Factors Affecting Kleptoparasitism and Predation Rates upon a Colony of Audouin's Gull (*Larus audouinii*) by Yellow-legged Gulls (*Larus cachinnans*) in Spain

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Abstract.—We studied part of the world's largest breeding colony of Audouin's Gull (*Larus audouinii*) in the Ebro Delta, NE Spain, in 1992, to evaluate predation and kleptoparasitism effects by Yellow-legged Gulls (*Larus cachinnans*). Kleptoparasitic attacks were the most frequent kind of disturbance, concentrated during the period when Yellow-legged Gull chicks were being raised. This also coincided with a moratorium period for commercial fisheries when the food resource provided by fishing vessels was unavailable. More attacks occurred either early or late in the day when the Audouin's Gulls returned to the colony from feeding sites. The success rate was higher for long chases and for large parasitic groups of gulls. Subadult and adult Yellow-legged Gulls had similar kleptoparasitic success. Yellow-legged Gull predation on Audouin's Gull eggs and chicks was low and appeared not to affect the breeding performance of Audouin's Gull.

Resumen.—Durante la primavera de 1992, se describieron y analizaron las formas de agresión de la Gaviota Patiamarilla *Larus cachinnans* sobre la Gaviota de Audouin *Larus audouinii* en la colonia de cría del Delta del Ebro, NE de España, la más importante del mundo. Los ataques de kleptoparasitismo fueron la forma de agresión más frecuente, concentrándose durante el periodo de crecimiento de los pollos de Gaviota Patiamarilla y coincidiendo con una moratoria de veda de los barcos de pesca de la zona, cuando el recurso alimenticio que supone el pescado que descartan no estaba disponible. La frecuencia de ataques fue mayor a primeras y últimas horas del día, cuando las Gaviotas de Audouin regresaban a la colonia desde los lugares de alimentación. La tasa de éxito fue mayor para ataques prolongados y para grupos grandes de parásitos. Adultos y subadultos de Gaviota Patiamarilla mostraron tasas de éxito similares. La predación de Gaviota Patiamarilla sobre huevos o pollos de Gaviota de Audouin fue aún mas baja. *Received 26 May 1993, accepted 20 January 1994.*

Key words.—Ebro Delta, kleptoparasitism, *Larus audouinii*, *Larus cachinnans*, predation, Spain.

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Gulls are highly gregarious birds, breeding in large, dense colonies and feeding in large flocks. They experience a wide range of intra- and interspecific relationships, especially during the breeding season when species select the same habitat and share available colony space with many other species (Burger 1979, Burger 1985, Vermeer *et al.* 1992).

Dominance interactions are usually directed from larger, more aggressive species to smaller species. Some well-documented types of aggression are kleptoparasitism (e.g., Källander 1977, Brockmann and Barnard 1979, Barnard and Thompson 1985) and predation upon eggs, chicks, or even adults (Southern and Southern 1984, Bradley 1986, Velarde 1992). Audouin's Gull (*Larus audouinii*) and the Yellow-legged Gull (*L. cachinnans*) are two sympatric species in the Mediterranean region (Cramp and Simmons 1983), differing considerably with regard to population status, feeding ecology, and movements. Whereas the Yellow-legged Gull is abundant and widespread throughout the Mediterranean region, the Audouin's Gull is an endangered species, considered rare on the ICBP (International Council for Bird Preservation) World Check-List of Threatened Birds (Collar and Andrew 1988). Yellow-legged Gull colonies occur at all sites of Audouin's Gull nesting (Witt 1977, Bradley 1986), but only at the colony in the Chafarinas Islands (SE Spain) have studies demonstrated the damage caused by predation on eggs and chicks by the large, aggressive Yellow-legged Gull upon the Audouin's Gull colony (Bradley 1986). The kleptoparasitic behavior of Yellow-legged Gull on Audouin's Gull has also been reported in the Chafarinas Islands (Witt *et al.* 1981), but the importance of this behavior is still not quantified.

During the 1992 breeding season, we recorded the kleptoparasitism and predation by Yellow-legged Gulls towards Au-

douin's Gulls breeding in a colony in the Ebro Delta, Spain to determine whether they affected the reproductive success of Audouin's Gulls.

