Breeding Biology and Population Dynamics of Slender-billed Gulls at the Ebro Delta (Northwestern Mediterranean)

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Abstract.—The breeding biology of the Slender-billed Gull (*Larus genei*) is poorly known. Several reproductive parameters have been recorded during ten years (from 1992 to 2001) at the Ebro Delta (northwestern Mediterranean), such as clutch size, egg size and breeding success, as well as the number of breeders during the study and their population dynamics. Average clutch size during the study was 2.57 eggs per nest, with three eggs being the modal size. Slender-billed Gulls can lay a second clutch after egg loss, although clutch size is decreased. Mean egg size for the period 1998-2001 was 38.50 ml (SE ± 0.11). Although breeding is highly synchronous, females laying first were probably those in best body condition. Average breeding success for the whole period was 0.71 chicks per nest (24% of eggs laid). Compared with other colonies, results suggest that on average, the site may be a high quality colony in terms of availability of food, nest sites and predation rates. However, most of the breeding parameters analyzed showed statistically significant differences between years, and also between breeding areas and sub-colonies within the delta. The number of breeding pairs increased slightly from 388 in 1992 to 468 in 2001 (mean annual growth rate was 1.02 per year), although the rate fluctuated greatly between years, these changes were probably related to emigration-immigration processes at a metapopulation level. *Received 1 August 2001, accepted 7 November 2001.*

Key words.—Slender-billed Gulls, habitat selection, *Larus genei*, breeding parameters, population dynamics.

Waterbirds 25(1): 67-77, 2002

Gulls are among the most extensively studied birds due to their worldwide distribution, abundance and colonial habits. However, the breeding biology of a number of small gull species remains poorly known. This is especially true for species with a scattered distribution such as the Slender-billed Gull (*Larus genei*). This species breeds in isolated localities from Senegal and Mauritania, throughout the Mediterranean, the Black Sea, Asia Minor, and Middle East to western India (Cramp and Simmons 1983). Most of the available information deals with the species in terms of both distribution and status in some of these areas (see Burger and Gochfeld [1996] and references therein). For instance, it is known that, contrary to most species of gulls, chicks form crèches looked after by a few adults, and that the nests are very closely packed (Isenmann 1976). Nevertheless, quantitative information about breeding parameters of the species is very scarce and always refers to small sample sizes (Isenmann 1976; Cramp and Simmons 1983; Fasola *et al.* 1993; Dies and Dies 2000). In the present study, a detailed account of the breeding biology of the Slender-billed Gull at the Ebro Delta (northwestern Mediterranean) is provided. Several reproductive parameters have been recorded during 10 years (from 1992 to 2001) such as clutch size, egg size (data from 1998 to 2001) and breeding success, as well as the number of breeders during the study and their population dynamics.

METHODS

Study Area

The study was conducted at the Ebro Delta in the Ebro Delta Natural Park (NE Spain: 40°37'N, 00°35'E) (see Fig. 1). The three study areas were La Banya, La Tancada and El Fangar. Although the three areas are within the limits of the Park, they showed differences in habitat, presence of terrestrial predators, level of human disturbances and access to foraging resources. La Banya was the main breeding area during the study. It is a peninsula connected to the rest of the Delta by a narrow 9 km long sand bar, which limits access of terrestrial predators, although feral cats were common until 1998. The habitat where the gulls breed is a flat sandy salt marsh of 2,500 ha with dunes covered by halophilous vegetation.

Approximately half of the surface is occupied by salinas (lagoons for salt production), where gulls breed on dikes and islets. The area is strictly protected and no human activities except salt extraction and scientific research are permitted during the breeding season.

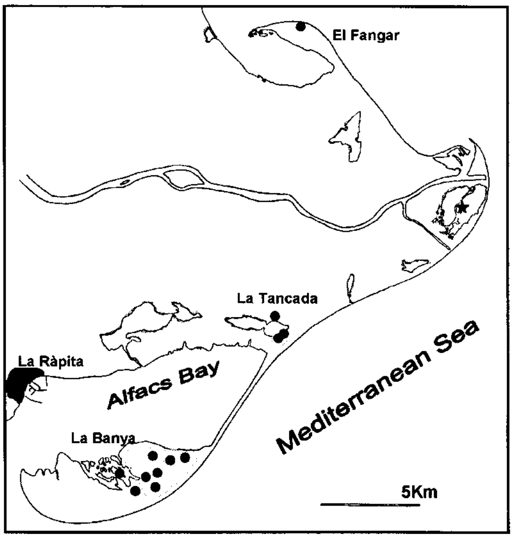

Fig. 1. Map of the Ebro Delta (western Mediterranean) showing the three breeding areas where Slender-billed Gulls have bred at least once during 1992-2001, as well as some sites cited in the text. The dots show the location of the different colonies within the breeding areas, while the shadow areas show the location of the two salinas. The star shows the location of one nest of Common Tern containing an egg of Slender-billed Gull in 2000 (see text).

