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ORIGINAL PAPER

Assessment of the impacts of hydrological fluctuations and salt pans abandonment on Greater flamingos in the Camargue, South of France

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Abstract Flamingos forage in both commercial salt pans and natural marshes and lagoons along the French Mediterranean coast. In order to assess the impact of changes in management of commercial salt pans and hydrological fluctuations on this flagship species, we evaluated the foraging areas of breeding flamingos using the resightings of 283 breeding flamingos marked with dye at the colony in 1987 and 1989, two years with

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contrasting hydrological conditions. Teams of observers searched all suitable habitats within 80 km of the colony during the four days following marking and recorded presence of off-duty flamingos. About one-third of the birds were found within 10 km of the colony, but some were seen up to 70 km away. About 24–54% of the birds were found in permanent brackish lagoons and 18–60% in the salt pans, the two most important habitats. In 1989, a dry year with lower water levels in the natural wetlands, the proportion of breeding flamingos using salt pans was twice as high [53%, range (47–60%)] as in 1987 [26%, range (18–29%)], this habitat thus acting as a refuge. Most of the feeding areas shown to be important for flamingos breeding in the Camargue are thus susceptible to variations according to rainfall and to transformations or drying out if the salt pans are abandoned. Our results provide essential benchmarks to reconsider the conservation of this flagship species when management of commercial salt pans changes.

Keywords Buffer · Dye · Mark-recapture · Global change · Mediterranean · Lagoon · Waterbirds

Introduction

Many species of birds exploit both natural and anthropogenic habitats. Agricultural lands, fish farms and salt pans for instance, have been shown to constitute habitats complementary to natural wetlands for several waterbird species (Glahn et al. 1995; Guzman et al. 1999; Tourenq et al. 2001; Masero 2003; Gauthier et al. 2005). While there may exist a competition for resources between waterbirds and human interests (e.g. goose or cormorant damage issues (Van Eerden 1990; Frederiksen et al. 2001)), anthropogenic habitats can often be beneficial to waterbirds with no direct cost to humans activities. Additionally, it has been argued that when managed adequately, man-made environments can be a substitute for natural habitat by providing foraging or nesting opportunities similar to those of natural wetlands (Masero 2003; Sánchez-Guzmán et al. 2007). However, while many species now depend on these anthropogenic habitats, the use of these habitats by people may change quickly due to world trade globalisation, market reorientations, price volatility, or shifts in subsidy policies (Gauthier et al. 2005; Gottschalk et al. 2007). It is therefore important to better evaluate how these habitats contribute to species and population survival and how their management affects their suitability for birds.

The breeding success of waterbirds directly depends on wetland availability and productivity during the breeding season (Cézilly et al. 1995). In the Mediterranean, water levels of coastal and estuarine lagoons in spring are often influenced by the amount of winter rain, which varies substantially from year to year. In contrast, the commercial production of salt guarantees the availability of water bodies of consistent area and salinity from spring to late summer each year by artificial pumping of seawater into large coastal salt pans. This predictability explains why salt pans accommodate a large breeding bird diversity, providing both breeding islands and foraging areas for several species (Britton and Johnson 1987). Therefore, salt pans are becoming increasingly important for the conservation of waterbirds because of the loss of many natural coastal wetlands drained or transformed to the benefit of agriculture extension, industrial development or urban sprawl. Furthermore, in the Mediterranean, salt pans may buffer environmental variations such as drought which, in some years, considerably reduces the area of temporary wetlands available for waterbirds (Masero 2003). However, in recent decades, the European salt industry has entered a phase of decline due to competition with countries having lower production costs. Thus, in many regions such as southern Spain and France, the majority of salt pans have been permanently abandoned (Sadoul et al. 1998; Paracuellos et al. 2002).