STUDY AREA AND METHODS

The study was conducted in the Ebro Delta (Parc Natural del Delta de l'Ebre, NE Spain). Audouin's Gull colonized the Ebro Delta in 1981. Since then, the growth of the colony has been constant and it now contains roughly 60% of the total world population, almost 7000 pairs (Oro and Martinez 1992). The Audouin's Gull colony is located in a 2500 ha peninsula distinguished by a mosaic of salt marsh and halophytic vegetation. Other species breeding here are Gull-billed Tern (*Gelochelidon nilotica*), Sandwich Tern (*Sterna sandvicensis*), Little Tern (*S. albifrons*), Common Tern (*S. hirundo*), and four other species of gull: Black-headed Gull (*L. ridibundus*), Slender-billed Gull (*L. genei*), Lesser Black-backed Gull (*L. fuscus*) and a colony of 1100 pairs of Yellow-legged Gull.

Observations were conducted by the same observer on 37 days between the beginning of April and the end of June in 1992 in a subcolony of 160 pairs. The subcolony was watched from dawn to sunset from an observation point 150 m away using 8×40 binoculars. For analyses, we grouped the samples into three groups of equal observation effort: early (0700-1100 h), middle (1200-1700 h) and late (1800-2100 h). Total observation time was 333 h, divided equally among the three months of the study.

During each observation period, we recorded the number of Audouin's Gulls arriving at the colony and two types of interspecific interactions with Yellow-legged Gulls, kleptoparasitic (including the attacks which ended with the death of the gull) and predation upon eggs and chicks of Audouin's Gulls. The data set included: time of day, stage of Audouin's and Yellow-legged Gulls breeding cycle, number of Yellow-legged Gulls involved in the attack (recording when possible the identity of the successful gull that obtained the food), age of the aggressors (adults (> 4 yrs) or subadults (2-4 yrs)), and duration of attack and its outcome. The criterion of success depended on the type of attack. For kleptoparasitism, it was the regurgitation of food by the host; for predation, the death of chicks or the destruction of eggs. Predation upon nests was recorded only for the subcolony, whereas the records of kleptoparasitism included all Audouin's Gulls crossing the observation point and arriving in the colony. For the nest predation records, we considered only the period beginning with the egg-laying stage of Audouin's Gulls. The relationships between success rates and duration of the chase, group size, and number of gulls arriving were examined using a Spearmann rank correlation test.

Data were collected during all stages of the breeding cycle of Audouin's Gull: nest building (4-6 May), egg laying (14-16 May), incubation (18-20 May), chick hatching (9-11 June) and pre-fledging (26-28 June). We also sampled during the main breeding stages for the Yellow-legged Gull: egg-laying (29-31 March), incubation (5-7 April), chick hatching (25-27 April), pre-fledging (13-15 May) and fledging of the juveniles (1-3 June). These periods were defined as the day when the modal number of nesting pairs in the subcolony had entered that stage, including ± 1 d.

We used two indices for the frequency of kleptoparasitic chases: the number of attacks per hour and the number of attacks per 1000 Audouin's Gulls crossing the observation point per hour, because the number of gulls arriving in the colony varied with time of day. Differences in frequency of attack and success rates between reproductive stages and between hours of day were analyzed by Chi-square tests. For some analyses, we formed two groups of data; the first from April to May, while the second to June. We divided the season because of a fishing moratorium imposed on the local inshore fleet during April and May which seemed to change the feeding behavior of the gulls (Paterson *et al.* 1992, Oro and Martinez 1992).

RESULTS

We recorded a total of 221 attacks by Yellow-legged Gulls on Audouin's Gulls of which 213 (96.4%) were kleptoparasitic (Table 1). Of the 213 kleptoparasitic chases, seven adult Audouin's Gulls were killed. Eight predation attempts upon nests were recorded inside the subcolony (3.6%), only two of which were successful (Table 1). All attacks observed were upon nests with eggs and no attempt at chick predation was seen.