La Tancada is a brackish and shallow lagoon of 195 ha surrounded mostly by vegetation of Glasswort (mainly *Arthrocnemum fruticosum*). A small area frequently occupied by gulls is the remains of ancient salinas and here some other human activities are allowed during the breeding season, such as fish farming or the cultivation of rice. Terrestrial predators (feral cats and dogs and especially foxes) occur. The breeding area at El Fangar is a flat, sandy peninsula of ca. 800 ha. The habitat is characterized by bare, open areas with a few dunes and some halophilous vegetation. Although it is a peninsula, the area is not as isolated as La Banya, and terrestrial predators are common. Shellfish exploitation in the mud and tourists on the beaches are both frequent.

Data Recording

The breeding areas were observed from mid March until early July during 1992-2001. A minimum of 59 days (corresponding to 223 h) was spent each year observing the birds. Observations were carried out from a distance using a car. The main goals of the observations were to locate the colonies and investigate their phenology based on courtship, copulatory behavior and nest building. The colony was entered only once each year to minimize disturbance (after observing a desertion of a colony in 1991 due to a photographer entering during laying). The colony was entered approximately 20 days after the first pairs were observed incubating; this delay was to ensure that most of the pairs had already completed their clutches, since incubation lasts 22 days (Cramp and Simmons 1983) (see below). When possible, data were recorded separately for each sub-colony (groups of nests clearly grouped and slightly separated from other group(s) of nests) and breeding areas (see Fig. 1). The high proportion of birds starting incubation the few days after the first pair laid suggested highly synchronous laying, and that the number of nests and eggs were a good estimator of colony size and clutch size respectively. However, colony and clutch sizes recorded could be slightly underestimated due to predation by Yellow-legged Gulls (*Larus cachinnans*) or by incomplete clutches. These potential biases were not assessed in order to avoid further disturbance, but I assumed that they were constant between the years. To avoid double counting of nests, each was marked with a bean during the censuses. Clutch size recorded in the Ebro Delta was compared with data from previous studies in Fuente de Piedra and Doñana (both in southern Spain) and Valencia Albufera (east Spain) (Studer-Thiersch 1968; Costa 1985; Dies and Dies 2000).

The breeding species associated with Slender-billed Gulls and the main features of the breeding habitat were recorded. Association between Slender-billed Gulls and other species was examined in several ways. First, I built a contingency table taking into account the total number of sub-colonies established during the study and the frequency of association with the other species. The species considered were the commonest colonial Charadriiformes breeding at the Ebro Delta: Avocets (*Recurvirostra avosetta*) and Black-winged Stilts (*Himantopus himantopus*); Yellow-legged Gulls, Audouin's Gulls (*Larus audouinii*), and Black-headed Gulls (*L. ridibundus*); Gull-billed Terns (*Sterna nilotica*), Sandwich Terns (*S. sandvicensis*), Common Terns (*S. hirundo*), and Little Terns (*S. albifrons*). An additional category of no association was also considered, by applying a chi-square statistic to test for the null hypothesis that the proportion of sub-colonies where Slender-billed Gulls associated with one species was the same as the proportion of sub-colonies where Slender-billed Gulls associated with the other species (see for instance Margalef 1982, p. 405). This analysis revealed which species were closely associated with Slender-billed Gulls. However, this analysis would preclude conclusions about whether there was a positive or negative association of Slender-billed Gulls with other species. To analyze the true associations between species, the locations of colonies of the species mentioned above were necessary to score the presence or absence of Slender-billed Gulls and associated species in each, taking into account all the dunes and sites where at least one of the species bred at least once during the study. This was possible only at La Banya, where fieldwork was more intense during the study. An index between a chi-square statistics applied to two contingency tables with and without double absences (Cole 1949; Margalef 1982) was applied for each of the commonest associated species at La Banya (in this case, for Avocets, Yellow-legged Gulls, Audouin's Gulls, and Sandwich Terns and Common Terns). Finally, and to take into account the abundance of each species breeding at the whole Ebro Delta, a goodness-of-fit test was applied to a contingency table of frequencies of sub-colonies associated with each species after expected values, taking into account the mean value of the counts of all the other species carried out during the study (Anonymous 1992, 1993, 1995; D. Oro, unpubl. data), were calculated.

