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THE BIOLOGY OF AN ISOLATED POPULATION OF THE AMERICAN FLAMINGO *PHOENICOPTERUS RUBER* IN THE GALAPAGOS ISLANDS

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SUMMARY

A genetically and morphologically divergent population of *c*. 500 American Flamingos, isolated from the parental Caribbean stock of Phoenicopterus ruber, occurs in the Galapagos archipelago. Based primarily on data from a 3-year study, we provide the first description of the feeding and breeding biology of this population. Galapagos provides a suitable habitat comprising lagoons on a number of islands, among which the flamingos travel in response to food and nest site availability. We identify putative food items. The occurrence and quantity of some food species was associated with the chlorosity of lagoon water, as was the distribution of flamingos. The flamingos bred opportunistically at five lagoons on four islands, sometimes simultaneously on more than one island. Group display usually involved ≤ 20 birds, and colonies contained as few as three nests. Laying occurred during nine months of the year, mainly August–January, coinciding with the coastal drier season and low lagoon water levels. On average *c*. 30 % of all adults incubated clutches each year, producing 0.37 fledglings per clutch. Recruitment is probably sufficient to sustain the population, which has been stable over at least c. 45 years, and is probably limited by suitable habitat. Moult to flightlessness was recorded among adults. We review potential dangers to this unique population and suggest conservation measures.

RESUMEN

Biología de una población aislada del Flamingo americano *Phoenicopterus ruber* en las Islas Galápagos. Una población morfológica y genéticamente divergente de *c*. 500 Flamingos americanos, aislada de la población originaria de *Phoenicopterus ruber* del Caribe, se encuentra en el archipiélago de Galápagos. Basándonos sobre todo en los datos provenientes de un estudio de tres años, presentamos la primera descripción de la biología de la alimentación y reproducción de esta población. Galápagos provee un hábitat apropiado que consiste de lagunas en varias islas, entre las cuales los flamingos viajan según la disponibilidad de alimento y sitios de anidación. Identificamos supuestos elementos alimenticios. La presencia y cantidad de algunas especies de alimento fueron relacionadas con la clorosidad del agua de las lagunas y con la distribución de los flamingos. Mediando las condiciones, los flamingos anidaron en cinco lagunas de cuatro islas, a veces simultaneamente en más de una isla. El despliegue en grupo a menudo involucró ≤ 20 aves, y las colonias podían ser de solamente tres nidos. Hubo puesta de huevos durante nueve meses del año, sobre todo de agosto a enero, coincidiendo con la estación costera más seca y con bajos niveles de agua en las lagunas. En promedio *c*. 30 % de los adultos incubaron nidadas cada año, produciendo 0.37 volantones por nidada. El reclutamiento probablemente es suficiente para sostener la población, la cual se ha mantenido estable por al menos *c*. 45 años, y probablemente es limitada por la disponibilidad de hábitat adecuado. Se observó en adultos la muda que imposibilita el vuelo. Analizamos amenazas potenciales a esta población única y sugerimos medidas para su conservación.

INTRODUCTION

The Galapagos archipelago (0°N, 90°W) supports a small population of the American Flamingo *Phoenicopterus ruber*, some 1500 km from its parental stock which is currently found in the Caribbean, Mexico, Colombia and Venezuela (Espinoza *et al*. 2000, Baldassarre & Arengo 2000, <http://www.flamingoresources.org/fsg.htm> consulted 27 Dec 2013). Microsatellite and mitochondrial DNA sequence data, and skeletal and egg measurements, showed that

the Galapagos population differs genetically and morphologically from that in the Caribbean (Frias-Soler *et al*. 2014), consistent with its reproductive isolation.

The age of the Galapagos population is unknown, though a genetic distance estimate suggests that the archipelago was colonized about 70,000 to 350,000 years ago by flamingos from the Caribbean (Frias-Soler *et al*. 2014). Flamingos were recorded in one of the earliest accounts of Galapagos, in the log of Captain Cowley's 1684 voyage (Salvin 1876), and they have been consistently

reported since. They are recorded over a c. 20,000 km² area that includes at least 37 beach, inland or volcanic crater lagoons, all within *c*. 2 km of the coast, at 24 locations on six of the major islands in the archipelago (Fig. 1). All lagoons where they occur fall within a circle of radius *c*. 100 km, and each lagoon is within *c*. 50 km of its nearest neighbouring lagoon. The population is stable, ranging from 371 to 696 birds in censuses conducted from 1967 to 2010 (Gordillo 1973, Tindle & Tindle 1977, Harcourt 1982, Valle & Coulter 1987, Vargas *et al*. 2008, unpublished annual census reports of the Charles Darwin Research Station (CDRS) 1981–2009, Jiménez-Uzcátegui & Naranjo 2010), in which (usually) simultaneous counts were made at most lagoons where flamingos primarily occur. Lower counts were associated with incomplete coverage. During this period, flamingos have bred on Isabela Island (three lagoons), Santiago (three), Floreana (one), Bainbridge (one) and Rábida (one).

While *P. ruber* throughout its range is listed as Least Concern on the IUCN Red List (<http://www.iucnredlist.org> consulted 11 Dec 2013), the population in Galapagos was considered Endangered by Granizo (2002) and Jiménez-Uzcátegui *et al*. (2007), because of its small size.

Unlike its populations in the Caribbean region (Rooth 1965, Ottenwalder *et al*. 1990, Espinoza *et al*. 2000), little is known of the biology of the American Flamingo in Galapagos apart from census information and an association of flamingo distribution with rainfall and lagoon water level: flamingo abundance was lower at lagoons when water levels were above their seasonal means (Vargas *et al*. 2008). The objectives of the present study were to describe the feeding ecology, breeding biology and population dynamics of the Galapagos birds, particularly in regard to their isolation from the ancestral

Figure 1. Occurrence of American Flamingos in Galapagos. Circles denote approximate locations of lagoons where flamingos have been regularly or occasionally seen. Solid circles denote lagoons where breeding occurred during 1970–9. Lagoons considered in the present study are named. Island names are in upper case (Bainbridge is on an islet off Santiago).

stock. The outcome is relevant to the management of this evolutionarily divergent population.

METHODS

Study Sites
The study focused on eight lagoons (Table 1, Fig. 1) which supported 70–90 % of the total Galapagos flamingo population during a 37-month study period (June 1976 to June 1979). These lagoons contain all the major sites at which flamingos are known to have bred in the archipelago (Harris 1973, Jiménez-Uzcátegui & Naranjo 2010). During the study period no nests were recorded at other lagoons examined.

Table 1. Characteristics of the main study lagoons during the study period.

Island	Lagoon	Coordinates	Length x representative width (m)	Lagoon type	Features[1]	Water level fluctuation	Flamingo flock
Isabela	Cementerio	0°57'13"S, 90°59'11"W	1702 x 689	Behind beach	Occasional flooding at spring tides. Tidal seepage.	Much	Itinerant
	Quinta Playa	1°0'14"S, 91°4'53"W	1102 x 259	Behind beach	Occasional flooding at spring tides. Tidal seepage.	Little	Permanent
	Barahona	0°59'16"S, 91°02'09"W	283 x 123	Behind beach	Inward tidal overspill. Tidal seepage.	Much	Unknown
Santiago	Sartén	0°13'5"S, 90°36'48"W	520 x 147	In lava field, *c*. 0.5 km inland	Tidal seepage.	Little	Permanent
	Mina de Sal	0°14'27"S, 90°50'14"W	295 x 269	Crater lake, *c*. 1 km inland	Much evaporation. Large rain catchment. Seawater seepage. Solar lake effect.	Much	Itinerant
	Espumilla	0°12'0"S, 90°49'41"W	353 x 101	Behind beach	Tidal overspill and seepage. Large rain catchment.	Much	Itinerant
Bainbridge 3	Bainbridge	0°21'6"S, 90°33'58"W	196 x 156	Crater lake	Evaporation. Large rain catchment. Seawater seepage? Solar lake effect.	Much	Itinerant
Floreana	Punta Cormorant	1°13'36"S, 90°25'38"W	519 x 272	Behind beach	Inward tidal overspill. Tidal seepage.	Little	Almost permanent

[1]Solar lake effect is stratification of lagoon water according to chlorosity and temperature.