Over their range, all flamingo species use wetlands that have often been modified for salt production, with operations ranging from small-scale use to large-scale commercial extraction. In the Mediterranean, five out of the nine regular breeding sites of the Greater Flamingo are located in commercial salt pans. One of the most important and regular of theses sites is the commercial salt pans at Salin-de-Giraud in the Camargue (southern France; Johnson and Cézilly 2007) where an average of 10,500 pairs have bred each year since 1969. Salin-de-Giraud holds the most extensive salt pans in Europe covering 11,000 ha with an annual production of up to 1,400,000 tons of salt (900,000 tons/year on average). In 2007, the salt company decided to reduce by 60% the production at this site and to sell up to 20% of the land. Evaluating how this change will affect the only French breeding population of flamingos has thus become a critical issue.

In Greater flamingos, both sexes contributes to incubation and there are several anecdotal accounts of breeding flamingos travelling to distant feeding grounds (up to 140 km away) during off-duty periods (Dement'ev et al. 1951; Rooth 1965; Brown et al. 1975). In the south of Spain, breeding adults tracked by satellite telemetry travelled up to 150 km from the colony to feeding areas (Rendon-Martos et al. 2000; Amat et al. 2005). In France, flamingos can be found up to 100 km or more from the colony in habitats that are diverse and include freshwater marshes, natural brackish lagoons and extensive areas of low halophytic vegetation within the delta which become temporarily flooded following heavy rains.

Hence, although previous studies have emphasised the importance of commercial salt pans as feeding areas for Camargue flamingos (Johnson 1983; Britton and Johnson 1987), breeding flamingos are not entirely reliant on salt pans for foraging. Yet, there has been no quantitative investigation of the relative importance of this and other habitats to the breeding birds. Such a study is complicated by the presence of large numbers of non-breeding flamingos which can not be distinguished from the breeding birds. To identify the foraging habitat requirements of breeding flamingos, we dye-marked incubating birds, searched for them away from the colony, and compared their distribution during two seasons, May 1987 and May 1989.

We contrast the distribution of flamingos observed in these two years which were characterised by contrasting rainfall accumulations during the preceding winter. Our results allow us to quantify the proportion of the breeding flamingos in France which relies on the salt pans for foraging and they allow us to anticipate the consequences of an expected change in the management of the salt pans.

Study area and species

The area of southern France in which flamingos can be seen regularly during the breeding season was divided into six geographical subdivisions: (i) east of the Rhone River, (ii) the île de Camargue, the roughly triangular area between the two arms of the Rhone but excluding the salt pans of Salin-de-Giraud, (iii) the salt pans of Salin-de-Giraud, (iv) the Petite Camargue, west of the Petit Rhone but excluding the salt pans of Aigues-Mortes, (v) the salt pans of Aigues-Mortes, and (vi) the Languedoc (Fig. 1).

Since 1974, flamingos have bred successfully every year on a purposely-built island in the Etang du Fangassier in the north-west of the salt pans of Salin-de-Giraud (Johnson

Fig. 1 Study area showing geographical subdivisions searched for dye-marked off-duty breeding flamingos in 1987 and 1989, South of France

1997; Fig. 1). Greater flamingos feed mainly on invertebrates which they filter from water or mud over a large range of habitats (Jenkin 1957; Zweer et al. 1995). Since 1950, the water levels and salinity of the Camargue wetlands have largely been influenced by infiltration of seawater through damaged sea defences and by freshwater inflow from the irrigation of neighbouring rice fields (Tamisier and Grillas 1994; Chauvelon et al. 2003). Flamingos have been observed foraging in four habitat types: (i) salt pans, (ii) permanent brackish lagoons, (iii) temporary marshland (including temporary brackish lagoons and temporary flooded sansouire) and (iv) freshwater marshes.

The two main salt pans in the study area, at Salin-de-Giraud and Aigues-Mortes together covered 21,000 ha (Lemaire et al. 1987). Salt pans consist of a series of about 100 shallow (<50 cm) evaporating lagoons up to 500 ha in area through which sea-water is pumped in sequence from March to September. The salt concentration of the water progressively increases through evaporation by wind and sun so that the lagoons increase in salinity from 40 to 320 g l^{-1} (see Britton and Johnson (1987)).

Permanent brackish lagoons vary in salinity from 5 to 35 g l^{-1} (Heurteaux 1989) and are found in all regions. All are fairly shallow (mean depths mostly 20–75 cm) and in direct or indirect communication with the sea.