To assess whether Slender-billed Gulls bred within the salinas more than expected, I constructed a contingency table of the number of different sub-colonies established in and outside of the salinas and calculated an expected value considering the total number of sites occupied by any colonial Charadriiformes breeding at the three areas considered (see list above).

During 1998-2001, eggs from a sample of clutches (mainly of two and three eggs, the main clutch sizes) were measured (length and maximum width) to the nearest 0.1 mm using digital calipers. Egg size was estimated by internal egg volume (cm^3) as determined by the equation: $V = 0.000485 \cdot \text{length} \cdot \text{breadth}^2$ used for Audouin's gulls *Larus audouinii* ($r^2 = 0.999$, n = 38; see Oro *et al.* 1999). In 1998, my entry into the colony was just prior to the hatching of the first eggs, and nests were classified as early clutches (when at least one egg was nearly hatched) and late clutches (when none of the eggs in the clutch had showed a broken shell typical of pre-hatching). Since Slender-billed Gulls exploit discards from trawlers (Oro 1999), I tested the potential effects on clutch size of a trawling moratorium that has been established in the area during two (but different) months each year, but which always overlapped with some of the reproductive stages of the gulls (see also Oro *et al.* 1999). In 1992 and 1994, the moratorium occurred during April and May and May and June respectively, overlapping with the pre-laying and laying stage of the gulls. The potential effect of trawling activity on egg size could not be tested during 1998-2001, since trawler activity was normal during pre-laying and laying periods.

A census of chicks in the crèche, counted from a distance, was performed ca. 30 days after the single entry and used to estimate the breeding success as number of chicks per breeding pair. Since the young in the crèche were normally closely packed and the habitat is flat, the number of chicks was probably underestimated, but it is assumed that the bias was constant throughout the study and the breeding success was a minimal value. An index of breeding success was calculated as the number of chicks fledged as a percentage of eggs laid estimated from the mean clutch size (see above). Breeding failure in one sub-colony in 1994 caused by a licensed photographer was not considered in the analysis.

Data Analysis

G-tests and chi-square tests were carried out for comparisons involving frequency data such as clutch size. The few four-egg clutches were not considered to avoid the violation about minimum expected frequencies of contingency tables and their applied G-tests. Since a large female effect in egg size variability is commonly found in birds (e.g., Jover *et al.* 1993), a random-effect one-way ANOVA was used to test for this effect in the different sub-samples defined by the combination of year and clutch size of two and three eggs. Thereafter, mean egg volume in the clutch was used to perform all subsequent analyses at inter-clutch level. One-way ANOVA and, when appropriate, an *a posteriori* Student-Newman-Keuls test procedure, was used to compare breeding areas, sub-colonies and years, as well as early and late clutches (see above). Mean and standard errors are presented unless otherwise stated.

The annual growth rates (λ) of Slender-billed Gulls in the Ebro Delta colonies between year t and $t + l$ was calculated as:

$$\lambda = N_{t+l}/N_t$$

using counts of nests at the Ebro Delta from 1992 to 2001 and λ for each pair of years in this time interval. The mean annual population growth rate over the study period was calculated as:

$$(N_{2001}/N_{1992})\cdot \exp^{1/9}$$

RESULTS

Colony Features, Size and Growth

The lowest number of pairs (388 nests) was recorded the first year of the study, 1992, whereas the maximum number was 605 pairs in 1995. During the study period, mean colony growth in pairs was 1.041 showing an average 4.1% increase in breeding numbers per year (Table 1). However, years with very small changes in colony size (e.g., 1% increase in 2001) have contrasted with years of extremely large changes (e.g., 50% increase in 1993, 30% decrease in 1997). One-tailed Spearman rank correlation of annual numbers nesting at La Banya and La Tancada during six years, 1995-2000 (Fig. 2) was negative but not significant ($r_{s\,6} = -0.71$, P = 0.055).

During the study, gulls always bred at La Banya, whereas La Tancada area was occupied since 1995 and birds only bred at El Fangar in 2000 and 2001 (see Table 1 and Fig. 1), although seven pairs had bred there in 1991 (A. Martínez-Vilalta, pers. comm.). In 2000, an egg of the Slender-billed Gull was found in a Common Tern nest in a small colony of five nests at Buda Island (Fig. 1), far from the three breeding areas.

Copulation was first observed in early April, and laying dates were always between late April and early May (median 28 April, range 24 April-8 May; N = 21 sub-colonies). Courtship behavior (displays, courtship feeding, copulation) was observed in dense groups and mostly occurred far from the breeding site.

