 2005 | Yes | 70.78 | 30 | -0.16 | Yes | Yes | No |
| 2006 | No | 70.10 | 35 | -0.34 | Yes | Yes | No |
| 2007 | Yes | 70.06 | 33 | -0.01 | Yes | Yes | No |
| 2008 | No | 69.63 | 40 | -0.35 | Yes | Yes | No |
| 2009 | No | 68.74 | 52 | -0.61 | Yes | No | No |
| 2010 | Yes | 68.53 | 56 | 0.11 | Yes | No | Yes |

Fig. 3 Successful breeding events, water level, water salinity, mudflat availability, and the presence of *Artemia* and silverside fish during the study period



made artesian wells. Relative to the breeding habitat requirements of flamingos, Mistolar was more like the mainland than offshore mudflats.

Steady decline (2004–2010)

The high-water level period continued until 2003, when for a few months the lake reached the highest level ever recorded. Since then, lake level has decreased steadily (Fig. 3). The silverside population declined rapidly after salinity surpassed 55 g l^{-1} and was again extinct by the time salinity reached 58 g l^{-1} (2009). *Artemia* then reappeared. The Chilean flamingo continued breeding intermittently on the northwestern islands (site 5) until 2009, when those islands were again connected with the mainland as the whole northern portion of the lake dried up. In 2010, new colonies appeared on other small islands closer to Mistolar (Fig. 1, site 5).

Feeding areas

Our observations indicate that flamingos breeding at Mar Chiquita fed exclusively in that lake and its wetlands. Aerial surveys showed that they usually fed around the mouths of the incoming rivers. Nesting sites were at distances of 40–60 km from these feeding sites, well within the range of daily flamingo flights (Amat et al., 2005). River deltas are likely to offer abundant food, besides being a source of drinking water. The steep salinity gradient associated with the mixing of inflowing fresh waters with highly saline

lake water may result in significant flocculation of organic matter that could provide both nutrients and energy. In addition, the higher nutrient levels typical of inflowing waters and the shallowness of these areas of sediment deposition may favor development of benthic algae, which in turn enhance development of invertebrate populations.

Flamingos preferred the larger Rio Dulce delta for feeding, followed by those of the Rio Segundo and finally the Rio Primero. This sequence correlates with the mean discharge volumes of the rivers (1967–1997 period) of 90.7 , 12.2 , and $9.7 \text{ m}^3 \text{ s}^{-1}$, respectively. An exception to this general pattern was observed during the 1969, 1970, and 1973 surveys, when the Rio Dulce flow was extremely low because water was being withheld upstream to fill the new Río Hondo reservoir. During this period, feeding flocks were more abundant around the mouths of the Segundo and Primero rivers.

Given the very large areas that flamingos used for feeding, no accurate assessment of the number of feeding individuals was possible for comparisons among years. Smaller feeding groups and isolated individuals were observed sporadically away from the river deltas, particularly along the southern and western coasts.

Environmental factors and flamingo breeding

Breeding habitat

All successful breeding colonies recorded during our study period were located on mudflats, particularly

offshore mudflats bordering islands. The only exception was the colony established on a shoreline peninsula at a time when no offshore mudflats were available (Fig. 2, site 1).

Breeding site fidelity

Breeding colonies were established at only five sites throughout the study period (Fig. 1). Once nesting was begun, a site was abandoned only if a change in water level caused it to be either flooded or surrounded by extensive dry flats. Preferred islands included both single, large mudflats (e.g., sites 2 and 3 in the rapid rise period), or archipelagos of several smaller mudflats close to each other (Fig. 1, sites 4 and 5). Changes in colony nesting sites were associated mostly with periods of declining lake level, when receding waters exposed new mudflats around islands (Fig. 2).

Limnological variables

During the study period, successful breeding occurred under a wide range of water level and salinity conditions little different from those when breeding did not occur. For successful breeding years, water level ranged from 62.7 to 70.8 m a.s.l. and salinity from 30 to 274 g l⁻¹, whereas for non-breeding years water level ranged from 62.8 to 71.8 m a.s.l. and salinity from 22 to 268 g l⁻¹.

Seasonal changes in the lake level between the beginning and end of flamingo breeding seasons varied considerably along the study period. When assessing their influence on flamingo breeding success, variations (both positive or negative) below 0.40 m should not be considered in the analysis because (1) variations of this order of magnitude are frequent during the breeding season caused by winds of over about 19 knots (meteorological tides) (Pozzi et al., 2006) and (2) our field observations indicate that flamingos build nests in places high enough to withstand water level increases up to about 0.40 m.