Temporary marshlands mainly consist of low-lying sansouire susceptible to shallow flooding following autumn and winter rains (Lemaire et al. 1987). This habitat is characterised by glasswort (*Arthrocnemum* spp. and *salicornia* spp.) which covers 50–80% of the otherwise bare mud or silt. Even after winters with above average rainfall, most of this area is dry by mid to late May. The water soon becomes brackish (1–5 g l^{-1}) and the salinity gradually increases as the water evaporates. Also in the temporary marshlands are many temporary brackish lagoons used by flamingos. All are dry by the end of July.

The freshwater marshes are mostly located in the upper part of the île de Camargue (>1 m above sea-level). They consist of a mosaic of reed beds (*Phragmites* and *Scirpus* spp.) and shallow open ponds which water levels are managed for hunting.

Methods

Rainfall and wetland availability

Rainfall in the Camargue was recorded at Tour du Valat meteorological station. We expected the wetlands of the île de Camargue to be the most sensitive to rainfall variations because that is where most of the temporary marshlands occur. Therefore, we evaluated water surface areas only within the two arms of the river. Wetland edges were digitized on a numerical topographic map (IGN Scan25). We classified wetland polygon according to four habitat types: salt pans, permanent brackish, temporary marshlands or freshwater marshes based on field observations. We estimated the availability of the different wetland types using Landsat TM5 of 5 June 1987 and spot images of 23 April 1989. We identified flooded areas using infrared channels with supervised classification methods. We coded classified images as either wet or dry. The area available to flamingos per wetland type was then simply calculated as the total wet area within each polygon type for each year.

Dye-marking

During the peak of hatching on 10–11 May 1987, and 27–28 May 1989, 153 and 130 flamingos respectively incubating close to the edge of the breeding island at the Etang du Fangassier were marked with a saturated solution of picric acid in ethanol. The dye was liberally applied to the back of each bird by means of a sprayer operated by an observer in a boat-hide from a range of 1–3 m. All but one of the dye-marked birds remained on the nest during the marking procedure; the exception returned within ten minutes. Subsequently the birds smeared the dye to most of their plumage during preening so that they were distinguishable from unmarked birds at ranges up to 1 km. The dye remained fast during the course of the study. The number of dye-marked birds present on the island was counted at 08:00 h and again at 19:00 h on each of the four days after marking. The difference between the mean of these two counts and the total number of birds marked was taken as the number of dyed birds available to be seen away from the colony on a given day. We restricted observations to four days because we believe this to be about the maximum attentive period by partners for successful breeding.

Habitat use of off-duty dye-marked flamingos

On each of the four days after marking, seven teams of ground-based observers systematically searched all suitable habitats for flamingos by vehicle within the areas described above (see Fig. 1). At each locality the number of dye-marked birds and the total number of flamingos present were recorded. Because the natural brackish lagoons of the Petite Camargue could not be observed from the ground, observations were made from the air in only one out of the four days in 1987 (14 May) but each day in 1989. Likewise, in the

Languedoc west of Sete surveys were also conducted by plane once during the four days (14 May in 1987 and 31 May in 1989). On the same day, an aerial photograph of the breeding colony was taken in order to count the number of incubating birds on the island.

Length of incubation shifts

From 1977 to 1985, 6,021 chicks were marked individually with Darvic bands engraved with a unique alphanumeric code (Johnson 2000). These bands can be read through a telescope at up to 400 m and many of these flamingos have returned to breed in the Camargue. In both 1987 and 1989 the colony at the Etang du Fangassier was observed daily from a tower hide 70 m away, from April to August, and the breeding activities of banded birds was recorded. The duration of incubation shifts was estimated by monitoring the presence of banded birds at nests that could be observed easily. Changeovers at the nest between the marked bird and its partner were recorded and the identity of the incubating bird checked at intervals of approximately two hours. Soon after egg-laying and also just before hatching, flamingos sometimes changed over at the nest every few hours, whereas much longer shifts were typical of the remainder of the 29 day incubation period (A. R. Johnson, unpublished data). Therefore, observations within two days of egg-laying or hatching were excluded from the analyses. Because incubations shifts of a given pair are not independent observations, we used linear mixed models to test for a difference of incubation shift length between the two years.

