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Despotic establishment of breeding colonies of greater flamingos, Phoenicopterus ruber, in southern Spain

Abstract The spatial distribution of individuals fits an ideal despotic distribution (IDD) model when some individuals prevent others from settling in a high-quality habitat, so that the last group of individuals is forced to use lower-quality habitats in which their fitness is lower. A critical assumption of the IDD model is that individuals using the lower-quality habitats must have attempted to settle first in the better habitats, but this has seldom been demonstrated. We tested key assumptions of the IDD model by using long-term data on choice of breeding sites by greater flamingos (*Phoenicopterus ruber*) in southern Spain, where these birds breed at Fuente de Piedra lake (FP) and the Guadalquivir marshes (GM). Based on the accessibility of terrestrial predators to breeding sites, the FP colony was of better quality than the GM colony. As expected from an IDD model, the flamingos settled first at FP than at GM. The order of settlement was probably not affected by differences in food availability between sites, since in most years, the flamingos breeding in FP obtained food in GM during the chick-rearing period, once the FP lake dried up. Furthermore, breeding success was much higher at FP than at GM. Another assumption of the model is that individuals are omniscient and that they should try to settle first in the best site. We recorded 18 individually marked flamingos prospecting for nest sites in FP in a season, when many birds had already settled in this colony. The same individuals were subsequently recorded breeding in the same season in GM, indicating that they had previous information on the availability of sites on which to breed. A third assumption of the IDD model is that as the density increases in a given habitat, the fitness of individuals should decrease. In accordance with this, we found a strong effect of bird density on egg losses. The individuals that were recorded prospecting for sites in FP and that later bred in GM were younger than flamingos that were breeding in FP. We suggest that age-related behavioral dominance may be a mechanism responsible for this despotic distribution.

Keywords Ideal despotic distribution · Colony choice · Breeding success · Density effects · Age-related dominance · Greater flamingo

Introduction

Several models have been proposed to explain how animals distribute themselves in their habitats (Karieva 1990). Fretwell and Lucas (1970) and Fretwell (1972) formulated an evolutionary theory of habitat selection in which they developed the ideal free distribution (IFD) model and an alternative, the ideal despotic distribution (IDD) model. These models have been expanded subsequently by considering unequal competitors (reviews in Bernstein et al. 1991; Tregenza 1995; Sutherland 1996). Under the IFD model, individuals occur in direct proportion to the availability of resources among habitats, there are no differences in quality among habitats once all habitats have been occupied, and there are no fitness differences between individuals in different habitats. The distribution of individuals is despotic when some individuals prevent others from settling in a given habitat. The last group of individuals is then forced to use lower-quality habitats in which their fitness is lower.

A critical assumption of the IDD model is that the individuals must be able to judge territory quality. This

Communicated by J.L. Dickinson

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has been shown in oystercatchers (*Haematopus ostralegus*) (Ens et al. 1995), but not in other studies on habitat distribution by birds which found that individuals of lower quality settled in habitats of lower quality (Andrén 1990; Møller 1995; Petit and Petit 1996). Although this finding is consistent with the IDD model, these studies did not document any single instance in which an individual breeding in a lower-quality habitat attempted to breed first in a better habitat.

Testing habitat choice models under field conditions may not be easy, because measuring resource distribution among habitats is difficult (Messier et al. 1990). Colonial waterbirds offer a good opportunity to test habitat choice models by studying the distribution of individuals among colonies (Brown et al. 1990). In many birds, the formation of nesting colonies is likely to result from individual decisions constrained by the spatial distribution of nesting sites, which are usually discrete and easily recognizable units. Here, we tested assumptions derived from the IDD model by using long-term data on choice of breeding sites by greater flamingos (*Phoenicopterus ruber*) in southern Spain.

Assumptions and tests of the model

Studer-Thiersch (1974) has shown that there is competition for nesting space among breeding greater flamingos. In colonial waterbirds, this type of interference may affect reproductive success (Inoue and Kawata 1997), as well as settlement decisions. Indeed, Nager et al. (1996) found that the proportion of greater flamingos that moved from their natal colony to start breeding elsewhere increased when access to breeding sites at the natal colony was more difficult due to the presence of conspecifics.