One to five visits of one day or less were made to seven of the study lagoons (not Barahona) each month over the study period; Barahona was visited monthly from Jan 1976 to Apr 1977. In addition, monthly visits were made to Cementerio lagoon over 13 years (1968–80). Less frequent visits to a further nine lagoons where flamingos have been recorded (Fig. 1) were made as transport allowed. A further ten lagoons were visited once during the study period. At each visit, the number of adult and juvenile birds was recorded and any active nests and their contents recorded. Lagoon water and mud samples were collected. The water level was measured at Cementerio lagoon during 1970–9.

Extended visits were made to five of the study lagoons during breeding (Table 2), when a team of 2–3 observers continuously monitored individual nests from vantage points within 3–20 m of the colonies, between 6h00 and 18h00 (approximately dawn to dusk) for 134 days and from 18h00 and 6h00 for 40 moonlit nights, totalling *c*. 14,500 nest-hours of observation. The locations of nests were mapped and data collected on nesting and parenting. The generally open aspect and small size of the lagoons allowed simultaneous observation of the activities of adult flamingos not directly engaged in nesting (the "flock"). Data from the flock were obtained on feeding behaviour, displays and copulation. A flock was defined as a group of ≥ 10 individuals within 20 m of each other.

Lagoon ecology
Water level in the lagoons was determined by a number of factors (Table 1). Water level at Cementerio lagoon was measured monthly to the nearest cm using a permanently located 0–150 cm rule. In other lagoons, water level was estimated as "high", "medium" or "low"' by the same observer (RWT) who was familiar with the lagoons.

Water samples (*c*. 200 ml) were collected from Quinta Playa and Espumilla lagoons monthly over 16 months during 1976–8 and from Mina de Sal, Punta Cormorant and Sartén lagoons opportunistically over 30 months during 1976–8, at 2–5 locations per lagoon. Chlorosity (g of chloride and chloride equivalents per litre) was determined by the method of Strickland & Parsons (1972), using International Association for Physical Sciences of the Ocean (IAPSO) sea water as standard (chlorosity 19.38 Cl$^-$/l). Salinity = 1.807 x chlorosity/density. Chlorosity is suggested as the preferred measure during mixing of fresh and salt water (Head 1985), as occurred in some lagoons.

Mud samples (*c*. 250 ml) were collected from beneath the lagoon water into a graduated container and strained through a 0.5 mm mesh. The retentates were dried at 60–80°C for 72 h and weighed (i). Organic matter was oxidized off by burning twice with absolute ethanol, followed by heating on a hotplate for 3 h, and the sample re-weighed (ii). Percent organic matter was determined as (ii)/(i) x 100.

To determine identity and concentration of organisms in lagoon water, five sweeps of water in the lagoon were

Table 2. Extended observation periods at breeding lagoons.

Lagoon	Observation periods	Stage of breeding cycle
Cementerio	17 Oct to 18 Nov 1976	Display, eggs, chicks 1–30 days
	17–24 Dec 1976	Chicks *c*. 60 days
	4–16 Dec 1978	Eggs, chicks *c*. 5–90 days
Quinta Playa	25–28 Aug 1976	Display
	7–16 Dec 1978	Display
Sartén	27 Jan to 10 Feb 1977	Chicks *c*. 20–60 days
	10–20 Mar 1977	Chicks *c*. 75–90 days
	3–19 Dec 1977	Display, chicks *c*.1–8 days
	20 Jan to 8 Feb 1978	Chicks *c*. 15–45 days
	22 Mar to 5 Apr 1978	Chicks *c*. 90 days
Mina de Sal	6–25 Jan 1977	Display, eggs, chicks *c*. 1–8 days
	20–22 Dec 1977	Display, eggs, chicks *c*. 2–12 days
	15–25 Feb 1978	Eggs, chicks *c*. 30 days
	13–14 May 1979	Display, eggs
Punta Cormorant	14–19 Mar 1979	Display, eggs
	28–31 Mar 1979	Eggs, chicks *c*. 1–10 days

made at least 5 cm above the lagoon bottom, using a plankton net of 0.1 mm mesh with a 25 cm diameter mouth (each sweep being previously calibrated to pass *c*. 2 l of water). Organisms were retrieved from the net and resuspended in 10 ml of 10 % formaldehyde in seawater. Mud samples were collected from 2–5 locations per lagoon by straining *c*. 250 ml mud taken from the top 5 cm of substratum through a 0.5 mm sieve. Eighteen 1-ml samples of strained mud from the sieve were bottled with 2 ml of 10 % formaldehyde in seawater. For identification of organisms in mud, 0.25 ml of the sample in formalin was diluted with 2 ml water.

Water, mud and aquatic organisms sampled from lagoons were returned to the laboratory within at most three days of collection for analysis of water chlorosity, identification of organisms in water and mud, and determination of mud organic content.

Organisms were identified and counted by binocular (10x objective) or monocular (10x eyepiece, 10x or 40x objective) microscopy depending on organism size. Samples were analyzed in duplicate, and mean values recorded. Some organisms were sent to the Smithsonian Institution, Washington DC (U.S.A.) for confirmation of identity. The occurrence in lagoon water of two predominant potential food items, the brine shrimp *Artemia salina* and the hemipteran *Trichocorixa reticulata* (Tindle & Tindle 1978), was used as a measure of food availability. *A. salina* is associated with a chlorosity of > 30 Cl$^-$/l, while *T. reticulata* is associated with chlorosity < 15 Cl$^-$/l (Davis 1966, Daintith 1996, Tripp & Collazo 2003).

Flamingo biology
Flock sizes and the numbers of adults ("grey" birds were considered sub-adult) in the flocks engaged in feeding and other behaviour (resting, preening, aggressive encounters,

alarm posture, flying, copulation, comfort movements; the birds engaged in nesting activities were excluded from this analysis) were recorded at Mina de Sal and Sartén lagoons at 20-min. intervals during the period 5h30–17h30 on 16 days at each lagoon during Jan–Feb 1977 and 1978. Food was abundant at each lagoon during these periods. Data for each hour period were recorded at least 32 times over the 16 days. In addition, data on the number of flamingos engaged in nocturnal feeding were collected over four nights (17h30–5h30) during these months at each lagoon. Data were expressed as the mean percentage of the flamingos in the flock involved in feeding and other activities during four 6-h time blocks covering the 24-h cycle (17h30–23h30, 23h30–5h30, 5h30–11h30, 11h30–17h30). The timing, location and number of birds involved in group display (Rooth 1965, Studer-Thiersch 1974, 2000, Kahl 1975) were recorded.