Distribution of off-duty breeding birds

We assumed that all the dye-marked birds seen away from the colony during the four days after marking were still breeding and that a negligible proportion failed during this period. We also assumed (a) that the population was closed during the study period which is likely to be verified because of the short time period considered, (b) that all dye-marked flamingos have the same probability of being detected in the resighting sessions and (c) that they do not loose their marking between sessions. We tested the assumption that dye-marked flamingos were homogeneously distributed among flocks. If this assumption is true, then the number of dye-marked birds encountered in each flock should approximate a Poisson distribution. We thus tested this assumption for each of the tracking days using an overdispersion score test developed by Dean and Lawless (1989), Dean (1992) and Rivest et al. (1998) (see also Béchet et al. (2004) appendix for an explicit formulation). As this latter assumption was met (z ranged from 0.02 to 0.36 and Ho is rejected only if $z > 1.645$), the proportion of breeding birds, $\pi_i$present in a particular area on a given day could be estimated by:

$$\pi_i = \frac{m_i T_i}{C_i M} \quad (1)$$

where m_i is the number of dye-marked flamingos counted in area i, C_i is the number of flamingos checked for marks in area i, and T_i the total number of flamingos counted in area i, and M is the number of dye-marked flamingos available (i.e. off-duty). In 1987, M was assumed to be equal to the total number of flamingos dye-marked minus the number observed incubating on a given day. In 1989, all flamingos encountered were checked for dye-marks which simplifies equation (1). Moreover, by adding the number incubating and the number of birds foraging gave a total greater than the total marked. This is likely due either to an overestimation of the number incubating (A. R. Johnson, pers. obs.), or to birds being seen on the nest before leaving to forage, or vice-versa. For simplicity and clarity of the results, we assumed in 1989 that the number available (M) was the total number observed foraging (i.e. no off-duty dye-marked flamingos were missed) these days. The variance of the proportion π_i is derived in the appendix. The results present the estimates of $\pi_i \pm$ SD.

Finally, we tested if habitat use varied between the two years using generalised linear models with the π_i in a given habitat a given year as the response variable and Habitat, Year and their interaction as the explanatory variables. Model selection relied on the small sample unbiased AIC_c, using both $\Delta\text{AIC}_\text{c}$ and $\text{AIC}_\text{c}\omega$. $\Delta\text{AIC}_\text{c}$ is the difference of AIC_c between a given model and the model with the smallest AIC values in the set of models. $\text{AIC}_\text{c}\omega$ is considered as the weight of evidence in favour of a given model being the best model among the set of models considered (Burnham and Anderson 2002).

Results

Rainfall and habitat availability

In 1989, accumulated winter rainfall in the Camargue (from September to April) was less than half (293.6 mm) that recorded in 1987 (611.3 mm). This reduced the water levels of the Vaccares lagoons considerably (Fig. 2) which in turn is known to considerably reduce water surface of the temporary marshlands of the Etang du Sud (Cézilly et al. 1995; Béchet and Johnson 2008). As predicted from the winter rainfall, wetland availability was considerably less in 1989 with 13.2 km^2 (8.5%) reduction compared to 1987, excluding the salt pans (Table 1). The main reduction of habitat availability concerned freshwater and temporary marshland habitats.

The 1989 image was obtained much earlier in the season (April) than in 1987 (June). But the amount of spring and summer rainfall was also less in 1989 (58.8 mm from April to August versus 109.2 for the same period in 1987), so there was no compensation for this dryer conditions by later rainfall.