Increases over 0.40 m were recorded in 11 years (3 in breeding years and 8 in non-breeding years). For breeding years, the highest level rise was 0.87 m in 1969. At this time, the lake was rapidly increasing from the 1968 very low levels (Bucher & Bucher, 2006). It is likely that nests in traditional breeding areas were not affected because they were at a relative

higher position in relation to the previous year. The same scenario applies to 1975 (0.7 m). The 1992 smaller increase (0.51 m) is close to the magnitude of meteorological tides and probably had little influence on the breeding colonies. No seasonal decreases in lake level were recorded in breeding years.

In non-breeding years, increases of over the 0.87-m record reached in breeding years occurred in 1973 (1.38 m), 1978 (1.26 m), and 2001 (1.05 m), all of them during periods of rapid inter-annual level increase (Fig. 1). As mentioned previously, it is likely that in these years all traditional breeding sites were flooded. The remaining three events (ranging between 0.73 and 0.43 m) were smaller than the peak value recorded during successful breeding years, suggesting that such a level of rise may not be high enough to be the key factor in flamingo breeding failure.

Decreases of over 0.4 m were recorded in non-breeding years only: 1995 (0.7 m) and 2009 (0.61 m). As mentioned before, significant decreases in water level could prevent flamingo breeding by either allowing a terrestrial connection between islands and the coast allowing invasion by predators, or through a fall in primary productivity following a reduced nutrient inflow from the incoming rivers.

Mean annual rainfall in the vicinity of the nesting areas was similar between breeding (662 mm) and non-breeding (756 mm) years, suggesting that in Mar Chiquita rainfall in the colony area may have little influence on the onset of flamingo breeding events.

With regard to the possible influence of other key species on flamingo breeding, *Artemia* and silverside were present in Mar Chiquita during both breeding and non-breeding events, although never simultaneously. Five flamingo breeding events were recorded over the 8 years when *Artemia* was present, whereas six breeding events took place during the 25 years of silverside presence in the lake. *Artemia* occurred with salinities above 55 g l⁻¹, whereas silverside invaded the lake only when salinity was <55 g l⁻¹. Absence of both *Artemia* and silverside in 2009 may have been due to rapidly changing water salinity conditions in the vicinity of this threshold for both species, and our observations could have missed the presence of either of them at low densities.

In summary, when breeding and non-breeding years are compared, the only environmental factor consistently associated with breeding events was availability of mudflats. Offshore island mudflats were clearly

preferred, the only exception being year 1969, when the breeding colony was located on the mudflats of a long peninsula or spit.

Discussion

The wide range of hydrological and limnological conditions recorded during the 41-year study period provided important clues for the understanding of the environmental factors that influence the onset of breeding by the Chilean flamingo in Mar Chiquita. The observed 11 breeding events in the 42-year study period confirm flamingo's well-known tendency to breed sporadically in large colonies, usually in a few places to which they tend to be faithful. The observed frequency of successful breeding attempts (once every 3.85 years) is very similar to that recorded for the closely related Greater Flamingo (*Phoenicopterus roseus*) during a 40-year period in Etosha National Park, Namibia (once every 3.64 years) and during a 26-year period at Fuente de Piedra, Spain (once every 4.33 years; Johnson & Cézilly, 2007, p. 147).

With regard to the possible influence of the studied environmental factors on flamingo breeding in Mar Chiquita, comparison of breeding and non-breeding years shows that availability of mudflats, particularly offshore mudflats on islands devoid of mammal predators, is the only habitat characteristic constantly associated with successful breeding events. A similar conclusion was reached in another important Chilean flamingo breeding site, Laguna Llanquanelo in western Argentina, which went through the same cycle of rapid increase of water level at the same time as did Mar Chiquita (Sosa, 1999). The breeding events also tended to take place after a few years of water level decline.

Availability of both shoreline and offshore mudflat depends on a very dynamic landscape and sedimentological process controlled primarily by water level. Of particular significance is the periodic generation and disappearance of islands with mudflats that in our study resulted in four changes in the location of breeding colonies.