A total of 24 sub-colonies of different sizes were formed during the study (median = 178 pairs; range = 3-582), with a maximum of four sub-colonies occupied in any year. From the twelve different sites (dunes, dikes, beaches) occupied at least once during the study, 67% were located within salinas areas; this proportion increased to 75% when considering the total number of occupied sites used at any time from 1992 to 2001 (24 sub-

Table 1. Estimated numbers of breeding pairs of Slender-billed Gulls at the Ebro Delta during the study, as well as the number of sub-colonies and breeding areas. λ is the population growth rate (see text). The species of breeding Charadriiformes associated with Slender-billed Gulls is also shown (AV = Avocet; BwS = Black-winged Stilt; ST = Sandwich Tern; GbT = Gull-billed Terns; CT = Common Tern; LT = Little Tern; BhG = Black-headed Gull; AG = Audouin's Gull). When more than one sub-colony was occupied, the number of sub-colonies in breeding association for each species is shown in brackets.

Year	Sub-colonies	Breeding areas	Species associated	Breeding pairs	λ
1992	1	La Banya	AV; ST; AG	388	
1993	1	La Banya	AV; ST; GT; AG	582	1.50
1994	3	La Banya	AV (2); ST (2); AG (1); no association (1)	573	0.98
1995	4	La Banya; La Tancada	AV (4); ST (2); CT (3); GbT (1); AG (2)	605	1.06
1996	2	La Banya; La Tancada	AV (2); ST (1); AG (1)	564	0.93
1997	2	La Banya; La Tancada	AV (2); ST (1); GbT (1)	393	0.70
1998	2	La Banya; La Tancada	AV (2); ST (1), CT (1); GbT (1)	406	1.03
1999	2	La Banya; La Tancada	AV (1); CT (1), LT (1); GbT (1); no association (1)	487	1.20
2000	4	La Banya; La Tancada; El Fangar	AV (1); BwS (1); ST (2), CT (1); GbT (1); BhG (1)	468	0.96
2001	3	La Tancada; El Fangar	AV (2); BwS (1); ST (1), CT (2); GbT (1); BhG (1)	473	1.01

colonies). Half of these sites were used only once during 1992-2001. From these twelve sites, five were totally surrounded by water (33% of the 21 total number of occupations), six were partially surrounded by water (52%) and only the El Fangar site was far from water (200 m from the open sea in this case). This was also the only colony on a sandy beach and on bare ground lacking vegetation. The rest of the sites were vegetated, most of them (9 of 12) with more or less dense small bushes of Glasswort, one on a salinas road with sparse Sea Purslane (*Atriplex portulacoides*), and one of them on a high dune with bushes of Egyptian Evergreen Shrub (*Thymelaea hirsuta*) and low vegetation dominated by herbaceous species, particularly European Beachgrass (*Ammophila arenaria*).

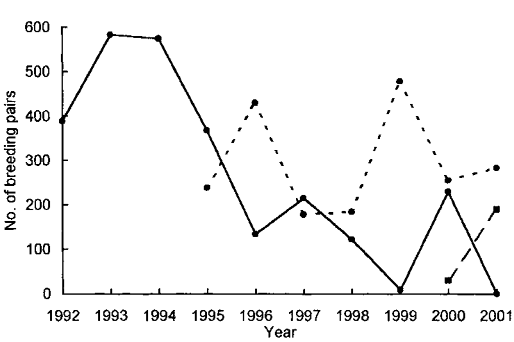

Fig. 2. Number of breeding pairs estimated in the two main breeding areas at the Ebro Delta (western Mediterranean) during 1992-2001. Solid line shows numbers at La Banya, dashed line shows those at La Tancada and solid squares those at El Fangar.

Colonies of the Slender-billed Gull were associated with all of the commonest species of colonial Charadriiformes except Yellow-legged Gulls (Table 1). Only in two cases (from the 24 sub-colonies occupied during the study) gulls bred in a single species colony. Avocets and Sandwich Terns were the commonest species associated with Slender-billed Gulls (in 75% and 51% of 24 sub-colonies respectively) (Table 1). The contingency table shows that significant differences were found in the frequency of association depending on the species (G_9 = 65.7, P < 0.0001). Avocets and Sandwich Terns were positively associated and Yellow-legged Gulls and Black-headed Gulls were negatively associated. An index of true associations also showed that the associations with Avocets and Sandwich Terns were positive and significant (χ^2_1 = 16.0, P < 0.001 and χ^2_1 = 163, P < 0.0001, respectively), whereas the associations with Common Terns, Yellow-legged Gulls and Audouin's Gulls were negative and not significant (χ^2_1 = 0.10, n.s., χ^2_1 = 0.03, n.s., and χ^2_1 = 0.12, n.s., respectively). Finally, statistical differences were found between the observed and expected number of associations depending on the abundance of each species (χ^2_8 = 339, P < 0.0001), and in this case Slender-billed Gulls were positively associated with all the species except the Common Tern, Yellow-legged Gull and Audouin's Gull.