Colony size

In 1987, egg-laying began in early April and almost all breeding birds were nearing the end of incubation during the dye-marking experiment and when the colony was photographed

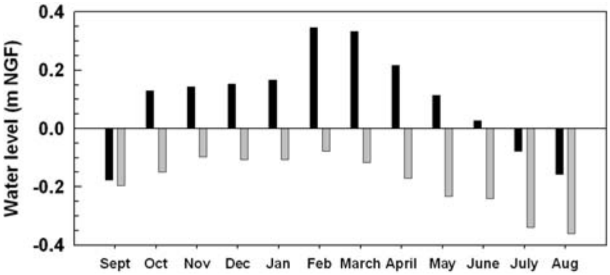

Fig. 2 Monthly water levels (m NGF) of the Vaccares lagoon recorded from September to August in 1987 (*black*) and 1989 (*grey*)

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Table 1 Area (km^2) of the different wetland types available for flamingos in the île de Camargue in 1987 and 1989 with the percentage of change between the two years

Wetland type	1987	1989	% Change
Freshwater marshes	23.8	17.3	−27.3
Permanent brackish	118.0	114.3	−3.1
Temporary marshlands	13.0	9.9	−23.3
Salt pans	83.4	83.0	−0.4
Total	246.1	227.3	

from the air. About a 25% of the pairs had hatched chicks and was brooding small young. We counted 9,537 incubating birds on the aerial photograph of the island on 14 May. In 1989, not only was April to August rainfall exceptionally low, but it never rained during the whole of the incubation period from early May to early July. Further, because of a strike by personnel of the salt company, flooding of the Etang du Fangassier was delayed by 15-days and egg laying did not begin until early May. Additionally, a Black Swan (*Cygnus atratus)* regularly disturbed the breeding flamingos, particularly but not solely the earlier breeders and at least 300 eggs were lost during the season. We counted 10,200 incubating birds on the island on the aerial photograph of 29 May.

Incubation shifts

We monitored incubation shifts at 17 nests in 1987 and at 14 nests in 1989 with 79 and 56 attentive periods of known duration was known to be within ± 2 h, respectively. Incubation shifts tended to be longer in 1989 (34.9 h ± 4.9) than in 1987 (29.3 h ± 4.2), but the difference was not significant (mixed model: $t = 1.15$, $df = 29$, $P = 0.25$).

Distribution of off-duty breeding birds

In both years the difference between the number of dye-marked flamingos observed incubating on the first and last day of the experiment was <2. Hence, there was no evidence that a significant proportion of the breeding attempts of marked birds failed during the experiment.

In 1987, we observed 58–92% of the marked birds daily while we located 100% of them in 1989 (Table 2). The smaller proportion of birds detected in 1987 was probably because of less thorough coverage of some sites. The main areas used by breeding flamingos in 1987 were the Languedoc (26–34% of off-duty flamingos were found in this region), the salt pans of Salin-de-Giraud (14–27%) and the rest of the île de Camargue (6–30%; Fig. 3). Only 7% of the off-duty flamingos this year were found at the Aigues-Mortes salt pans. In 1989, the proportion of dye-marked flamingos encountered at Salin-de-Giraud was much higher (32–50%) and so was the proportion using the salt pans of Aigues-Mortes (10–15%). The Languedoc remained an important region for off-duty flamingos (14–25%) together with the île de Camargue (20–27%). In both years, the east of Rhône and Petite Camargue regions accommodated < 4% of the off-duty flamingos. No additional picric-marked flamingos were observed when flying over the west of Sete in both years.

The wetland types used by flamingos differed markedly between the two years as the best model retained the interaction between Year and Habitat ($\mathrm{AIC_c}\omega = 0.99$ and $\Delta\mathrm{AIC_c}$

Table 2 Number of flamingos counted (*T*) in the study area, number checked for dye-marks (*C*), number of dye-marked birds found in the study area (*m*) number of dye-marked flamingos observed incubating (*I*), number assumed to be off-duty (*M*) and estimated proportion found (π) among the 153 and 125 birds dye-marked at the colony site in 1987 and 1989, respectively