The number of attacks on Audouin's Gull arriving in the colony was significantly higher during early and late periods in the day ($\chi^2=30.9$, d.f.=2, $P<0.001$). However, considering that the number of Audouin's Gulls returning to the colony changed with the time of day, the conformity test between the observed attacks and the expected attacks in relation to the number of Audouin's Gulls returning to the colony showed that the number of attacks did not differ significantly among the three periods of time considered ($\chi^2=1.16$, d.f.=2, $P=0.5$). Moreover, the number of attacks on Audouin's Gulls was higher during the moratorium than during the fishing season ($\chi^2=28.4$, d.f.=3, $P<0.001$, Fig. 1). No more than three attacks were ever recorded in any one hour.

The mean success rate of kleptoparasitic attacks was high (40.8%), with no difference detected in the number of attacks observed for the three periods of the day considered ($\chi^2=0.14$, d.f.=2, $P=0.9$). In all successful attacks, only one bird of the attacking group obtained the food.

The number of attacks and their success rates are expressed as a function of the duration of the chase (Fig. 2A) and

Table 1. Details of kleptoparasitism and predation on Audouin's Gulls by Yellow-legged Gulls.

Parameters	Time[1] Early	Mid	Late	Total
Kleptoparasitism:				
No. of hours sampled	111	111	111	333
No. of attacks	119	28	66	213
Attacks/hour ($\bar{X} \pm SD$)	107 ± 0.93	0.3 ± 0.4	0.55 ± 0.72	0.73 ± 0.63
Successful events (%)	47 (39)	11 (39)	29 (44)	87 (41)
No. of Audouin's Gulls arriving ($x10^3$)	32.9	6.6	14.5	53.9
Attacks/1000 birds	3.01	0.67	4.07	2.58
Nest predation[2]:				
No. of hours sampled	72	72	72	216
No. of attacks	2	6	0	8
Successful events (%)	1 (50)	1 (17)	0	2 (25)

[1]Early = 0700-1100 h; mid = 1200-1700 h; late = 1800-2100 h.
[2]Based on study of a 160-pair subcolony.

Yellow-legged Gull group size (Fig. 2B). Success rate increased with both the duration of the attack (Spearmann rank test r_s=0.980, N=16, P<0.01) and group size (r_s=0.803, N=16, P<0.01). Of 60 successful attacks by groups of Yellow-legged Gulls, we were able to identify the bird who benefited from the stolen food on 14 occasions. In only two cases (14.3%) was this the initiator of the chase.

Of 746 Yellow-legged Gulls observed participating in kleptoparasitic attacks, 21.1% were subadults. We found no difference between the success rates of adult and subadult attacks (χ^2=0.22, d.f.=1, P=0.6). Mixed-age groups were not considered.

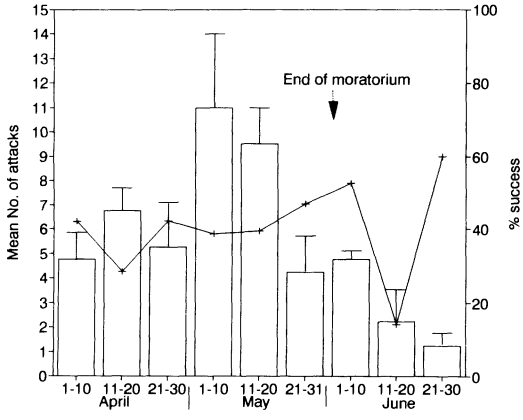

Figure 1. Mean number of attacks (bars showing ± 1SD) and success rates (line) depending on the fishing moratorium period (the arrow shows the end of May).

The frequency of attacks differed significantly between the different breeding stages of Audouin's Gull (χ^2=22.84, d.f.=4, P<0.001) and the Yellow-legged Gull (χ^2=10.47, d.f.=4, P<0.05) (Table 2).

The kleptoparasitic attacks were concentrated on Audouin's Gulls returning to the colony and so was correlated with the number of arriving gulls (r_s=0.81, N=9, P<0.01, Fig. 3). The number of both attacks and number of Audouin's Gulls departing to feeding sites was not significantly correlated (r_s=-0.20, N=9, P>0.10, Fig. 3).