Slender-billed Gulls bred on dikes and islets within the salinas more frequently than expected by the availability of these sites (see methods) (Goodness of Fit χ^2_1 = 8.74, P < 0.003).

Clutch and Egg Size

Clutch size was significantly different among years (G_{18} = 128, P < 0.0001). Modal clutch size was three eggs for all years except 2001, being, on average, 64.5% of total sampled clutches (Table 2). Standardized residuals showed that in 1992, 1994 and especially in 2001 three-egg clutches appeared at significant lower frequencies than expected (55%, 56% and 44%, respectively), whereas in 1997 their frequency was significantly higher than expected (84%). As expected, the trend was the opposite for two-egg clutches in 1992, 1994, 2001 and 1997 (38%, 36%, 46% and 13.2%, respectively, 31.2% of two-egg clutches for all years). Years when the trawling moratorium overlapped with the pre-laying stage showed a significantly lower clutch size than in normal years (G_2 = 7.36, P < 0.03). However, a significant difference between years still existed when only those with normal trawler activity were compared (G_{14} = 120, P < 0.0001). Clutch size in 1994 was probably lower due to the desertion of the first breeding site selected by gulls after predation by a feral cat on five consecutive nights. Eight corpses of adult Sandwich Terns and three Slender-billed Gulls were found in one of the dikes, together with droppings and tracks of the cat (D. Oro, pers. obs.). The site was abandoned 16 days after the first adult was observed incubating and clutch size was estimated for that year in the two sub-colonies subsequently occupied. When 1994 was excluded from the analysis, statistical differences between 1992, affected by the trawling moratorium, and the

Table 2. Clutch size of Slender-billed gulls at the Ebro Delta, 1992-2001. Percentages of clutch size for each year are shown in parentheses.

	Clutch size					
Year	1	2	3	4	Mean	N
1992	17	85	123	0	2.47	225
	(7)	(38)	(55)	(0)		
1993	15	68	138	2	2.57	223
	(7)	(30)	(62)	(1)		
1994	48	37	57	0	2.48	102
	(8)	(36)	(56)	(0)		
1995	15	109	194	3	2.58	321
	(5)	(34)	(60)	(1)		
1996	7	21	60	2	2.63	90
	(8)	(23)	(67)	(2)		
1997	6	28	178	3	2.83	215
	(3)	(13)	(83)	(1)		
1998	12	23	81	1	2.61	117
	(10)	(20)	(69)	(1)		
1999	11	74	200	1	2.50	286
	(4)	(26)	(70)	(0)		
2000	28	146	284	2	2.57	460
	(6)	(32)	(62)	(0)		
2001	37	155	148	12	2.38	352
	(11)	(44)	(42)	(3)		
Total	156	746	1463	26	2.57	2391
	(6.5)	(31.2)	(61.5)	(1.1)		

other years, were still significant ($G_2 = 5.83$, $P < 0.05$). Statistical differences in clutch size were detected between sub-colonies in 2001 ($G_4 = 13.9$, $P < 0.01$), but not in 1995 or in 2000 ($G_2 = 4.14$, n.s.; $G_4 = 6.79$, n.s., respectively). Significant differences in clutch size between the breeding areas of La Banya and La Tancada in 2000 ($G_2 = 0.62$, n.s.), and between La Tancada and El Fangar in 2001 ($G_2 = 0.30$, n.s.) were not found.

Average clutch size during the study (2.57 eggs per nest) was significantly higher than that recorded in small colonies in Fuente de Piedra and Doñana (southern Spain) (2.4 and 2.3) and in a small colony in Valencia Albufera (2.3) ($G_6 = 14.2$, $P < 0.03$). However, these differences could be due to the different recording biases at each colony, and they have to be interpreted with caution.

As expected, a highly significant female effect on egg size was detected in each year for two- and three-egg clutches, with the exception of two-egg clutch in 1998 which may have been probably due to the small sample size for this year (Table 3). Average clutch volume was significantly different between years ($F_{3,293} = 2.80$, $P < 0.04$) but no effects of either clutch size ($F_{1,293} = 2.12$, n.s.) or of its interaction with the year effect were found ($F_{1,293} = 0.68$, n.s.). The *a posteriori* SNK tests showed that the mean egg volume in three-egg clutches was significantly smaller in 1999 and 2001 (0.7 cm^3 in average) than in 1998 and 2000 (see Table 4). Data from 2000 showed that average volume in three-egg clutches was significantly different between La Banya and La Tancada ($F_{1,69} = 7.38$, $p < 0.01$). Average clutch volume at La Banya was significantly larger than those at Tancada (39.45 ± 0.39 [mean and SE, in cm^3], N = 51; 37.56 ± 0.47, N = 19, respectively). No effect of sub-colony on average volume in three-egg clutches was detected in 1999, or in 2000 or in 2001 ($F_{2,93} = 1.24$, n.s.; $F_{1,18} = 0.42$, n.s.; $F_{1,78} = 2.45$, n.s., respectively).