If the distribution of individuals among colonies is despotic, we should expect that individuals attempting breeding in the lower-quality site should be of lower quality than those breeding in the best site. A factor responsible for this type of distribution might be age-related competitive ability (Goss-Custard et al. 1982; Bildstein et al. 1991), with younger birds being excluded by older ones from the best sites. This may be a mechanism generating a despotic distribution (Ens et al. 1995). If flamingos settle in their colonies according to an IDD, the following predictions can be made: (1) fitness will be lower in less preferred colonies; (2) the colonies should be sequentially occupied according to their quality; (3) younger birds should be prevented from settling in the best sites, and (4) the higher the density in a given colony, the lower the fitness of individuals in that colony.

Methods

Study sites

In southern Spain, the greater flamingo breeds at two sites, Fuente de Piedra lake (Málaga province, 37°06’ N, 4°45’ W), and the Guadalquivir marshes (Sevilla and Huelva provinces, 36°57’ N, 6°23’ W). Rendón-Martos (1996) showed that the colony size of greater flamingos at Fuente de Piedra was affected by water levels in the Guadalquivir marshes, located 140 km away. Because the Fuente de Piedra lake usually dries up during the late breeding season, flamingos breeding in this locality obtain their food in the Guadalquivir marshes during the chick-rearing period (Rendón-Martos et al. 2000). Greater flamingos have also established breeding colonies in the Guadalquivir marshes, but only in years of high water levels (Rodríguez de los Santos 1983; Máñez 1991).

Fuente de Piedra is a shallow and saline lake covering 13.5 km². The water level experiences both seasonal and annual variations depending on the amount of rainfall. During the study period (1977–1999), the lake dried up in every summer except in 1990, 1997, and 1998. In some years (1980, 1981, 1983, 1989, 1992, 1993, and 1995), water levels in spring were very low, preventing settlement by flamingos. There are some islands and dikes in the lake that were constructed during the last century, when the salt was exploited commercially. Natural islands are found in the southwestern sector of the lake. These islands and dikes are used by greater flamingos as breeding sites and are rarely entered by ground predators during the incubation period. Furthermore, some management measures are adopted to prevent ground predators entering breeding sites (Rendón-Martos and Johnson 1996). Indeed, during 16 breeding seasons, we saw dogs during a single day only in each of two seasons. We did not detect any other evidence of predator presence, such as footprints on islands that must be crossed by predators to reach the breeding sites. However, as the lake usually dries up through the breeding season, red foxes (*Vulpes vulpes*) may eventually enter breeding sites and prey on flamingo chicks during the crèche phase. Nevertheless, the incidence of this type of predation on breeding success at the colony level is very small. In Fuente de Piedra lake, the colony is established either as a single unit or in two to ten subcolonies (Valverde 1964; Rendón-Martos 1996).

The Guadalquivir marshes are a complex of wetlands (>500 km²) that dry up to a large extent every summer. In this locality, greater flamingos have bred at two islands during the study period, always establishing a single colony. The sites are accessible to ground predators, mainly wild boars (*Sus scrofa*), especially late in the breeding season when water levels around breeding sites are usually low (Fernández Cruz 1982; Máñez 1991). In addition, livestock entered breeding sites in some years, causing flamingos to desert the colony (Rodríguez de los Santos 1983). Due to a rise in water levels during the 1996 incubation period, flooding of nests caused the complete failure of the colony.

Breeding parameters

Information on breeding greater flamingos at Fuente de Piedra was obtained from the literature (Sánchez et al. 1986; Rendón-Martos 1996), or during fieldwork conducted by us. Information on breeding flamingos at Guadalquivir was obtained from published reports (Fernández Cruz 1982; Rodríguez de los Santos 1983; Máñez 1991), from the files of the Estación Biológica de Doñana (CSIC, Sevilla), or during fieldwork conducted by us.

Every season, the date of breeding colony establishment at both Fuente de Piedra and the Guadalquivir marshes was considered as the date on which the first birds were recorded incubating, or by backdating from the first hatching. To record the date of establishment as accurately as possible, we monitored breeding sites almost daily from the moment those sites were occupied by courting birds.