DISCUSSION

Although other studies have demonstrated that food obtained by kleptoparasitism constitutes a significant proportion of the diet of some species of gulls (Hatch 1970, Fuchs 1977, Barnard and Thompson 1985) low rates of kleptoparasitism and predation were recorded at the Ebro Delta (Table 1). Predation by Yellow-legged Gulls on Audouin's Gull eggs was low and predation on chicks was not detected, unlike the situation in the Chafarinas Islands. Bradley (1986) recorded different rates of Audouin's Gull chicks killed by Yellow-legged Gulls depending on the habitat characteristics of the colony and nest density. Predation rates of chicks killed at the Chafarinas Islands were higher with lower nesting densities (2.3 nests/3 m radius), reaching 64% of the total chick mortality

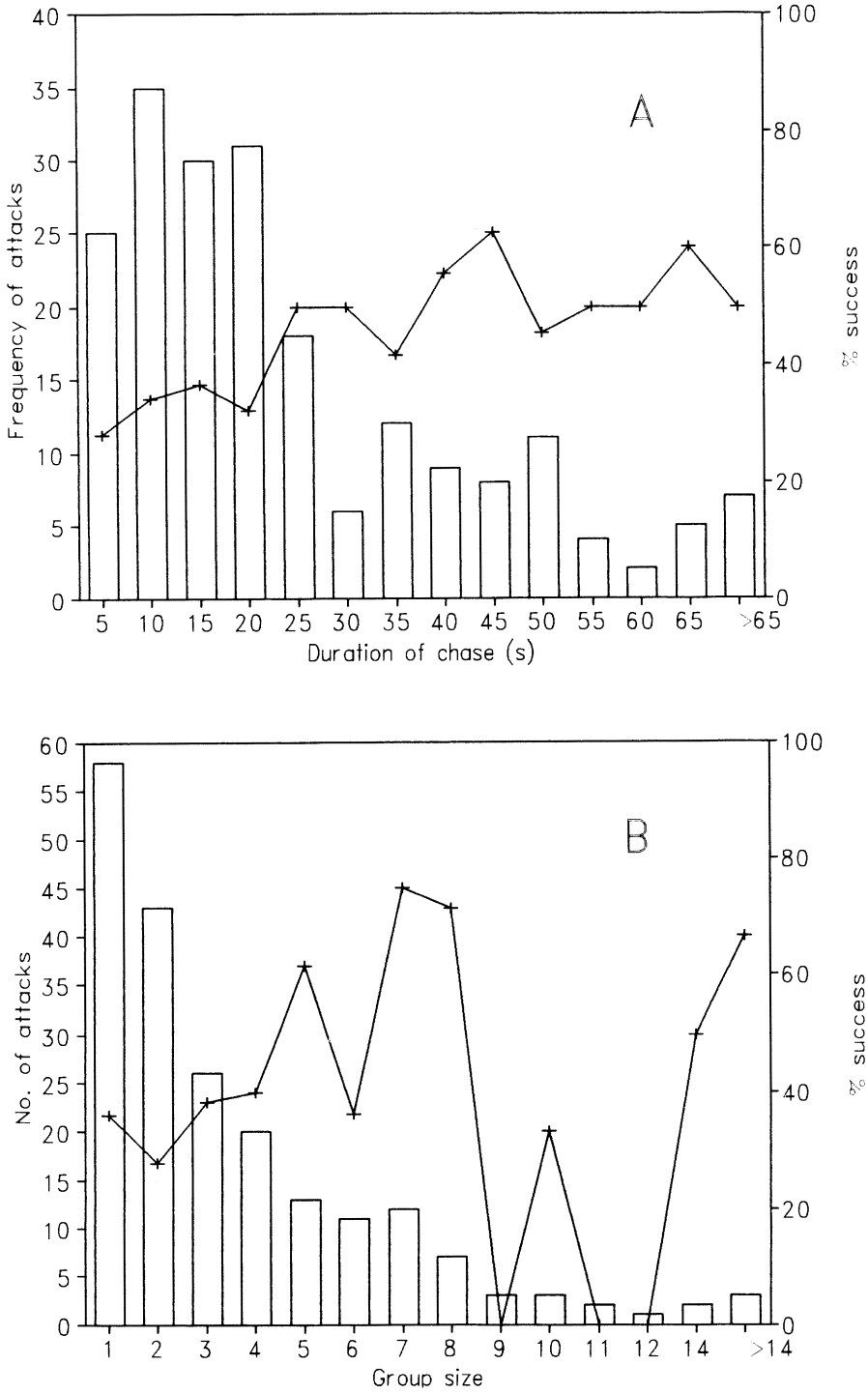

Figure 2. Frequency of attacks (bars) and success rates (line) as a function of the (A) duration of the chase and (B) size of the piratic Yellow-legged Gull groups.