Data from 1998 showed that average volume in early three-egg clutches was significantly greater (41.33 cm^3, SE ± 0.99, N = 16) than that in later clutches (38.78 cm^3, SE ± 0.36, N = 35) ($F_{1,50} = 7.03$, $P < 0.02$).

Breeding Success

Table 5 shows the average number of fledglings per breeding pair (laying at least one egg) during the study. The average productivity for the whole period was 0.71 chicks fledged per pair. The method of productivity estimation does not allow statistical comparison, but results indicate a high yearly variation in breeding success. Results also show differences within years depending on the sub-colonies and especially the breeding areas. Chicks were able to fly at 28 days of age when provoked by approach, and the crèche moved far from the nests (more than 200 m, even crossing dikes and tracks) if disturbed by man or predators.

DISCUSSION

Disturbance and Data Quality

I recorded the desertion of most of the breeding pairs in one colony before this study commenced and again in a sub-colony of

Table 3. Results of one-way ANOVA on two- and three-egg clutches to assess the female effect on egg volume and the estimated percentage of variability explained by the female effect. FV shows the component of variance explained by female effect as a percentage.

Clutch size	Year	F	df	P	FV (%)
Two-egg clutches	1998	0.80	9	n.s.	42
	1999	4.73	42	<0.0001	82
	2000	9.33	8	<0.001	89
	2001	2.24	43	<0.005	57
Three-egg clutches	1998	4.91	40	<0.0001	71
	1999	3.14	50	<0.0001	61
	2000	3.62	60	<0.0001	64
	2001	3.07	34	<0.0001	59

Table 4. Average egg length, width (in mm) and volume (mean and SD) (in cm^3) in two- and three-egg clutches of Slender-billed Gulls at the Ebro Delta for the period 1998-2001. The number of clutches sampled (N) is shown.

Year	Clutch size	N	Length	SD	Width	SD	Volume	SD
1998	1	3	54.46	3.76	36.30	0.42	34.84	3.22
	2	10	54.55	1.73	38.72	0.96	39.65	1.74
	3	41	54.17	1.91	38.58	1.02	39.16	2.75
	Total	54	54.22	1.92	38.55	1.05	39.01	2.71
1999	1	3	55.70	3.84	38.17	0.97	39.31	1.59
	2	43	54.08	2.19	37.82	1.20	37.57	3.03
	3	51	53.65	2.45	38.36	1.09	38.33	2.82
	Total	97	53.83	2.38	38.16	1.16	38.07	2.90
2000	1	—	—	—	—	—	—	—
	2	9	53.75	2.45	38.07	1.23	37.84	3.14
	3	61	53.88	2.33	38.65	1.30	39.10	3.28
	Total	70	53.86	2.34	38.60	1.30	38.94	3.27
2001	1	10	53.65	1.43	38.19	1.41	38.04	3.38
	2	44	53.37	2.19	38.12	1.48	37.69	3.37
	3	35	53.51	2.62	38.42	1.52	38.38	3.75
	Total	89	53.46	2.39	38.28	1.50	38.06	3.57
Total 1998-2001		310	53.82	2.30	38.38	1.28	38.50	3.18

incubating adults in 1994, both caused by licensed photographers. Thus, the species seemed sensitive to human disturbance. Although the species is not threatened, the birds are protected by law and the colony in the Ebro Delta is one of the largest in the western Mediterranean (Isenmann and Goutner 1993). As a result, reduced disturbance was given priority over high data quality in this study (see Nisbet 2000). I believe that the biases were not large and I assumed that they were similar in each year. The census method, and, in turn, the estimation of clutch size, were probably biased and perhaps explained some of the variation in colony size between years. In contrast, average volume in a clutch (especially in three-egg clutches) was probably not or little biased, since the assumption that these were complete clutches was robust, since most laying had ceased.