Inter-nest distances were measured centre-to-centre at newly vacated colonies (Sartén, n = 42 nests; Cementerio, n = 48; Mina de Sal, n=14; Bainbridge, n = 4). Distances separating groups of nests were measured as the distance between the nearest nests per group. Data were pooled and the mean inter-nest distance was used to calculate the density of nests per m². Only nest mounds used that season were recorded.

Nest contents (egg or chick) were noted. The length and greatest width of eggs which had rolled from nests or were abandoned because of colony flooding, at Cementerio, Sartén, Mina de Sal and Bainbridge lagoons, were measured using callipers. Chick age was determined from time of hatching (where known) or estimated from chick size, plumage characteristics, bill shape, and colour of leg skin (Johnson & Cézilly 2007). The small size of the colonies allowed recognition of individual parent birds by reference to nest, individual plumage colour and pattern, and bill markings. The sex of individual parents was determined by body size (males were almost invariably larger) and/or call (males had a deeper vocalization). In most cases, after leaving the nest at age 7–11 days to join the nearby crèches, individual chicks could be recognized by their body size relative to other chicks within the crèche (owing to asynchronous hatching) or by reference to their parents when being fed.

The timing of arrival and departure of parents at the nest was recorded. Where it was not possible to determine exact durations of nest site attendance (because of arrivals or departures when the colony was not being observed), minimum and maximum durations were derived by recording the sex of the parent in residence when observations resumed. The timing and duration of feeds given to the offspring (grouped as age 1–3, 4–9,10–11, 12–30, 31–60, 61–90, 91–105 days) at the nest and in the crèche were recorded.

Synchronous moult of flight feathers was determined by the inability of flocks of flamingos to take flight and by the visible absence or partial re-growth of flight feathers of individual birds.

Twenty-two flightless adult flamingos and ten *c.* 2-month old chicks were banded with site-specific coloured plastic rings at Sartén and Cementerio lagoons during Jan–Mar 1978. Seventeen flightless adults were banded at Quinta Playa lagoon in Dec 1978. Banded birds were re-sighted with binoculars. Inter-lagoon and inter-island travel was demonstrated by re-sightings of banded birds, by parent birds leaving nesting lagoons to feed at lagoons elsewhere, by juvenile dispersal and by gut contents.

Statistics

Data are expressed as means ± SD. A surrogate Poisson generalized linear model was used to compare breeding outcomes (fledglings per clutch). Because expected values were sometimes small (< 5), the analyses were verified using a Pearson's chi-square contingency table analysis with *P* values calculated by Monte Carlo simulation (Hope 1968). These tests were also used to compare the number of attentive periods at the nest, and the number of feeds given to offspring by paired male and female parents. The frequency of nest building by male and female partners was compared using a paired two-tailed t-test. Minimum/maximum durations of attentive periods were grouped into four classes (in all cases the minimum and maximum derived period for each observation both fell into the same class) and compared using the log-likelihood (LogLik) ratio statistic, while exact durations of attentive periods at the nest by males and females were compared using a two-tailed Mann-Whitney U-test. Data from members of the same pair were not included in comparison of exact durations of attentive periods.

RESULTS

Distribution

Punta Cormorant, Quinta Playa and Sartén lagoons supported flocks for all or most of the year, while Mina de Sal, Cementerio and Espumilla lagoons supported itinerant flocks of usually < 30 flamingos (Fig. 2). The largest flocks (100–350 birds) occurred at Quinta Playa.

Lagoon water chlorosity, the abundance of food items, and flamingo numbers were related. At Espumilla, two blooms of *A. salina* occurred in the latter parts of 1976 and 1977, coinciding with high chlorosity of lagoon water (Fig. 3). The blooms were separated by a period of lower chlorosity during which the concentration of *A. salina* fell considerably, or was entirely absent. For part of this low-chlorosity period, a bloom of *T. reticulata* occurred (Fig. 3). The flamingo population size fluctuated extensively, with larger numbers following *A. salina* blooms (Fig. 3), and an absence of flamingos (during July–September) following a near absence of both *A. salina* and *T. reticulata*. At Quinta Playa, chlorosity remained stable at < 30 Cl⁻/l, a population of *T. reticulata* persisted throughout the 15-month period, and the flamingo population size remained relatively stable (Fig. 3).
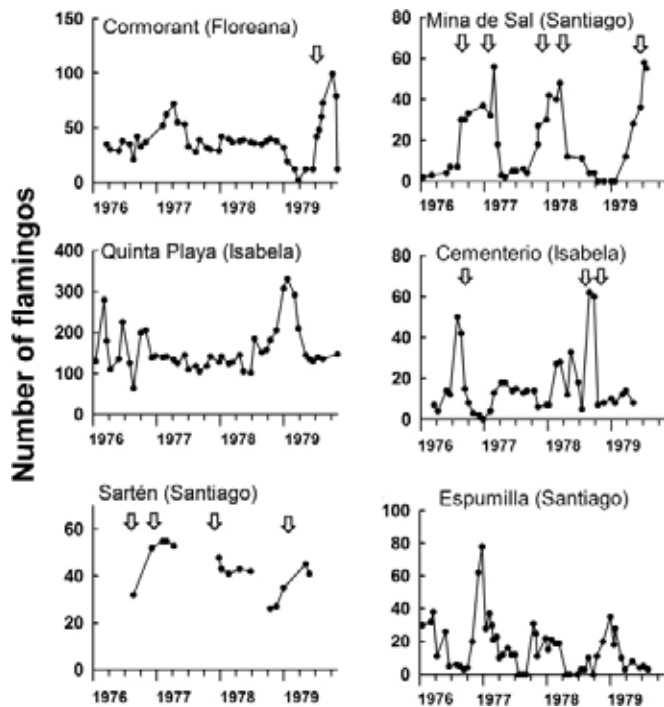
Figure 2. Distribution and egg laying peaks (arrows) of Galapagos flamingos in six study lagoons during 1976–9. Data from Quinta Playa and Cementerio lagoons are monthly counts. Data from other lagoons are highest counts of 2–5 counts per month, except where there was a difference of > 15 birds between highest and lowest counts for any one month, when both highest and lowest counts are plotted. Gaps of > 1 month occurred in visits to Sartén in 1977 and 1978, but local fisherman reported that flamingos were always present.

Chlorosity at Mina de Sal varied widely, with corresponding fluctuations in the concentration of *A. salina* and *T. reticulata* and in flamingo numbers: the highest flamingo counts coincided with periods of higher *A. salina* concentrations (Fig. 3), and when both *A. salina* and *T. reticulata* were scarce or absent flamingos were also absent (Aug 1978). In contrast, at Sartén and Punta Cormorant lagoons chlorosity was consistently < 30 CL⁻/l with little fluctuation, populations of *T. reticulata* were consistently recorded, *A. salina* was absent and flamingo populations fluctuated considerably less (Fig 3). These two lagoons provided a more consistent potential food supply than at Mina de Sal, where food supply fluctuated in both composition and concentration (Fig. 3).

A. salina was present in four out of 15 lagoons examined and *T. reticulata* in 13 of them. Other putative food items were frequently recorded (Table 3). Mud containing algal debris, bacteria, seeds, plant and animal remains occurred in varying amounts on the floor of all lagoons, and varied in organic content: single samples from Quinta Playa, Barahona, Cementerio and Punta Cormorant lagoons contained 9.8 %, 45.9 %, 26.2 % and 5.5 % organic material respectively. Water samples taken from the ten lagoons visited only one once during the study period ranged widely in chlorosity from 5.2 to 46.6 Cl⁻/l.