in one breeding season (N=58)(Bradley 1986). In the subcolony study at the Ebro Delta, a lower density of nests was recorded (1.9 ± 0.3 nests/3 m radius) and so one might expect higher predation on Audouin's Gull chicks. The availability of

Table 2. Kleptoparasitic and predation parameters related to the reproductive stages of Audouin's Gulls and Yellow-legged Gulls.

	Period[1]					
	NB	EL	IN	CH	PF	FL
Audouin's Gull:						
Modal date	5 May	15 May	19 May	10 June	27 June	-
No. of attacks received	7	19	27	11	6	-
Attacks/hour	0.24	0.65	1.0	0.38	0.20	-
Yellow-legged Gulls:						
Modal date	-	30 March	6 April	26 April	14 May	2 June
No. of attacks initiated	-	7	8	18	18	9
Attacks/hour	-	0.24	0.27	0.62	0.62	0.31

[1]Periods: NB= nest building; EL= egg laying; IN= incubation; CH= chick hatching; PF= pre-fledging; FL= fledging.

food from refuse tips and offal from fishing vessels (Ruiz *et al.* in press) could explain the low predation rates by Yellow-legged Gulls.

Indeed, the frequency of kleptoparasitism was higher during the moratorium season and differed significantly between the breeding periods of the two species of gull. Such an increase in attacks when the local fleet was inactive (Fig. 1) coincided with chick hatching and early growth stages of Yellow-legged Gull chicks (Table 2), i.e., the period of highest energy demand by chicks. This may be a period of food short-

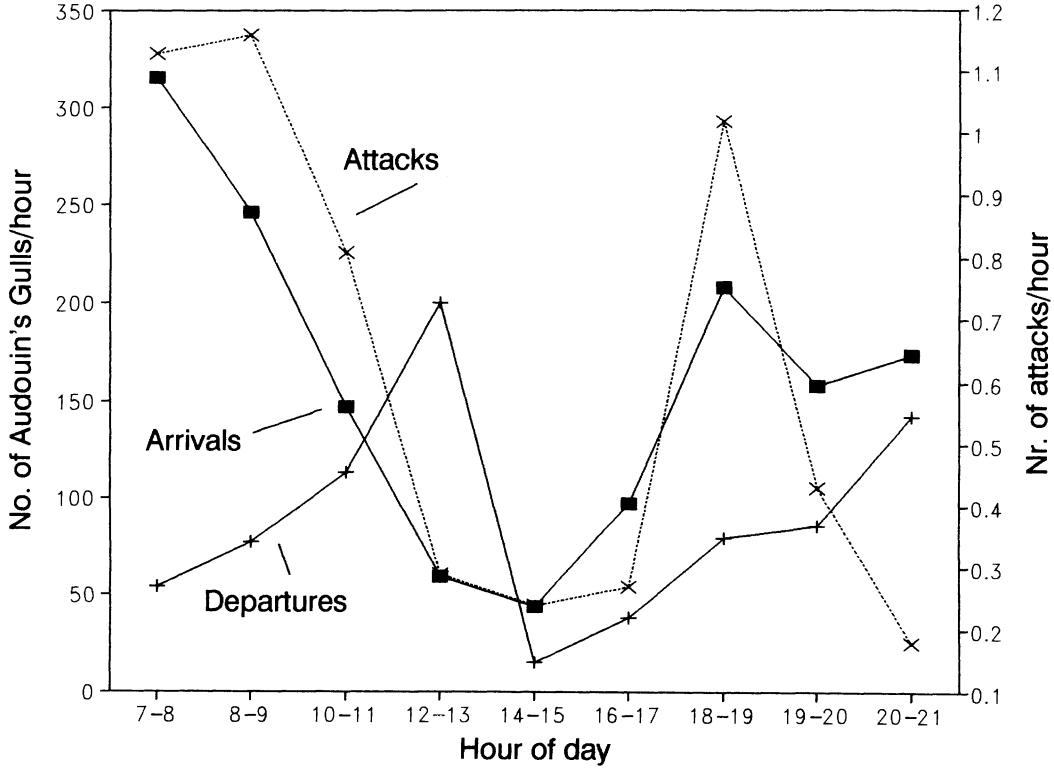

Figure 3. Mean frequency of Yellow-legged Gull attacks and mean frequency of Audouin's Gull arrivals and departures at the Ebro Delta colony.