Clutch and Egg Size

Clutch and egg size normally indicate the environmental conditions during laying, and both parameters increase as food availability increases, until a plateau is reached (e.g., Bolton *et al.* 1992; Oro *et al.* 1999). Results suggested that food supply varied greatly between years. Clutch size was lower when the trawling moratorium overlapped with the pre-laying stage (even when excluding results from 1994), but its effects were small. Clutch size differences also occurred in years with normal trawling activity, and exploitation of fish waste was probably much lower in this gull than that in typical scavenging species (Oro 1999). Results from 1994 confirmed that Slender-billed Gulls might lay replacement clutches after egg loss (see also Cramp and Simmons 1983), although clutch size decreased as a result. Egg size also suggested that food availability may vary not only between years, but also in the same year within the study area, where environmental conditions are probably similar between sub-colonies. Studies on other larids show that egg size is reduced before clutch size when resources for egg formation are limited (e.g., Bolton 1991; Bolton *et al.* 1992), and this probably explains why effects of sub-colony were not detected in clutch size. Mean egg size was significantly lower in 1999, when 99% of birds bred at La Tancada, whereas in 2000, egg size was significantly lower at La Tancada than at La Banya. These results

Table 5. Mean number of chicks fledged per breeding pair of Slender-billed Gulls during the study (1992-2001) at the Ebro Delta. Breeding success as average percentage of chicks raised per egg laid is also shown. For some years, data are separated by sub-colony and/or breeding areas. The total for these years was the average estimator weighted by the number of breeding pairs at each sub-colony or breeding area.

Year	Sub-colony	Breeding area	Estimation of crèche size	Mean number of chicks fledged per pair	Breeding success (%)
1992		La Banya	394	1.06	42
1993		La Banya	451	0.79	31
1994	Salinas 1	La Banya	0	0	0
	Maputo	La Banya	2	0.07	3
1994 total				0.003	0.1
1995	Juan Perro	La Banya	201	1.02	39
	Curroc	La Banya	124	1.25	48
1995 total				1.13	44
1996		La Banya	148	1.13	43
		La Tancada	24	0.05	2
1996 total				0.32	8
1997		La Banya	240	1.12	40
1998		La Banya	108	0.89	37
1999		La Tancada	372	0.87	35
2000		La Banya	76	0.33	13
		La Tancada	120	0.52	21
2000 total				0.43	17
2001	Baladres	La Tancada	64	0.56	27
		El Fangar	101	0.53	22
2001 total				0.54	25
Total 1992-2001				0.715	23.6

could be explained by differences in foraging habitats close to the breeding areas, rather than potential differences in phenotypic quality or age structure of birds breeding in different areas. Birds breeding at La Banya have faster and probably greater access to brackish ponds at the salinas and to trawlers from La Ràpita (see Fig. 1) (Oro 1999) than birds breeding at La Tancada.

Although breeding was highly synchronous (e.g., Cramp and Simmons 1983), data on egg size for clutches of three eggs suggested that among the females, those laying first are probably in the best body condition (see also Bolton *et al.* 1992). These females and their mates may be those that select the place for breeding, which changed from year to year owing to the high breeding site turnover rate in Slender-billed Gulls (see below).

When average clutch size during the study was compared with available results from other colonies (all very small), the results suggested two non-exclusive hypotheses: environmental conditions at the Ebro Delta are better than in these colonies or age structure is different among them. Egg size was also larger at the Ebro Delta (especially width and in turn egg volume), although available data from elsewhere were based on very small sample sizes (Cramp and Simmons 1983; Costa 1985; Dies and Dies 2000) (Table 6). The Ebro Delta has been described as a high quality environment owing to oceanographic features and the high availability of both foraging habitats and nest sites, which allow several seabird species to breed more successfully than in other colonies (see Oro 1999 and references therein). Moreover, a relatively large colony of Slender-billed Gulls, such as that at the Ebro Delta, enhances the social influences that may improve the reproductive performance.

Breeding Success

Breeding success varied markedly between years. Previous studies recorded that human activities, flooding and predators were the main causes of decreasing breeding success (see revision in Burger and Gochfeld [1996] and references therein). During the study, flooding occurred only in two sub-colonies with very low islets, although it affected only 2% and 4% of the nests. When colonies were abandoned, eggs were probably taken by Yellow-legged Gulls, which were observed attacking both nest contents and chicks at the crèche. However, predation was not high and breeding success at the Ebro Delta was higher than in colonies in western Africa (Gowthorpe 1979) or southern Spain (Costa 1985), and similar to that recorded in Valencia Albufera (Dies and Dies 2000) or the Black Sea (Cramp and Simmons 1983; Chernichko 1993). Where data for several years were available, breeding success in other colonies showed large fluctuations (e.g., Chernichko 1993; Dies and Dies 2000).