Date	T	C	*m*	I	M^a	π
1987						
12 May	21,486	20,800	31	98	55	0.58 ± 0.04
13 May	24,403	24,162	50	92	61	0.82 ± 0.03
14 May	36,694	30,623	38	81	72	0.63 ± 0.04
15 May	28,232	27,609	49	99	54	0.92 ± 0.02
1989						
29 May	33,270	33,270	48	93	48	_
30 May	34,497	34,497	84	70	84	_
31 May	34,596	34,596	72	54	72	_
1 June	35,250	35,250	56	95	56	_

[a] The number available is assumed to be the total number marked minus the number observed incubating in 1987 and the number observed foraging in 1989 (see text for details)

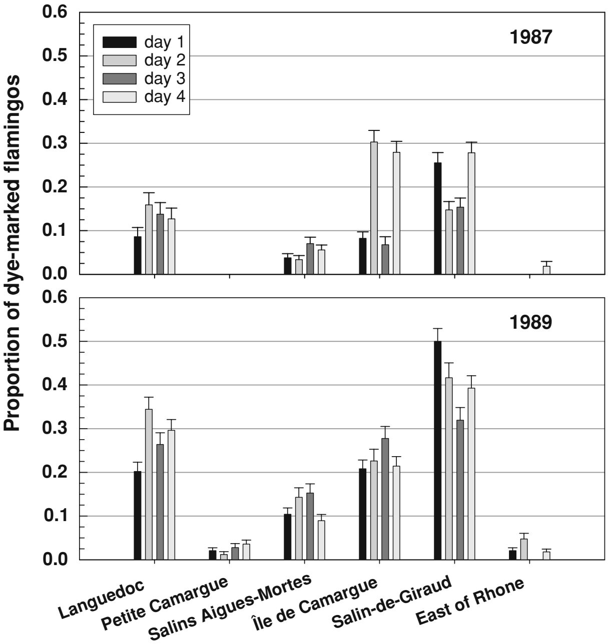
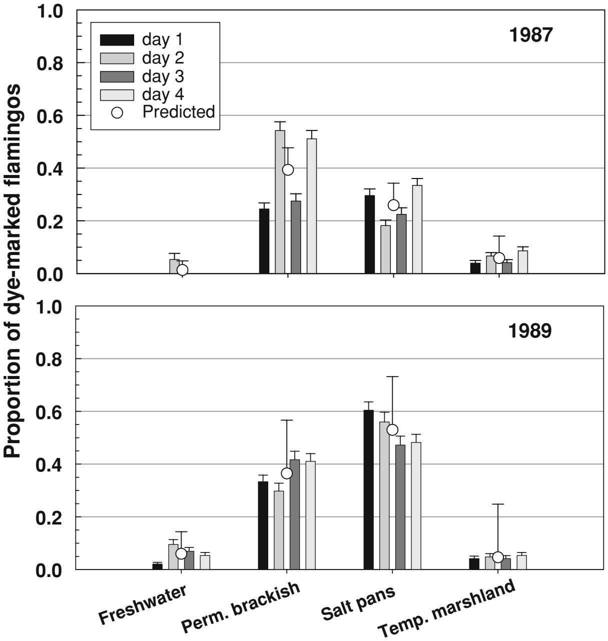


Fig. 3 Proportions (±SD) of off-duty flamingos encountered in the different regions of the South of France in 1987 and 1989. Note that it is assumed that all dye-marked flamingos were detected in 1989