Lagoon water levels and flamingo numbers were also related. Records over a 9-year period at Cementerio lagoon show that flamingos accumulated with falling water level in eight of the nine years (not 1977), with breeding occurring on islets exposed by falling water level in five or six years (Fig. 4). This lagoon experiences a quasi-annual cycle of water level due to the 'rainy' season (*c.* Dec–Jun); it is also affected by tidal seepage and periodic breaching
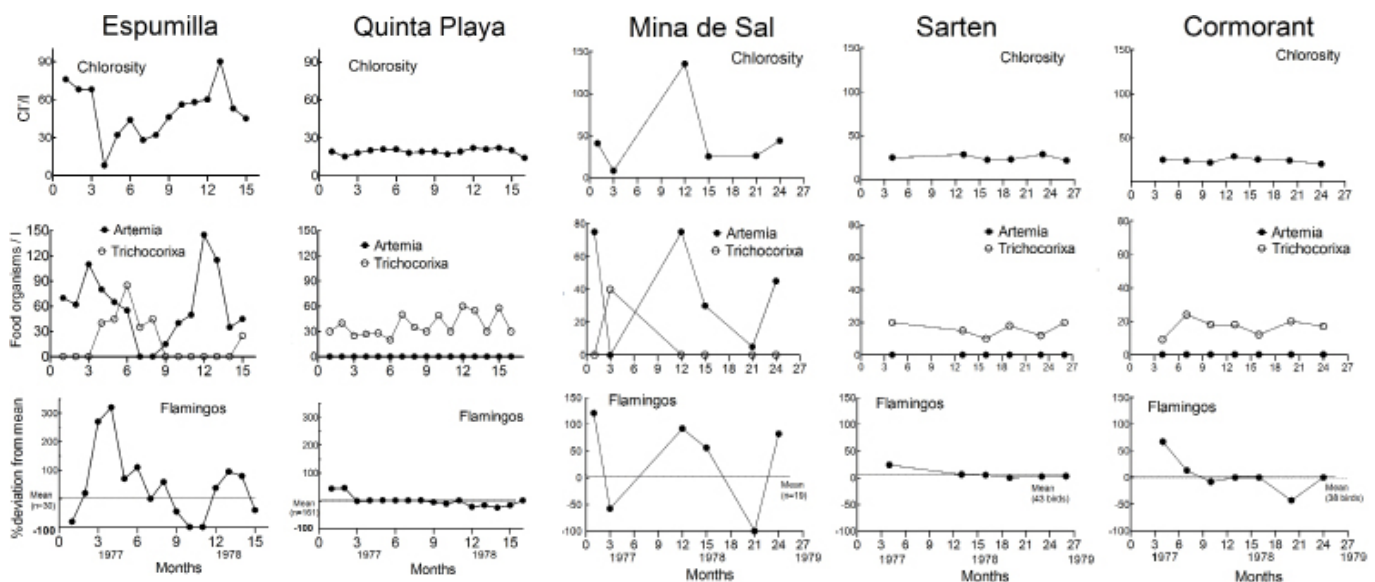

Figure 3. Fluctuation in the abundance of Galapagos flamingos relative to chlorosity of lagoon water and concentrations of *Artemia salina* and *Trichocorixa reticulata* at five lagoons: Espumilla, Quinta Playa (Oct 1976 to Dec 1978), Mina de Sal, Sartén, and Punta Cormorant (Oct 1976 to Dec 1979). The horizontal lines in the lower graphs indicate the mean numbers of flamingos at each lagoon over the duration of observations (n = 15 or 27 months).

Table 3. Potential food items of flamingos, in water and mud samples from Galapagos lagoons.

Food item	Typical amounts
Water	
Artemia salina	30–100/l
Trichocorixa reticulata (instar:adult ratio varied from 0:1 to 25:1)	5–30/l
Mud	
Copepoda (cyclopoid and harpacticoid)	1350 ± 1060/l*
Ostracoda	155,000 ± 145,876/l*
Brachyuran zooea and megalopa larvae	≥ 10 per sample
Palaemonetes sp. (Malacostraca) nymphs	≥ 10 per sample
Enochrus sp (Coleoptera) larvae and adults	< 10 per sample
Ochthebius sp. (Coleoptera)	< 10 per sample
Dytiscus sp. (Coleoptera) larvae	< 10 per sample
Dasyhelea sp. (Diptera) larvae and pupae	< 10 per sample
Scatella sp. (Diptera) pupae	< 10 per sample
Filamentous and globular algae	≥ 10 per sample
Diatoms	≥ 10 per sample

*n = 32 (16 monthly samples from each of Quinta Playa and Barahona).

Figure 4. Numbers of flamingos and lagoon water level at Cementerio lagoon. Breeding attempts are indicated by arrows with the number of occupied nests per attempt. It is not known whether breeding occurred in 1971, indicated as "nd"; no breeding occurred in 1974, 1975 and 1977.

by extreme high tides. Lower water level occurs during *c.* Jul–Nov. This lagoon provides a poor feeding environment for flamingos because of periodic explosive populations of invertebrate- and detritus-eating euryhaline marine fish (*Chanos* sp. and *Mugil* sp.) trapped in the lagoon as juveniles. No *A. salina* and few *T. reticulata* (5.1 ± 0.8/l, n = 30) and few other food organisms were recorded over a 15-month period in 1978–9. Nearly all birds at Cementerio nested, and breeding birds travelled to feed at lagoons elsewhere. Potential feeding lagoons are within 20 km of the Cementerio colony, so a round-trip journey flying at 40–50 km per hour (Bruderer & Boldt 2001) would take ≤ 1 h.

Movement
Four adult birds banded at Sartén lagoon were re-sighted at Espumilla (*c.* 24 km distant), one was re-sighted at Mina de Sal (*c.* 25 km), and one at Punta Cormorant (*c.* 113 km), 16, 15 and 0.5 months later, respectively. A male sighted at Sartén, identifiable by a neck deformity, was recorded 0.5 months later at Mina de Sal. Juvenile flamingos were recorded in several lagoons on southern Isabela in 1976, and at Punta Cormorant lagoon in 1977, even though no breeding occurred on these islands in the current or preceding year. The crop of a freshly dead flamingo at Cementerio contained abundant green olivine crystals (magnesium iron silicate), which occur in the mud at Punta Cormorant lagoon but not at lagoons on Isabela Island. These observations indicate that travel among lagoons and islands was common.

Activity budget
During daylight hours (5h30–17h30) feeding (Table 4), resting and preening (not shown) were the major activities in which adult flamingos in the non-breeding
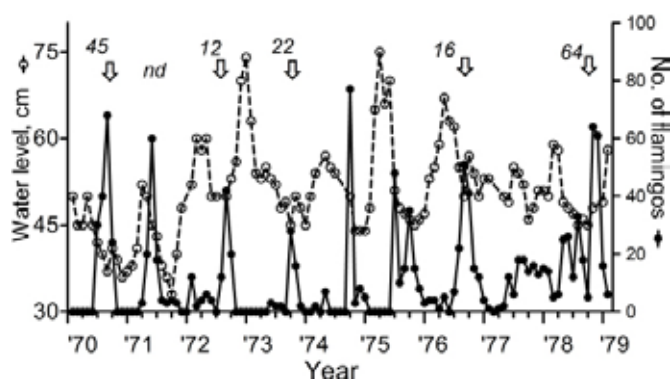
flock engaged. Other activities (see Methods) contributed < 8% of the activity budget. At both Sartén lagoon (where the predominant potential food-item was *T. reticulata*) and Mina de Sal lagoon (predominant potential food-item, *A. salina*) on average *c.* 40 % of the activity budget during daylight hours was taken up with feeding; feeding activity increased at night, particularly at Sartén (Table 4).