Colony Features and Population Dynamics

Several life-history traits recorded in this study seem to suggest that the ecology of the Slender-billed Gull is typical of a species reproducing in habitats where environmental conditions (probably related mainly to availability of food), vary with breeding seasons. Similar cases occur in other Laridae such as Gull-billed Tern (*Gelochelidon nilotica*) (Erwin *et al.* 1998) or Black-billed Gulls (*Larus bulleri*) (Evans 1982). However, little is known about the forces driving population dynamics in this species. Although the mean annual colony growth was 4%, some years have shown dramatic changes in breeding numbers. These sharp changes seem common for the species (e.g., Chernichko 1993; Isenmann and Goutner 1993), and are not probably the result of changes in survival (either adult or immature), productivity or local recruitment rates, but likely the result of two non-exclusive phenomenon; immigration-emigration processes between different colonies, and extensive and fluctuating numbers of non-breeding adults. The transfer of individuals is probably a behavioral response of individuals to spatial and temporal heterogeneity in environmental features and also indicates a high capability of dispersing between colonies. The relationship in changes of colony size between La Banya and La Tancada supports this at a smaller geographical scale. Several authors agree that the general increase at all the main colonies in the western Mediterranean (Camargue, Doñana, Po Delta, Valencia Albufera) during the last two decades has been the result of immigration from already established large colonies (e.g., Ferrer and Martínez-Vilalta 1986; Fasola *et al.* 1993; Sadoul 1997; Dies and Dies 2000). Moreover, few sites have been used more than once during the study (see also Schenk 1986; Fasola and Canova 1992; Chernichko 1993; Isenmann and Goutner 1993; Sadoul *et al.* 1996). Little is known about the factors influencing this high turnover rate, but the La Tancada breeding area was first used after 1994, when gulls at the three sub-colonies in La Banya failed to raise chicks. Breeding failure is one of the main factors driving dispersal of seabirds looking for more suitable places to breed in the future (e.g., Aebischer 1995; Oro *et al.* 1999). Another cause of breeding nomadism can be interspecific competition

Table 6. Available data on estimated egg size of Slender-billed Gulls in different colonies. Since no studies give the clutch size of the eggs measured during 1998-2000. Thus, the sample size refers to number of eggs measured.

Colony	Sample size	Length	SD	Width	SD
Ebro Delta (Spain)	589	53.94	2.26	38.41	1.20
Banc d'Arguin (Mauritania)[1]	NA	54	NA	39	NA
Doñana (Spain)[2]	33	54.3	1.86	37.9	2.12
Valencia Albufera (Spain)[3]	11	54.5	2.69	37.6	1.87

[1]Cramp and Simmons 1983.
[2]Costa 1985.
[3]Dies and Dies 2000.

for breeding space (e.g., Crawford *et al.* 1994; Sadoul *et al.* 1996) although further research is needed to assess this hypothesis.

During the study, most of the sub-colonies showed similar habitat features. First, they were established within salinas more frequently than expected, probably to have better access to Brine-Shrimps (mainly *Artemia salina*) growing in the salinas, one of the main foraging resources of the species (Burger and Gochfeld 1996). Second, most of the sub-colonies were placed very close to water (probably to increase protection against terrestrial predators), which probably determined the vegetation associated with these sub-colonies. Finally, Slender-billed Gulls were associated with Avocets and Sandwich Terns. Observations during the study suggested that Slender-billed Gulls chose to nest near colonies of Avocets which at that time of year were already established, probably taking advantage of their aggressive defense of their breeding areas against aerial predators. In contrast, Slender-billed Gulls normally preceded Sandwich Terns in selection of nesting areas and the latter probably searched for the protection supplied by Avocets and Slender-billed Gulls. Some abundant species were rarely associated; Little Terns probably avoided Slender-billed Gulls because of the gulls' kleptoparasitic behavior, whereas Black-headed Gulls mostly breed in fresh water lagoons at the Ebro Delta and were themselves kleptoparasites of, and even egg predators on, Slender-billed Gulls (D. Oro, pers. obs.). Slender-billed Gulls never bred associated with Yellow-legged Gulls, the largest and most aggressive gull species in the Delta. Similar results have also been recorded in the Po Delta (Fasola and Canova 1992; Fasola *et al.* 1993), in the Camargue (Sadoul *et al.* 1996) and in the Valencia Albufera (Dies and Dies 2000).

ACKNOWLEDGMENTS

This work would not had been possible with the invaluable help of Meritxell Genovart and Albert Bertolero in the field work. Many other people kindly helped in the field, especially David Bigas and Miquel Angel Franch. I also thank Diana Bowler for improving the English text, and John Coulson, Norman Ratcliffe and Nicolas Sadoul for helpful comments on the manuscript. I dedicate this work to Albert Martínez-Vilalta for his honest and professional defense of the conservation and research at the Ebro Delta during the years.

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