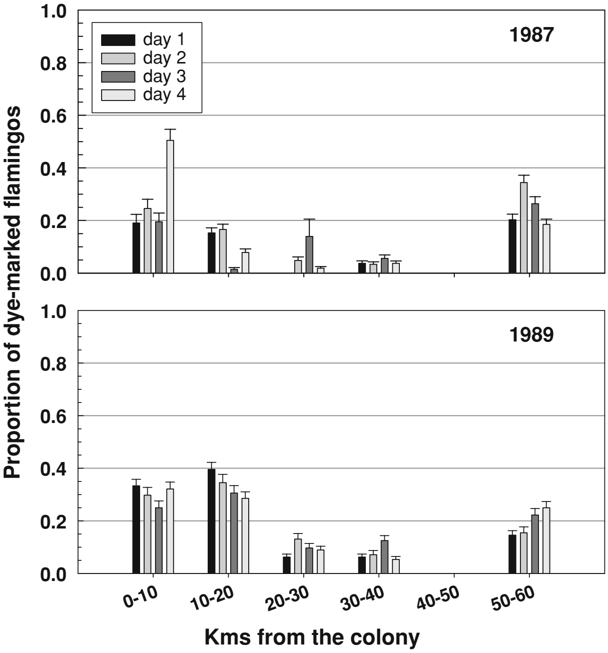
with the second best model (Habitat only) = 16.05). In particular the proportion of off-duty birds encountered in the salt pans times was twice as high in 1989 (53%, range (47–60%)) as in 1987 (26%, range (18–29%); Fig 4). Thus salt pans became by far the main habitat used in 1989 compared to 1987 when flamingos were more often encountered in permanent brackish lagoons (39%, range (24–54%) of the off-duty flamingos; Fig. 4).

Fig. 4 Observed (*vertical bars* ±SD) and predicted (*empty circle*) proportions of off-duty flamingos encountered in the different habitats of the South of France in 1987 and 1989



Finally, as a result, off-duty flamingos were more concentrated within 20 km of the colony in 1989 (55–72%) than in 1987 (20–58%). Our study however confirms that a non-negligible proportion of off-duty breeding flamingos (from 14 to 34% when combining 1987 and 1989) can fly up to 70 km to forage in the Languedoc lagoons (Fig. 5).

Fig. 5 Proportion (±SD) of off-duty flamingos encountered at different distances of the breeding colony in 1987 and 1989



Discussion

Our results show that salt pans accounted for 18–60% of the habitat used by breeding Greater flamingos depending on the year. In 1989, a dry year characterised by lower water levels in the natural wetlands, salt pans acted as a refuge accommodating a twice as high proportion of off-duty flamingos as in 1987, a more “normal” year. In particular, up to 50% of the breeding Greater flamingos foraged in the salt pans of Salin-de-Giraud.

Our results thus highlight the importance of salt pans during the incubation period. It is likely that the flamingos use this habitat increasingly during the chick rearing period since population density of their main prey, *Artemia* sp., increases and temporarily flooded habitats dry out (Britton and Johnson 1987). The loss of part of this important salt pan complex would thus have an important impact on the carrying capacity of the Camargue for this species. Flamingos may experience negative feedback from processes such as depletion, interference or competition exacerbated by higher densities in the other habitat types (Sutherland and Anderson 1993). The relative influence of these processes is not known in the Greater flamingo so that the relationship between habitat availability and flamingo number and density is not straight forward. Further research is thus needed to determine the impact of wetland loss on flamingo numbers in the Camargue.

Permanent brackish lagoons were the main habitat used by flamingos in 1987 [39%, range (24–54%)] and the second in importance in 1989 [36%, range (29–41%)]. Previous studies have shown that flamingo colony size is positively correlated with the water levels of the Vaccares lagoon in spring (Cézilly et al. 1995; Béchet and Johnson 2008). In these studies, these water levels were used as surrogates for both the availability of permanent and temporary brackish lagoons. Therefore, besides the importance of salt pans demonstrated by our study, the availability of permanent and temporary brackish lagoons remains critical for the flamingo population productivity.

The most important feeding areas for flamingos breeding in the Camargue are susceptible to alteration as a result of human activity. About 45% of the low-lying sansouire prone to flooding was reclaimed between 1942 and 1976 (Lemaire et al. 1987), while the salinity of the permanent brackish lagoons of île de Camargue has been subject to drastic fluctuations resulting primarily from variation in the quantity of freshwater entering them from irrigated rice fields and from large flooding events (Chauvelon et al. 2003; Poizat et al. 2004). Today, it is the decline of salt production which could cause major changes in the population dynamics of the Greater flamingos by decreasing significant foraging habitat for breeding birds.