At Fuente de Piedra, the number of breeding pairs was estimated by counting the number of incubating birds, and mapping the breeding sites twice a week. The censuses were made using binoculars and a spotting scope from a hide located about 300 m from breeding colonies and from vantage points around the lake. Care was taken to note the number of nests reused within breeding seasons, which some years may be >50% (Rendón-Martos 1996). After breeding had finished every year, breeding sites were entered to count the actual number of nests and to record the number of eggs lost and the number of dead chicks. Although both deserted eggs and dead chicks were scavenged to some extent, our procedure for estimating breeding failures was accurate, since the only scavengers recorded at colony sites were yellow-legged gulls (*Larus cachinnans*), which do not carry eggs or chicks away from nesting sites, and always leave egg or chick remains (Rendón-Martos 1996). At this colony, predation by mammals on chicks is very rare (see above). Clutch size of the greater flamingo is one egg (Cramp and Simmons 1977), and breeding success was estimated as the number of chicks that fledged relative to the number of breeding pairs. The number of chicks in the crèches was estimated from aerial photographs, which were taken after the last chicks had hatched, but before fledging of the first-hatched chicks.

The number of breeding pairs at the Guadalquivir marshes was estimated using different procedures. In 4 years, colony size was estimated using binoculars and a spotting scope from a hide erected about 400 m from nesting sites. In 6 years in which there was no hide, the colonies were approached by a small boat, and the number of incubating birds counted using binoculars while the observers were hidden among emergent vegetation. Breeding at the marshes is rarely successful (see below). In the few years in which the colony was successful, once the chicks had fledged, we entered the colony sites to count the number of lost eggs and depredated chicks. Breeding success was determined as in Fuente de Piedra. In 3 years, all surviving chicks (19 in 1988, 19 in 1997, and 138 in 1998) were captured and reared in captivity until fledging, because the crèches were being attacked by predators, or the wetlands around nesting sites had dried up. Breeding success in those years was considered nil, as all chicks are likely to have died.

Greater flamingos have been individually marked with darvic bands since 1977 in the Camargue (France), and since 1986 in Fuente de Piedra. Some of the flamingos from the Camargue have bred in Fuente de Piedra (Nager et al. 1996). At Fuente de Piedra, we searched for banded flamingos 4 days per week throughout the 1986–1999 breeding seasons. Searches for banded flamingos at the Guadalquivir marshes were made only in 1997. We considered as potential settlers those birds that entered, either singly or in pairs, sites occupied by breeding birds. These potential settlers did not stay in or near a nest and were frequently attacked by birds that had already settled when they moved through occupied territories. Potential settlers eventually attempted to construct nests. By recording bands at both Fuente de Piedra and the Guadalquivir marshes, we were able to document the age of breeding flamingos, as well as the age of birds trying to settle in a colony. By recording the individual identity of birds, we were also able to determine whether the timing of occupation of colonies was age related.

We used ordinal logistic regression to test whether there were differences among flamingo cohorts in their timing of settlement at Fuente de Piedra. In this kind of regression, the ordinal responses are modeled by fitting a series of parallel logistic curves to the cumulative probabilities. Each curve has the same design parameters but a different intercept (SAS 1989). In our case, we had six cohorts of flamingos that were banded as chicks in Fuente de Piedra.

In 1997 and 1998, we established a grid of quadrats (10×10 m) on an island of Fuente de Piedra by positioning marked wooden sticks before breeding started, which allowed us to test for density-dependent effects on breeding success. In each of the 2 years, once breeding had finished, we counted the number of nests and the number of eggs displaced outside nests in each quadrat. We also counted the number of eggs preyed upon by yellow-legged gulls. Because there is within-breeding season reutilization of nests by late-nesting pairs at this lake (Rendón-Martos 1996), direct comparison between egg losses and nest density could lead to misleading results. To control for the effects of nest reuse, we divided the number of egg losses within quadrats by the number of days that each quadrat had been occupied by adult birds on nests.

Sample sizes may differ in different analyses because not all information was available in some years. Thus, we had no estimates of breeding success for the Fuente de Piedra colony in 1977–1979, nor on laying dates in the marshes in 1979 and 1985. Throughout the paper, mean values are presented ±1 SD.