Local rainfall is another factor that could influence flamingo breeding, as shown for other saline wetlands in arid regions, such as Etosha National Park, Namibia. However, local rainfall does not appear to be a significant factor in the case of the more stable,

permanent Mar Chiquita, where local rainfall variations have much less influence on the lake's water level than does the inflow from rivers, as shown by detailed hydrological data and simulation analysis of the Mar Chiquita system (Rodríguez et al., 2006). Lake level variations during the breeding season may affect breeding when they go over a critical threshold of about 0.90 m, flooding nesting areas.

In summary, our results indicate that flamingos are capable of breeding under a wide range of limnological conditions in terms of level, salinity, and the presence of fish and invertebrates, as long as suitable breeding habitat is available, and the nesting areas are not flooded or affected by lake level decreases during the breeding season (both factors are rare in Mar Chiquita).

However, even if the presence of offshore mudflats appears as an essential habitat requirement, it does not guarantee flamingo breeding. Since captivity studies have shown that flamingos have the physiological capability to breed every year under optimal conditions (Studer-Thiersch, 2000), it is clear that other factors must influence the onset of successful breeding in wild populations.

No doubt, food availability remains a potential key factor to be considered. Studies in the Camargue have shown that flamingos are typical opportunistic breeders, capable of exploiting highly unpredictable and short-lived resources that appear over a wide area in the general region of nesting sites and that this ability favors regularity in breeding (Johnson & Cézilly, 2007; Bechet & Johnson, 2008). Moreover, Tutte (2000) found that the density of lesser flamingo (*Phoeniconais minor*) in East Africa lakes correlates with density and productivity of two preferred food items, *Spirulina* and benthic diatoms. Unfortunately, food availability is extremely difficult to measure in Mar Chiquita, given the size of the lake and the inaccessibility of colonies and most feeding areas except by air. However, the possible influence of food availability on Chilean flamingo breeding is supported by the shift of location of breeding colonies from islands close to mouth of the Rio Dulce to sites near the mouths of Segundo and Primero rivers at a time when the Rio Dulce discharges were minimal to non-existent.

Another result of our research is the observed replacement of *Artemia* by silverside and vice versa at $\sim 55 \text{ g l}^{-1}$. A similar phenomenon was documented

at Great Salt Lake in Utah, USA (Gliwicz et al., 2010). Also, Hart et al. (1998) found, in microecosystems simulating response of the Salton Sea (California) ecosystem to different salinities (30, 39, 48, 57, and 65 g l⁻¹), that *Artemia* developed substantial populations only at salinities (>48 g l⁻¹) high enough to exclude predaceous amphipods (*Gammarus mucronatus*) and prior to the development of predaceous copepod (*Apocyclops dengizicus*) populations at the higher salinities. They speculated that in the lake itself *Artemia* populations would not appear until salinity had risen high enough (60–70 g l⁻¹) to eliminate both fish (tilapia, *Oreochromis mossambicus*) and predaceous invertebrates.

Moreover, the observed coexistence of silverside fish and flamingo breeding colonies relates to the suggestion (Hurlbert et al., 1986) that distribution of the Chilean flamingo is determined primarily by the distribution of fish, with which it competes for invertebrate prey. They noted that flamingos were usually absent or scarce on lakes with fish and present in large numbers where fish were absent. In the case of Mar Chiquita, spatial heterogeneity, especially the existence of very extensive shallow areas where water is only a few centimeter deep may facilitate coexistence of fish and flamingos. These areas provide an ideal feeding habitat for flamingos, while they are probably avoided by fish, which would be easy prey there of fish-eating birds, particularly herons.

From the conservation perspective, management and conservation of the Mar Chiquita Ramsar site should give priority attention to the risks factors that have emerged from our analyses of records of the past 40 years. Although the observed changes in Mar Chiquita water level during 1969–2010 suggest a long-term cycle rather than a simple trend to new, permanent conditions, it is worth considering that climatic oscillations of the magnitude recorded in Mar Chiquita catchment may become increasingly common according to the predictions of global climate models (IPCC, 2001).

We offer two principal conclusions. First, habitat suitability analysis of wetlands like Mar Chiquita in environmental impact assessments should consider that although flamingos are very adaptable and opportunistic species, availability of offshore mudflats free of vertebrate predators is an essential requirement for flamingo conservation. Second, drastic and rapid increases or decreases in water level due to human

control of river inflows should be evaluated carefully. In the case of Mar Chiquita, in particular, there is a growing threat of increasing water diversion and regulation of the Rio Dulce for expansion of irrigated agriculture (Bucher et al., 2006), which may affect not only breeding habitat availability but also food availability near the river deltas, the preferred flamingo feeding sites.

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