age for breeding Yellow-legged Gulls that forces them to increase the number of kleptoparasitic attacks. The maximum attack rates also coincided with the egg-laying stage of Audouin's Gull (Table 2) but this may not have affected piracy rates. If the frequency of attacks depended on the breeding cycle of Audouin's Gull, maximum rates would be expected at chick hatching and the first stages of chick growth, when the arrival rates of adults feeding chicks are highest.

Kleptoparasitism by Yellow-legged Gulls on Audouin's Gulls was more common than predation on nests. The success rate of kleptoparasitic attacks was high (>20%) as in other gulls (Hatch 1970, 1975, Fuchs 1977, Verbeek 1977, Amat and Aguilera 1990). This contrasts with lower success rates for intraspecific piracy in gulls (Hockey *et al.* 1989) and for certain kleptoparasitic specialists such as frigatebirds (*Fregata* spp.) (Diamond 1975, Osorno *et al.* 1992). High success rates combined with low frequencies of attack suggests that some individual Yellow-legged Gulls may specialize in kleptoparasitism. Negro *et al.* (1992), studying kleptoparasitism in the Lesser Kestrel (*Falco naumanni*) found that some individuals specialized as kleptoparasites (see also review in Brockmann and Barnard 1979).

The success rate was higher for larger groups of Yellow-legged Gulls and also increased with the length of chases (Figs. 2A and 2B). However, duration of chases and group size were intercorrelated because attacks were commonly initiated by one or two gulls, who were then followed within moments by a number of others. In these cases, the initiators did not normally benefit from the regurgitated food. When gulls kleptoparasitize waders or terns, successful chases tend to be shorter than unsuccessful ones unlike the situation in the Ebro Delta, where the physical abilities of pirate and host are probably more similar. Therefore, kleptoparasitic success also depends on the flight speed and agility of the host. The success rates of adults and subadults (most of them nonbreeders) did not differ significantly, in contrast with the results recorded by Burger and Gochfeld (1981) for four species of gulls. At the breeding colony, we did not observe Yellow-legged Gulls younger than second year attacking Audouin's Gulls or joining chase groups.

Yellow-legged Gulls patrolled for incoming hosts by flying around the perimeter of the colony. Pirates concentrated on Audouin's Gulls returning to the colony (Fig. 3) probably because they were returning from feeding places and were likely to be carrying food. Evasive behaviors used by Audouin's Gulls were flying fast and dodging the pirate. There was a correlation between long chases and predation, and the fatigue of the host could facilitate the predation by the pirate. In all these cases (N=7, 3.2% of total attacks), the host did not regurgitate food. This fact suggests that the parasite would be not always able to distinguish whether the Audouin's Gulls were carrying food or not, as in other hosts (e.g., terns (Fuchs 1977) or lapwings (Källander 1977)). We assume that the goal of the parasite is the regurgitated food and not the predation of the host. At the same time, it is not clear whether the parasites could know the physical condition of the host and predation probably started as a kleptoparasitic attack. Brockmann and Barnard (1979) suggest that visible food is one factor that could make kleptoparasitism a more profitable strategy, although skuas and other specialist kleptoparasites may be able to distinguish profitable and non-profitable hosts (Furness 1987).

How the food stolen from the Audouin's Gulls and the predation upon nests influences their breeding success is still unknown. However, the low rates of predation and kleptoparasitism recorded and other indirect evidence, such as the dramatic growth of the Audouin's Gull colony in relation to the Yellow-legged Gull colony growth or the high Audouin's Gull breeding success at the Ebro Delta (Oro and Martinez 1992), suggest a low negative effect upon this species. In contrast to several colonies, where culling has been practiced to control the Yellow-legged Gull population, at the Ebro Delta colony no intervention of any kind has taken place. Such actions to control the Yellow-legged Gull populations should be used only on a case by case basis.

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