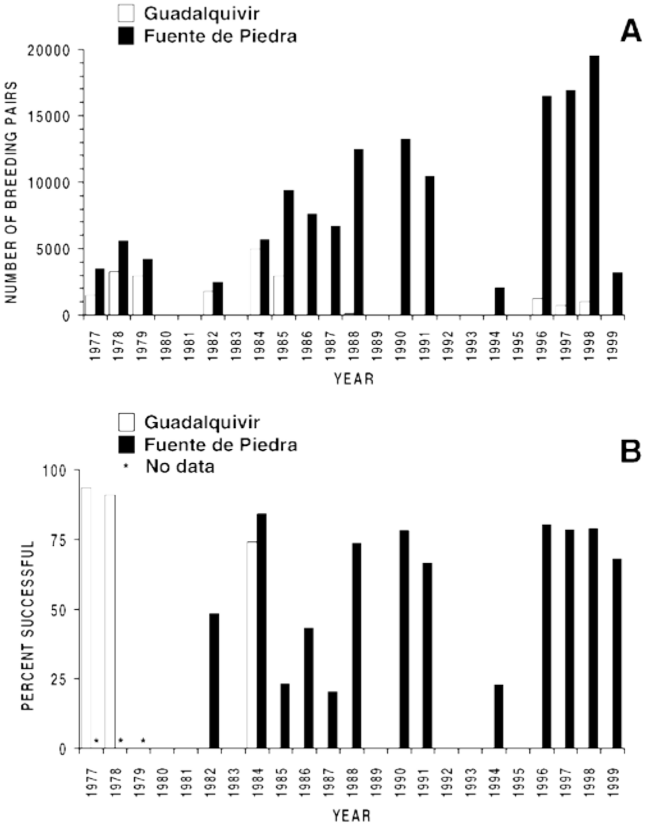

Fig. 1 Yearly distribution in the number of breeding pairs (**A**) and breeding success (**B**) of greater flamingos in Fuente de Piedra lake and the Guadalquivir marshes during 1977–1999. Breeding success is expressed as the percentage of nesting pairs that fledged a chick. Breeding success was not estimated in Fuente de Piedra during 1977–1979

Results

The flamingos established breeding colonies in the Guadalquivir marshes in 10 of the 23 years from 1977–1999, whereas they did so in Fuente de Piedra lake in 16 of those years (Fig. 1). Mean colony size was greater in Fuente de Piedra (8,731±5,582 nesting pairs, *n*=16) than in the Guadalquivir marshes (2,065±1483, *n*=10; Mann-Whitney *U*-test, *U*=6.0, *P*=0.001).

To demonstrate that the establishment of flamingo colonies is despotic, the sites must first be shown to differ in quality. The degree of accessibility of terrestrial predators to nesting sites is a critical aspect of site quality for colonial nesting waterbirds (Wittenberger and Hunt 1985). Based on this, Fuente de Piedra was of better quality than the Guadalquivir marshes (see above). According to the IDD model, the fitness of individuals should be higher in the best site. In years in which the flamingos settled in both sites, breeding success was much higher at Fuente de Piedra (66.7±22.5%, *n*=7) than at the Guadalquivir marshes (10.6±28.0%, *n*=7; *U*=3.0, *P*=0.004; Fig. 1).

A critical assumption inherent in the IDD model is that individuals should be omniscient, and that they

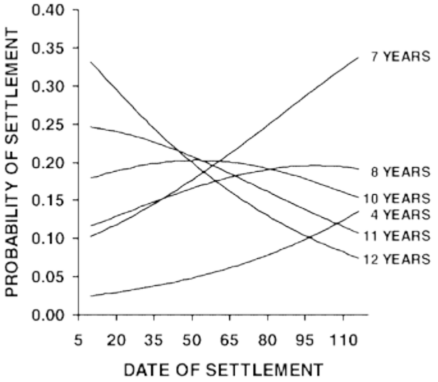

Fig. 2 Relationship between the probability of settlement and timing of settlement of greater flamingos at Fuente de Piedra in 1998, according to flamingo age. A logistic curve was produced by an ordinal logistic regression for each of the cohorts. Date of settlement is represented as number of days from 1 March

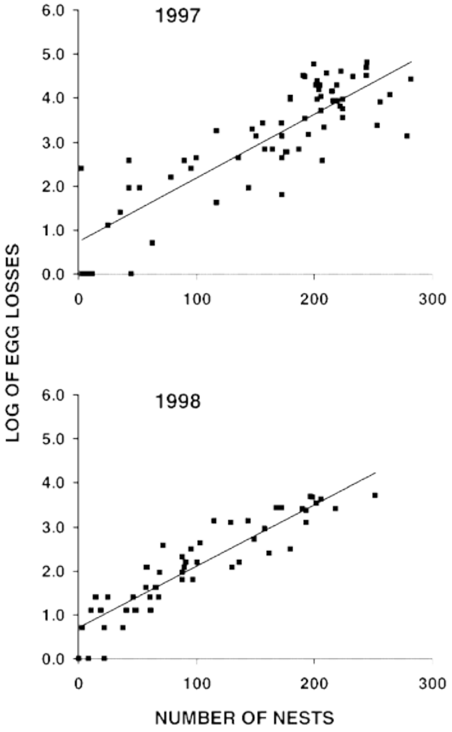

Fig. 3 Breeding failures of greater flamingos, expressed as number of eggs displaced outside nests (log-transformed) in relation to nest density in 10×10 m quadrats on an island in Fuente de Piedra lake in 1997 and 1998