Breeding
Group displays involved a mean of 12 birds (range 4–22, n = 30 display bouts) and occurred in all months except June and July, with most observed during the peak months of egg-laying. Display bouts were recorded during all daylight hours, and at all study sites, including those at which no nesting occurred (Espumilla, Quinta Playa).

Flamingos nested at five lagoons on four islands during 1976–9 (Table 5). Nesting occurred in all three years at Sartén and Mina de Sal, in two of the three years at Cementerio, and once each at Punta Cormorant and Bainbridge. Most laying (77.4 %) occurred Oct–Dec, although laying was recorded in all months except Apr–Jun (Table 5). Breeding sometimes occurred simultaneously at more than one lagoon: *e.g.* during Aug–Sep 1976, laying occurred at four sites on three different islands (Table 5). At individual lagoons, eggs were laid in batches; for example, of the 20 eggs laid at Mina de Sal during 1977–8, seven were laid during the first week of

Table 4. Percentage of flamingos in the flock engaged in feeding at Sartén and Mina de Sal lagoons during 6-h blocks over the 24-h cycle. Data are mean ± SD (n periods).

Period	Sartén	Mina de Sal
17h30–23h30	82.8 ± 14.5 (4)	56.0 ± 6.3 (4)
23h30–5h30	91.3 ± 4.2 (4)	78.6 ± 23.4 (4)
5h30–11h30	49.5 ± 27.0 (16)	49.6 ± 15.7 (16)
11h30–17h30	15.5 ± 9.4 (16)	37.9 ± 10.2 (16)
Overall	60.9 ± 33.5 (40)	62.5 ± 22.5 (40)

Table 5. Season totals of clutches laid and fledglings (= offspring that reached age 70 days) produced per breeding lagoon during 1976–9.

Lagoon	Season	Number of clutches laid (% of clutches at all sites that season)	Number of chicks hatched	Number of fledglings (fledglings per clutch)	Laying period
Cementerio[1]	1976–7	16 (22.2)	7	4 (0.25)	Sep 1976
	1977–8	0 (0)	0	0 (0)	
	1978–9	64 (51.6)	35	30 (0.47)	Aug, Nov 1978
	Total	80 (33.4)	42	34 (0.43)	
Sartén	1976–7	24 (33.4)	14	11 (0.46)	Sep 1976
	1977–8	23 (53.4)	15	12 (0.52)	Nov–Dec 1977
	1978–9	17 (13.7)	12	11 (0.65)	Sep–Dec 1978
	Total	64 (26.7)	41	34 (0.53)	
Mina de Sal	1976–7	16 (22.2)	6	1 (0.06)	Aug, Dec 1976
	1977–8	20 (46.5)	5	2 (0.10)	Nov 1977 to Feb 1978
	1978–9	12 (9.7)	?2	1 (0.08)	Nov 1978
	Total	48 (20.0)	?13	4 (0.08)	
Bainbridge	1976–7	16 (22.2)	9	?5 (?0.31)	Aug, Nov 1976
	1977–8	0 (0)	0	0 (0)	
	1978–9	0 (0)	0	0 (0)	
	Total	16 (6.7)	9	?5 (?0.31)	
Punta Cormorant	1976–7	0 (0)	0	0 (0)	
	1977–8	0 (0)	0	0 (0)	
	1978–9	31 (25.3)	?	-	Feb–Mar 1979
	Total	31 (12.9)	?	-	
All sites	1976–7	72	36	?21 (?0.29)	
	1977–8	43	20	14 (0.32)	
	1978–9	124	?49[2]	42 (0.45)[2]	
	Total	239		77 (0.37)[2]	

[1]23.6 ± 28.5 clutches per annum were laid in a total of eight breeding attempts at Cementerio lagoon during 1968–81 (including the three years for this lagoon in this table), producing 0.32 fledglings per clutch in the seven attempts for which outcomes were known.
[2]Punta Cormorant not included.

Nov, seven during the second half of Dec, and six from the last week in Jan to first week in Feb. Two, more-clearly distinct, periods of laying occurred at some lagoons in some years (Mina de Sal 1976, Bainbridge 1976, Cementerio 1978, Table 5), though this pattern was not consistent throughout the islands.

The colonies (one lagoon = one colony) comprised 1–5 groups of nests of mud, sand or gravel, containing 3–16 nests per group (n = 5 lagoons) at a within-group, nearest-neighbour inter-nest distance of 88.3 ± 18.4 cm and a mean within-group density of 1.16 nests per m² (n = 108 nests). The separation of groups of nests was associated with local physical features (rocky outcrops, protruding mangrove roots). Where measured, distances between nearest-neighbour groups was 178 ± 66 cm (n = 7 groups). The frequency of nest-building bouts did not differ significantly between male and female partners of individual pairs (t_{13} = –1.098, P = 0.292) (15 pairs: male 0.068 ± 0.034 bouts.nest^{-1}.h^{-1}, n = 136 bouts; female 0.094 ± 0.054 bouts.nest^{-1}.h^{-1}, n = 188 bouts). Nest building occurred primarily between 5h00 and 10h00 (mean = 0.28 bouts.nest^{-1}.h^{-1}, n = 324 bouts).

The single egg (mean size 88.1 x 51.5 mm, n = 58) was attended constantly by alternating parents. The durations of attentive periods at the nest, measured as maximum and minimum values, did not differ significantly between male and female partners of individual pairs ($LogLik_3$ = –234.19, Dev = 5.178, P = 0.159). Most derived attentive periods lasted 21–60 h (Table 6). In 15 cases (out of 147, = 10.2 %) where the exact durations of attentive periods were known there was also no significant difference between males and females (male 57.7 ± 10.3 h, n = 9; female 62.6 ± 6.06 h, n = 6; Mann-Whitney U = 18.50, P = 0.345).

Comparison of attentive periods between a colony where parents fed in the same lagoon (Sartén) (n = 103 attentive periods) and a colony where parents travelled to other lagoons to feed (Cementerio) (n = 44 attentive periods) indicated some evidence for a longer attentive period for females (Pearson's χ^2_1 = 8.47, P = 0.033) but not males (Pearson's χ^2_1 = 6.18, P = 0.099) at the latter.

Table 6. Number (%) of nest-attendance periods of different durations (derived maximum/minimum values) during incubation and brooding, until chick left nest at age 7–11 days.

| Duration of attentive periods (h) | Incubation | | Brooding | |
	Male (n = 70)	Female (n = 77)	Male (n = 32)	Female (n = 27)
≤ 20	13 (19)	9 (12)	4 (12)	5 (18)
21–60	48 (69)	50 (65)	27 (84)	21 (78)
61–90	6 (9)	8 (10)	0 (0)	1 (4)
> 90	3 (4)	10 (13)	1 (3)	0 (0)

Chicks on the nest were attended constantly by one or other parent, up to 7–11 days of age. The duration of attentive periods measured as maximum and minimum values did not differ significantly between male and female partners of individual pairs ($LogLik_3 = -57.54$, $Dev = 6.259$, $P = 0.398$) (Table 6). In the 12 cases (of 59, = 20.3%) where the exact durations of attentive periods were known there was also no significant difference between males and females (male 28.7 ± 6.1 h, n = 6; female 21.7 ± 2.2 h, n = 6; Mann-Whitney $U = 10.50$, $P = 0.262$). The duration of attentive periods measured as maximum and minimum values did not differ between a colony where parents fed in the lagoon (Sartén, n = 35 attentive periods) and a colony where parents travelled to other lagoons to feed (Cementerio, n = 24 attentive periods) ($LogLik_3 = -57.54$, $Dev = 6.124$, $P = 0.101$).