Potential bias may caution interpretation of our results. Greater flamingos are long-lived birds and ringing began comparatively recently so that ringed birds observed in this study are likely younger than the average for breeding birds. Incubating birds can only be dye marked close to the edge of the colony and it is known for other species that birds differ in their position within the colony according to age or breeding experience (Coulson and Porter 1985). The method also assumed that the distribution of birds by day was a good indication of where they were feeding. Britton et al. (1986) found that flamingos fed mainly at night in late summer, but G. Hirons and R. Green (pers. obs.) found a high proportion of birds feeding by day during April and May. Additionally, a comparison of counts made in April and May showed that the distribution of birds within a salt pan complex was similar by day and night. Finally, the important daily variations of the π_i likely resulted from a combination of two phenomena. First, these variations certainly reflect movements of off-duty flamingos between habitats from day to day. Second, in 1987, the resighting probability of off-duty flamingos was <1 (Table 2) so that some birds may have been found one day and missed the day after. However, both of the salt pans areas (Salin-de-Giraud and Aigues Mortes) were covered very thoroughly in both years, so our conclusion about the importance of salt pans is not affected by this.

This study confirms previous qualitative observations in showing that flamingos may feed at considerable distance from the breeding colony (Rooth 1965; Brown et al. 1975; Rendon-Martos et al. 2000; Amat et al. 2005). Yet, although some incubating flamingos travelled up to 70 km from the nest during off-duty periods, about one-third of them were found within 10 km.

At present, the west Mediterranean population of the Greater flamingo has increased to >100,000 birds (Delany and Scott 2006). However, even though the number of colonies has recently increased (Johnson 1997), it remains low with more than half of them located in commercial salt pans. It is likely that the changes of the salt market will seriously affect the maintenance of current management practices in what have become flamingos' traditional feeding grounds. Our results indicate that while salt pans have certainly contributed to the increase of the flamingo population, their abandonment may likewise negatively affect the number of breeding pairs. We thus urge conservationists to use these results as benchmarks to reconsider the conservation strategy of flamingos and other waterbird species which used to rely on these now threaten habitats that have become commercial salt pans. Our results also advocate for an integrated management planning aimed at ensuring the long-term persistence of the wetland complexes required by flamingos. In the Camargue, this may imply recreating the natural hydrological dynamics of the delta, something that has been lost since the embankment of the Rhone river and the building of dykes along the sea (Béchet and Johnson 2008).

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Appendix

If M_i is the number of dye-marked flamingos present in area i, m_i is the number of dye-marked flamingos counted in area i, C_i is the number of flamingos checked for marks in area i, and T_i the total number of flamingos counted in area i, then we can make the assumption that M_i follows a binomial distribution $\mathrm{B}(M,\pi_i)$. m_i follows a binomial distribution $\mathrm{B}(M_i,\rho_i)$ and C_i follows a binomial distribution $\mathrm{B}(T_i,\rho_i)$.

Then, the proportion of dye-marked flamingos present in area i, π_i can be estimated as

$$\pi_i = \frac{m_i}{\rho_i M} = \frac{m_i T_i}{C_i M}.$$

Then making the assumption that the C_i and m_i are independent, the delta method gives

$$V(\pi_i) = \left(\frac{T_i}{M}\right)^2 \left[\frac{1}{C_i^2} V(m_i) + m_i^2 \frac{V(C_i)}{C_i^4}\right]. \quad (1)$$

Besides, as the distribution of the m_i is conditional on the M_i and V(X) = V(E(X|Y)) + E(V(X|Y)), then $V(m_i) = V(M_i\rho_i) + E(M_i\rho_i(1-\rho_i))$, and thus $V(m_i) = \rho_i^2 M\pi_i(1-\pi)_i + M\pi_i\rho_i(1-\rho_i))$.

Developing and replacing the π_i and ρ_i by their estimates,

$$V(m_i) = \frac{m_i}{T_i M}(T_i M - m_i T_i). \tag{2}$$

Finally, $V(C_i) = T_i\rho_i(1-\rho_i)$ and thus replacing ρ_i by its estimate,

$$V(C_i) = \frac{C_i}{T_i}(T_i - C_i). \tag{3}$$

Calculating (1) and (2) allows estimating $V(\pi_i)$ with (3).

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