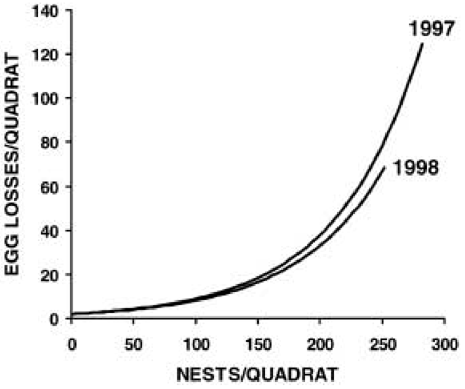

Fig. 4 Relationship between the number of egg losses and the density of nests in 10×10 m quadrats on an island in Fuente de Piedra lake in 1997 and 1998. Lines were obtained by fitting the data to an exponential function

should try to settle first in the best site. In 1997, we recorded 18 individually marked flamingos trying to settle at Fuente de Piedra when the colony was already established. These same individuals were subsequently recorded breeding in the same year in the Guadalquivir marshes, indicating that they had tried to settle first in Fuente de Piedra. None of 79 marked individuals that were first seen at Guadalquivir bred later at Fuente de Piedra.

As expected from an IDD, in those years in which the flamingos nested in both sites, they started laying earlier in the Fuente de Piedra colony (16 March±15 days, n=8) than in the Guadalquivir marshes (27 April±16 days, n=8), a significant difference (U=60.0, P=0.003). We stress that differences in food availability between sites were not affecting this type of settlement, since in most years, the flamingos from Fuente de Piedra obtained most of their food during the chick-rearing period in the Guadalquivir marshes (Rendón-Martos 1996; Rendón-Martos et al. 2000).

If colony establishment is despotic, age-related behavioral dominance may be a mechanism responsible for this type of distribution. Based on an ordinal logistic regression, we found that the timing of settlement of breeding flamingos at the Fuente de Piedra colony was age related (Fig. 2; n=251, χ^2=10.52, df=1, P=0.001). Furthermore, the flamingos recorded breeding in the Guadalquivir marshes in 1997 were younger (8.4±2.7 years old, n=18) than those breeding in the same year at Fuente de Piedra (10.8±3.1 years old; n=96, t=3.11, P=0.002). For this last comparison, we considered only the flamingos breeding before 1 May in Fuente de Piedra, because most of the flamingos that subsequently bred in the Guadalquivir were recorded visiting Fuente de Piedra before that date.

Another assumption of the IDD model is that as density at a given site increases, the fitness of individuals should decrease. When breeding sites are limiting, competition for nesting space may be an important factor affecting colony size. The rates of daily egg loss (log-transformed) in relation to nest density were similar in 1997 and 1998 ($F_{1,96}$=0.02, P=0.878; Fig. 3). There was a strong effect of the number of birds per quadrat on egg losses, both in 1997 (r^2=0.72, n=67, P<0.001) and 1998 (r^2=0.84, n=54, P<0.001; Fig. 3). In 1997, the flamingos breeding in Fuente de Piedra settled on two islands, whereas in 1998 their nesting was distributed in ten subcolonies. One of the islands was occupied on both years, but at a much higher density in 1997 than in 1998. In 1997 in particular, the number of egg losses inside quadrats increased sharply when nest density was >2 nests m^{-2} (Fig. 4).

Discussion

The pattern of settlement by breeding greater flamingos recorded during our study is consistent with assumptions of the IDD model: breeding success was higher in the best site (Fuente de Piedra), flamingos occupied the best site first, lower-quality individuals, i.e., younger ones, were displaced to lower-quality nesting colonies (Guadalquivir marshes) and, as density increased, breeding success diminished.

Although some studies have claimed that the distribution of studied organisms conformed to an IDD (Andrén 1990; Møller 1995; Petit and Petit 1996), such studies did not actually demonstrate the critical assumption of the IDD model that lower-quality individuals should first try to settle in the best habitat. Nor is the rapid occupation of vacant territories by floater individuals an unambiguous demonstration of an IDD unless they are shown to actually contest for occupied territories.