During incubation, nest relief took place predominantly in late afternoon at colonies where parents fed in the lagoon (Sartén and Mina de Sal) and predominantly in early morning at the colony (Cementerio) where parents travelled to other lagoons to feed (Table 7, $\chi^2_2 = 35.5$, $P < 0.0001$; nocturnal (18h30–5h30) period excluded from the analysis because expected values too low). During brooding of chicks aged 7–11 days, nest relief was spread throughout the day at the colonies where parents fed in the lagoon and was predominantly nocturnal at the colony where parents travelled to other lagoons to feed (Table 7, $\chi^2_3 = 17.93$, $P < 0.0005$).

The frequency with which chicks received feeds from their parents fell dramatically between day 3 and leaving the nest to form crèches, and progressively reduced to near zero at age c. 105 days (n = 701 feeds) (Fig. 5). The duration of individual feeds received by chicks increased until they reached age c. 45 days, and then remained more

Table 7. Number (%) of nest reliefs at different times of the day during incubation and brooding of chicks aged 7–11 days. (A) colonies where adults fed in their nesting lagoon and (B) colony where they fed in other lagoons.

Time of day	Incubation		Brooding	
	A (n = 41)	B (n = 59)	A (n = 25)	B (n = 33)
5h30– 9h30	7 (17)	45 (76)	7 (28)	5 (15)
9h30–14h00	5 (12)	4 (7)	6 (24)	2 (6)
14h00–18h30	28 (68)	9 (15)	9 (36)	4 (12)
18h30–5h30	1 (2)	1 (2)	3 (12)	22 (67)

or less constant (Fig. 5). Overall, the amount of time spent receiving food from parents decreased from hatching to c. 105 days, and the decrease was greatest after the chick left the nest at 7–11 days (Fig. 5). By 105 days of age, individual chicks had received 265 ± 82 feeds from parents, lasting a total of 1921 ± 551 minutes. Beyond three weeks of age, chicks also foraged for themselves.

In 197 (out of 701, = 28.1%) feeds where the sex of the parent and the identity of the chick were known, the frequency of feeds by male and female partners (n = 12 pairs) did not differ significantly ($\chi^2_1 = 0.081$, $P = 0.775$) (males, n = 93 feeds; females, n = 104 feeds), nor did the duration of these feeds ($\chi^2_9 = 0.159$, $P = 1.000$). There was no significant difference in the frequency with which chicks in the various age groups were fed at a colony where parents were resident in the lagoon (Sartén, n = 254 feeds) and a colony where parents travelled to other lagoons to feed (Cementerio, n = 243 feeds) ($\chi^2_7 = 1.01$, $P = 0.995$). Before chicks left the nests, feeds were spread over 24 hours, but thereafter feeds were predominantly
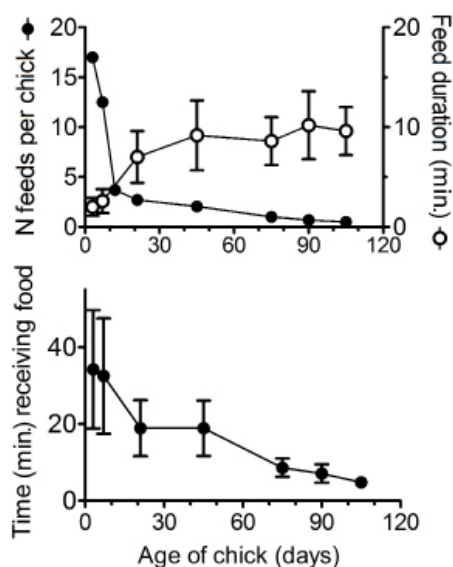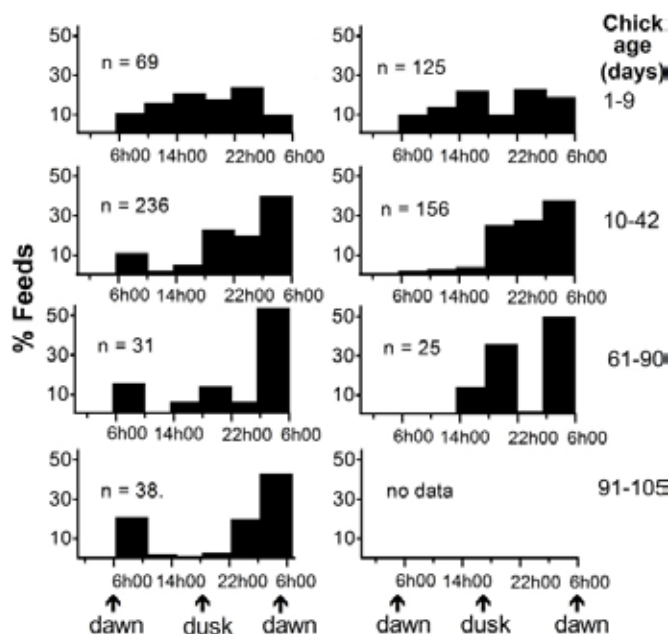

Figure 5. Chick feeding by Galapagos flamingos: mean number of feeds received per chick per 24 h, mean duration of feeds and mean amount of time spent receiving food per chick per 24 h (n = 701 feeds).

Figure 6. Timing of feeding of Galapagos flamingo chicks. Left: colonies where adults fed in the nesting lagoon. Right: Cementerio colony, from which adults travelled to other lagoons to feed.

nocturnal, peaking toward dawn (Fig. 6). Parents who foraged in other lagoons returned to the colony lagoon predominantly in the evening (17h00–20h30; 57.1 % of arrivals) or at dawn (5h00–6h30; 28.6 % of arrivals). Chicks were fed more than once by an individual parent at each visit to the nest.

Breeding outcome averaged 0.37 young fledged per clutch, being highest at Sartén (0.53) and lowest at Mina de Sal (0.08) (Table 5). Breeding outcome barely differed between a colony where parents were resident in the lagoon (Sartén) and a colony where parents travelled to other lagoons to feed (Cementerio) (χ^2_1 = 3.94, P = 0.047).

Several nests and eggs were abandoned after tidal floods at Cementerio and Punta Cormorant lagoons. Eggs which rolled from nests were usually abandoned. In crèches, older chicks harassed later-hatching chicks, which in some cases showed signs of emaciation. Chicks that became separated from the crèche usually died. Some died following accident to legs or wings entangled among roots and tree debris in some lagoons or (rare) predation by Galapagos Hawks *Buteo galapagoensis*. Some starved at the Cementerio colony, when parents failed to return from feeding lagoons to feed them. At Mina de Sal most eggs and nests were submerged by rainwater accumulating in the crater in all three years of the study; of the few hatchlings, most perished (Table 5).

Moult

Synchronous moulting of flight feathers occurred in at least some adult birds. Between 18 and 37 flightless flamingos were recorded at Sartén during Jan–Feb in all three years of the study, 200–250 at Quinta Playa in Dec 1978, and two at Bainbridge in Feb 1979. Birds at various stages of moult (from complete absence of primaries and secondaries to advanced regrowth) were recorded.

DISCUSSION

Distribution

Fluctuating physical conditions resulting from the interplay of tidal seepage and overspill, irregular precipitation, and varying topography determining the extent of rainwater drainage into Galapagos lagoons predispose them to highly variable water level and productivity. These conditions do not affect all lagoons to the same extent, leading to spatially and temporally fluctuating availability of suitable feeding and nest locations within the archipelago. The distribution of Galapagos flamingos was associated with lagoon water chlorosity which determines the occurrence of putative food items, and with low lagoon water level exposing breeding sites. Galapagos flamingos take opportunistic advantage of any abundant population of aquatic invertebrates. Flamingos elsewhere have evolved to exploit such locally unpredictable feeding conditions: while primarily philopatric, they quickly become nomadic, moving to sample food and water level if local conditions deteriorate (Rooth 1965, Arengo

& Baldassarre 1995, Bildstein *et al.* 2000, Bruderer & Boldt 2001, Johnson & Cézilly 2007, Béchet *et al.* 2009). Radio-tagged American Flamingos in the Yucatán changed sites up to seven times a year (Baldassarre & Arengo 2000).

Census results since 1981 have demonstrated that Quinta Playa and Cementerio lagoons together account for as much of the total Galapagos flamingo population as all other lagoons combined. Vargas *et al.* (2008) demonstrated significant correlations between flamingo abundance and rainfall, lagoon water level and temperature at these lagoons: flamingo numbers fell at some lagoons during rainy seasons and particularly during the severe El Niño Southern Oscillation (ENSO) event in 1982–3. However, the total population did not fall: when numbers at Cementerio and Quinta Playa decreased, the combined population at other lagoons increased, presumably as birds sought feeding lagoons less affected by heavy rainfall (Vargas et al. 2008). Similarly, the total flamingo population in Galapagos was not reduced following a severe ENSO event in 1997–8 (unpublished census reports of CDRS). Our observations of flamingos moving between lagoons and islands also indicate that the flamingo population is mobile and opportunistic. Our visits to some lagoons were infrequent, so our re-sightings after banding are probably underestimates. All Galapagos lagoons containing putative food items are visited by flamingos. The population is probably a single dispersive panmictic unit which tracks patchy resources, resembling an "ideal free distribution" model (Fretwell & Lucas 1970). However we cannot discount an "ideal despotic distribution" model in which some dominant individuals prevent others from occupying high-quality habitat, as described for the Greater Flamingo in southern Spain (Rendón *et al.* 2001).

The lagoons frequented by *c*. 90 % of the current flamingo population have existed since observations began, and the pattern of flamingo distribution among them has remained relatively constant. However, in earlier times, suitable lagoons may have differed in number and location from those seen today, given the topographic volatility of the archipelago's volcanic landscape. This may have affected the size of the total flamingo population.

Feeding

The classes of potential food item available in Galapagos are broadly similar to those elsewhere in the range of the American Flamingo, including organic mud, crustaceans, annelids, insect larvae, molluscs and plant seeds (Arengo & Baldassarre 1995). While *A. salina* and *T. reticulata* are major potential food items, it is unlikely that food was restricted to these two organisms since in a given lagoon flamingos displayed other feeding techniques in addition to "skimming", e.g. "stamping" and "walking, leaving tracks of bill" (Jenkin 1957, Rooth 1965, Mascitti & Kravetz 2002), known to be associated with different classes of food. Furthermore, additional food items may be swallowed simultaneously with major food items (Jenkin 1957, Tuite 2000).

The contribution of foraging to the activity budget of Galapagos flamingos (Table 4) is similar to that at a major feeding lagoon in the Yucatán where 5000–8000 American Flamingos accumulate to breed (Espino-Barros & Baldasssarre 1989). The percent time spent foraging may be inversely related to food abundance (Arengo & Baldasssarre 1999). However since the activity budget also reflects competition with behavioural patterns other than foraging, one cannot infer that food availability at the Galapagos lagoons is similar to the Yucatán feeding site, without further investigation.

The contribution of feeding to the daily activity budget was similar in a lagoon where *A. salina* was the most abundant potential food item (Mina de Sal) and a lagoon where *T. reticulata* was the most abundant (Sartén) (Table 4). However, whether *A. salina* and *T. reticulata* provide comparable nutritional benefits requires additional investigation. Other factors, not so far studied, which might affect food availability include large flocks accumulating at sites of high food density and causing food depletion, and competition for food. An interplay of these factors could contribute to an equilibrium between abundance and quality of food and flamingo distribution among Galapagos lagoons.

The reasons for the observed extensive nocturnal feeding by Galapagos flamingos are unclear. Diurnally fluctuating food availability (Johnson & Cézilly 2007), predator avoidance (Beauchamp & McNeil 2003) and thermoregulation (Jutglar 1992) have all been suggested to predispose to nocturnal feeding. If nocturnal foraging allows individuals to supplement inadequate diurnal food intake (McNeil *et al*. 1992), then only less successful foragers should forage at night. At Sartén lagoon nearly all the flock foraged during the night, suggesting that the flock was unable to obtain enough food by day (Table 4). There are no regular predators of adult flamingos in Galapagos, and daytime temperature rarely exceeded 30°C at either of the study lagoons, so these two factors are unlikely to preclude daytime feeding.

When food was abundant, nesting flamingos fed in the lagoon along with a non-breeding flock. When a lagoon was poor in food items, one parent attended the nest while the other left the colony to feed elsewhere, so enabling them to breed at locations that were sub-optimal for feeding, as has been reported elsewhere (Rooth 1965, Rendón-Martos *et al*. 2000, Amat *et al*. 2005, Johnson & Cézilly 2007, Béchet *et al*. 2009).

Breeding
Our data (*e.g*. Fig. 4) suggest that flamingos accumulate and breed when falling lagoon water level exposes suitable nest sites. The pattern we report of intermittent breeding, shifting of nesting location, rapid onset of breeding when conditions become favourable, and use of both food-rich and food-poor lagoons for breeding is typical of flamingos elsewhere. The clutches we recorded at Punta Cormorant in 1978 were the first at that site for 13 years. Breeding has been sporadic at Quinta Playa, Mina de Sal and Cementerio over the last 45 years.

In contrast to other populations of American Flamingo (<http://aviansag.org/Husbandry/> consulted 28 Aug 2014), Galapagos birds undertake group display involving *c*. 20 birds or less and colonies may contain as few as three concurrently active nests. Flamingos have populated at least 11 islands or groups of islands worldwide. Founder populations on distant islands would presumably have been small and infrequent (Johnson & Cézilly 2007) and breeding may have been limited by the habit of group display involving large numbers of birds. The size of the original (and any subsequent) flamingo colonization of Galapagos is unknown, but as well as facilitating establishment, the capacity to breed in low numbers is vital to the present small population.

The group display of Galápagos flamingos was not restricted to either onset of breeding or locations of nesting sites, and presumably maintained the birds in a state of near-readiness for breeding. By reacting quickly to improving local conditions the flamingos were able to breed somewhere in the archipelago for nine months of the year. Breeding started with onset of the coastal drier season, which provided suitable areas for nesting. Elsewhere, flamingo breeding is strongly associated with high water level and consequent high food availability, determined by local precipitation, managed sea-water flooding of salt pans, and fresh water from irrigated rice fields (Gerharts & Voous 1968, Cézilly *et al*. 1995, Béchet & Johnson 2008, Béchet *et al*. 2009). In contrast, in Galapagos most egg-laying occurred in the season when low precipitation occurs at low altitudes (Trueman & d'Ozouville 2010).