Ens et al. (1995) indicated that six questions should be addressed when attempting to document a despotic distribution in any long-lived species. (1) Are there consistent differences between habitats in terms of long-term reproductive success? In line with this, we found that breeding success in the most preferred site was higher during most years in which breeding took place in the two sites. (2) Are competitors able to discriminate between habitats of different quality? Prior to starting to breed in the Guadalquivir marshes, individual flamingos were recorded in the Fuente de Piedra colony, where they might have tried to settle. (3) Are the differences in habitat quality large enough to risk a fight for achieving access to a good habitat? We have no direct evidence of this. At Fuente de Piedra, egg losses are the main cause of breeding failure (Rendón-Martos 1996). Eggs are displaced outside nests during contests, and this may be considered circumstantial evidence that flamingos risk a fight to breed in a good site. (4) Do owners win because of phenotypic superiority? Our data and those of Nager et al. (1996) indicate that older birds usually breed in the best sites. (5) Do breeding skills improve the effectiveness of individuals in their competition for access to habitats of high quality? We have no data on this. (6) Can recruits opt for all sites with a reasonable chance of success, or do they have to concentrate on specific sites? In accordance with assumptions of the IDD, greater flamingos in southern Spain have to concentrate on a specific site (Fuente de Piedra) to have a reasonable chance of success.

The main assumptions of some habitat choice models that account for interference among individiduals are that individuals are omniscient, and that they have a perfect knowledge of patch profitabilities (e.g., Tregenza 1995). Such assumptions may represent an insurmountable complication when attempting to test habitat choice models in many organisms. However, such conditions may be easy to find in habitats with little complexity, such as those studied by us or by Ens et al. (1995). Breeding greater flamingos exhibit high fidelity to natal colonies (Nager et al. 1996). The number of sites at which flamingos may breed in southern Spain is very limited, and individually marked birds are relatively easy to observe, which facilitates documentation of the turnover of individuals between sites (i.e., unequivocal evidence that individuals are omniscient), as well as knowledge of site profitability. Omniscience is suggested by the fact that before reaching reproductive age, flamingos are recorded in breeding colonies, probably prospecting for potential breeding sites (own unpublished data; see also Nager et al. 1996). One of the functions of site prospecting is presumably to gain experience about the quality of future breeding sites (Schjørring et al. 1999). But more importantly, individual flamingos were recorded visiting the colony in Fuente de Piedra, where breeding success is better, just before being recorded breeding in the Guadalquivir marshes, suggesting that they had knowledge of site profitabilities.

In our study, a relevant resource affecting settlement by greater flamingos was nesting space. Given that greater flamingos are long-lived birds (Johnson 1997), the assessment of potential breeding sites may be based on past experience. Experienced individuals should therefore be better able to assess breeding site quality, and this may confer on them an advantage over less experienced individuals. The latter may then benefit from the settlement decisions of experienced individuals by what has been considered “public” information (Valone 1989). However, when nesting space is limiting, later incoming individuals may be constrained in their choice of breeding sites by competition with experienced individuals (Nager et al. 1996). Individuals probably acquire experience with age. Because of this, age and experience may be intimately linked, so that for an individual the decision as at what age to settle cannot be separated from the decision on where to settle (Ens et al. 1995).

Acknowledgements Several people, but especially the late Antonio Herrera, collected data in the colonies of the Guadalquivir marshes. In the marshes, Héctor Garrido read many rings of marked flamingos that greatly facilitated the documentation of settlement patterns. Juan J. Chans facilitated our access to the files of Estación Biológica de Doñana. During field work in Fuente de Piedra we were assisted by Antonio Arroyo, Rafael Camerana, and Juan Rubio. The Consejería de Medio Ambiente (CMA) of the Junta de Andalucía (Monitoring Program of the flamingo colony of Fuente de Piedra, and an agreement CMA-CSIC), and Plan Andaluz de Investigación (research group RNM 0105) provided funds that supported the study. During manuscript preparation we were supported by Dirección de Enseñanza Superior e Investigación Científica (grants PB97-1083 and PB98-0494-C02-01). We would also like to thank Christophe Barbraud, Janis Dickinson, R. Michael Erwin, Alan R. Johnson, Arja Kaitala, and an anonymous referee for helpful comments on previous versions of this paper.

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