Of the estimated total population of *c*. 500 adult birds, *c*. 30 % incubated clutches per year (Table 5) (= 45 % of adults capable of breeding; see "Population" below). The laying period of a colony varied from a week to *c*. 3 months, the longer spreads probably reflecting the persistence of available nesting areas, as illustrated by Cementerio (Fig. 4) and Mina de Sal. The period from laying to chick independence per individual breeding pair lasted *c*. 4 months. Breeding success varied considerably between nesting locations (Table 5), characteristic of opportunistic breeding (Johnson & Cézilly 2007). The overall average nesting success of 0.37 juveniles per clutch (Table 5) in Galapagos is similar to that of large flamingo colonies elsewhere, *e.g*. the Greater Flamingo colony at Elmenteita, east Africa (historically 0.32: Brown 1975) or the American Flamingo in the Caribbean (0.41–0.44: Sprunt 1975). The nesting success we report for Galapagos may have been lower than usual over a longer term because of flooding at the Mina de Sal colony in all three years of the study, where most eggs and chicks perished (Table 5).

There was little evidence that absences from the nest site by off-duty parents during incubation and brooding were longer at a colony where parents travelled to other lagoons to feed, compared with a colony in a lagoon where

parents fed. The time an off-duty parent spends away from the nest during brooding depends on food availability (Johnson & Cézilly 2007) and the periods of absence we report are similar to those for Greater Flamingos which successfully raised offspring in the Carmargue (Johnson 2000). The frequency, timing, and duration of feeds to offspring that we report are similar to those observed for other populations of American Flamingo (Rooth 1965, Studer-Thiersch 1975).

Population

The estimated total population of *c*. 250 pairs produced 25.7 fledglings per annum (data from Table 5), *i.e.* 0.103 fledglings per pair per annum. Allowing for survival from fledgling to breeding (at five years old: Johnson & Cézilly 2007) of 46.06 % (Johnson et al. 1993), the likely recruitment rate of replacement breeders into the population is 0.047 breeders per adult per annum. An adult flamingo in Galapagos would thus probably replace itself with a five year-old offspring breeding for the first time, in *c*. 21 years.

Approximately 370 of *c*. 500 adult birds (74 %) will be old enough to breed (≥ 5 years) at a given time. During the study, on average 168 birds bred per annum, which is 45.3 % of 370. Assuming a conservatively estimated longevity of 20–30 years (as reported for Greater Flamingo) and little decline in reproduction in older birds (Johnson & Cézilly 2007), the growth rate of the population would approximate to zero, which accords with the census results of the past 45 years. Growth of the population is probably restricted by the low recruitment by reproduction, which is typical of Phoenicopterus spp. (Simmons 1996). However, inter-island movements within the archipelago and the likely annual mate changing (observed for Greater Flamingo: Cézilly & Johnson 1995) will enhance genetic mixing in this small isolated population.

Moult

It has been debated to what extent flamingos moult to flightlessness in the wild (Ogilvie & Ogilvie 1986). Allen (1956) reported a flock of *c.* 2000 flightless American Flamingos away from breeding sites in Cuba. We encountered flightless birds in Galapagos both at a breeding lagoon (Sartén), and at a lagoon where breeding did not occur that year (Quinta Playa). In the former, the flightless birds were encountered while young chicks were being reared there, although flightless birds were not engaged in parenting. We were unable to determine whether the flightless birds had been breeding earlier that year. In flamingos elsewhere, simultaneous flight feather moult has been recorded before, during, or after breeding (Shannon 2000). That we did not record synchronous moult outside of the breeding season may reflect fewer observations during those months. At least two of the three lagoons where flightless birds were recorded contained relatively high and stable levels of food organisms (Fig 3; no data for Bainbridge); it seems unlikely that birds apparently needing to spend *c*. 60 % of their time feeding could afford a period of flightlessness in a food-impoverished lagoon.

The Future

The population is considered at risk because of its small size and therefore management is important, particularly in view of the population's genetic uniqueness. The current census programme should be maintained. Based on early censuses, which showed that most of the flamingo population was found at the same ten lagoons, a standard procedure for the census has been followed since 1995, in which lagoons are simultaneously surveyed once a year (Jiménez-Uzcátegui & Naranjo 2010). However, regular monitoring of breeding effort and success is also required, which would require more than one visit to each breeding lagoon per season, particularly since a wide spread of laying may occur (Table 5).

El Niño Southern Oscillation climatic events have occurred in the Galapagos Islands for at least the last 6000 years (Riedinger *et al*. 2002) and are predicted to continue (Sachs & Ladd 2010). The events of 1982–3 and 1997–8, in which many Galapagos seabirds suffered reduced populations (Valle & Coulter 1987, unpublished reports at CDRS), did not grossly affect the size of the flamingo population. The distribution of flamingos changed temporarily as they sought feeding lagoons less heavily affected by extreme heavy rainfall. Their nomadic opportunistic behaviour probably facilitates their survival in such climatic conditions. However, possible rising of sea-level and increased precipitation associated with global climate change (Sachs & Ladd 2010) pose a threat of flooding at important lagoons, and concomitant reduction in breeding success. Natural changes to physical characteristics of lagoons may have impacts on the flamingo population; Espumilla lagoon has been dry for most of the last 20 years probably due to some local hydrological change.

The distribution, opportunistic breeding, and pattern of nest attendance and chick provisioning of the Galapagos flamingo population are similar to those of its conspecifics in the Caribbean. However, this unique population is extremely vulnerable to local habitat disturbance whereas in the Caribbean flamingos can readily move greater distances in response to decrease in habitat quality. Periods of reduced food abundance in Galapagos would probably lead to reduced reproduction and productivity, with severe effects, since flamingos reproduce slowly and show deferred maturity (Cézilly *et al*. 1995). Conservation of the Galapagos flamingo requires that the protection of habitat by the Galapagos National Park Directorate (GNPD) be maintained over the whole range of the population, to accommodate fluctuations in food availability and nesting conditions. This is necessary even though particular sites might not be in use at a given time. Enough habitat needs to be available to provide *c*. 50 t food per year (assuming

an estimated consumption per flamingo per day of 270 g: Rooth 1976). Long term trends in food availability at major feeding lagoons need to be estimated.

The threat from introduced land mammals is small at two of the most successful and regularly used breeding sites (Sartén and Cementerio), because flamingos nest on islets within the lagoons. Only sporadic breeding occurred at Quinta Playa and Espumilla lagoons, which were devoid of islets, and where nests located along the shores have been susceptible to trampling and predation by introduced pigs, donkeys, goats, cats or rats (Lévêque 1964, Jiménez-Uzcátegui *et al.* 2007). Mammalian incursion could be counteracted by construction of artificial islets and/or mud nests within some lagoons, as in the Carmargue (Johnson 1982).

Disturbance of flamingo habitat by humans in Galapagos has hitherto been local, such as at lagoons where fish were salted or salt collected by local inhabitants. They were disturbed by clearing of vegetation for a chicken farm at Cementerio in the 1960s (Tupiza 1965). These activities have now ceased. Tourist groups visit several lagoons which support *c*. 10 % of the total flamingo population. Tourists are restricted to trails located so as not to disturb the fauna, and access to most such sites must be in the company of licensed guides. Tourism has so far posed little or no threat to the flamingo population (Tindle 1978). However, flamingos are stress-prone (*e.g.* Galicia & Baldassarre 1997), and would be vulnerable were current high standards of tourist management to lapse.

ACKNOWLEDGMENTS

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