

Daniel Oro · Roger Pradel · Jean-Dominique Lebreton

Food availability and nest predation influence life history traits in Audouin's gull, *Larus audouinii*

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Abstract The effects of food availability and nest predation on several life history traits such as adult survival, dispersal, and reproductive performance were assessed in an Audouin's gull (*Larus audouinii*) colony during the period 1992–1997. The amounts of fish discarded from trawlers were used as a measure of food availability, and a trawling moratorium which partially overlapped with the breeding season of the gulls was taken into account. The effects of nest predation were assessed in 1994, when a terrestrial predator entered the colony and remained for the whole breeding season preying on both eggs and chicks. Using the moratorium and the predatory event as natural experiments, several hypotheses were tested: (a) food supply would affect breeding performance but not adult survival (independently of age and sex), since gulls are long-lived and adult survival is the most sensitive demographic parameter in their population dynamics; (b) the predator would trigger breeding dispersal (although gulls are mostly philopatric, they are known to abandon their natal colony after breeding failure instigated by events such as this). If breeding dispersal occurs, the rate is expected to be higher in females than in males, and higher in new breeders than in more experienced breeding birds, as is usually recorded in colonial seabirds. Probabilities of resighting and survival were estimated separately, using capture-recapture models. As expected, changes in food availability did not affect adult survival, whereas they influenced egg volume,

clutch size, and breeding success. Local adult survival was estimated to be 0.908 (SD = 0.007) for males and females, and it did not change significantly with the age of individuals (range 3–8 years). The predator significantly decreased breeding success, and caused the dispersal of a number of adults probably to breed in another colony; this rate was estimated at an average of 0.10 (SD = 0.02). As expected, inexperienced breeders dispersed significantly more (14%) than more experienced breeders (8%) after the predator event, but dispersal was not sex biased. Recapture probabilities after the predator event suggest that birds that left the colony still had not returned. Results confirm that population dynamics of ground-nesting seabirds are sensitive to terrestrial predation, even when predation caused only a partial breeding failure.

Key words Adult survival · Breeding dispersal · Population dynamics · Reproductive performance

Introduction

Breeding success (number of offspring per female) and survival are two of the most important life history traits in organisms. Species differ in the manner that these two traits combine to optimize fitness (Stearns 1992). Environmental conditions may influence these traits, and they are not to be considered constant in the real world (Benton and Grant 1996; McNamara and Houston 1996). As such, variations in food availability and nest predation rates may affect reproductive strategies in birds and the evolution of avian life histories (Martin 1987, 1995; Sæther 1996). In long-lived species such as seabirds, the theory of life history evolution predicts that a deterioration in environmental conditions, for example a decrease in food availability, would affect fecundity before survival (Stearns 1976). Although it is well known that food supply affects reproduction and population dynamics of seabirds (Hamer et al. 1991; Spaans 1971;

D. Oro (✉) · R. Pradel · J.-D. Lebreton
Centre d'Ecologie Fonctionnelle et Evolutive, CNRS,
1919 route de Mende, F-34293 Montpellier cedex 5, France

Present address:

D. Oro
Dept. Biologia Animal, Vertebrats, Universitat de Barcelona,
Diagonal 645, E-08028 Barcelona, Spain
e-mail: daniel@porthos.bio.ub.es

Division of Environmental and Evolutionary Biology,
Graham Kerr Building, University of Glasgow,
Glasgow G12 8QQ, UK

Sydeman et al. 1991; Monaghan et al. 1992; Oro et al. 1996a; Phillips et al. 1996), only Pons and Migot (1995) have tested this prediction by assessing its influence simultaneously on breeding parameters and adult survival. In relation to nest predation, studies have concentrated on short-lived species such as passerines (e.g., Martin 1993; Sæther 1996), demonstrating that higher adult survival and lower fecundity are associated with nests that are better protected against predation. However, the effects of nest predation in the evolution of life histories in colonial seabirds are slightly different (Clode 1993). Coloniality in birds appears to be highly correlated with exposure of nests to predators (see also Rolland et al. 1998). Seabirds breed mostly in colonies, and colonial nesting seems to lead to increased vulnerability to predation. Seabird colonies seem to be able to sustain predation by conspecifics (i.e., cannibalism) or other avian species, such as raptors or other seabirds (e.g., skuas, large gulls), whereas they seem very sensitive to terrestrial predation (Croxall and Rothery 1991). Thus, colonies are normally placed in sites protected against terrestrial predators such as mammalian carnivores, although many cases of predation have been reported (e.g., Southern et al. 1985; Bloomer and Bester 1992; Burness and Morris 1993; Hartman et al. 1997). However, little is known about the effects of such predation on demographic parameters or the population dynamics of the colonies affected (Côté and Sutherland 1997).

Audouin's gull *Larus audouinii* is a medium-size gull species (average weight 570 g), and is monogamous, with a modal clutch size of three eggs (for details see Oro 1998). The species is an endangered endemic seabird of the Mediterranean region, and it was considered to be threatened with extinction in the late 1960s (600–800 pairs; de Juana et al. 1984). It is still considered endangered (Tucker and Heath 1995), although the establishment in 1981 of a new colony in the Ebro Delta (northwestern Mediterranean) has dramatically increased the total number of breeding pairs, estimated at about 16,000 pairs in 1996 (D. Oro, unpublished data). Although Audouin's gulls are specialist foragers taking clupeoids during the night, at this colony they largely exploit discards from trawler fisheries, probably because discarded fish represent a very predictable foraging resource in both space and time (Oro 1995; Oro and Ruiz 1997; Oro et al. 1997). However, since 1991, a trawling moratorium that overlaps with the breeding season of Audouin's gull has affected its breeding and feeding ecology (Oro et al. 1996a,b). Fish availability in the Mediterranean sea has decreased in the last few decades as a consequence of overfishing (Palomera 1992; Safina 1995; Leonart and Recasens 1996) and, in turn, dependence of Audouin's gull on trawler discards has probably increased. In this study, the trawling moratorium has been used as a natural experiment to assess the influence of different levels of food supply (as changes in trawler discard availability; see Oro and Ruiz 1997) on several life history traits in Audouin's gull such as adult survival and breeding performance. We first tested the

hypothesis that food supply would affect breeding performance but not adult survival, since gulls are long lived and adult survival is the most sensitive demographic parameter in their population dynamics (Stearns 1992). If we assume that costs of reproduction are similar for both sexes and independent of their age, as recorded for other gull species (e.g., Pons and Migot 1995; Pugsek et al. 1995; Rattiste and Lilleht 1995; Prévot-Julliard 1996; Wanless et al. 1996), adult survival is expected to be constant with age (before the effects of senescence for the oldest ages) and sex (although see Aebischer and Coulson 1990; Pugsek and Diem 1990; Pyle et al. 1997).

The presence of a European badger *Meles meles* that remained in the colony during one of the field seasons was used as a second natural experiment to assess the effects of nest predation on breeding performance and breeding dispersal in Audouin's gull. Audouin's gull breeding colonies are located mostly on islets where there are no terrestrial predators. However, the Ebro Delta colony is not totally isolated from the mainland (see below) and is accessible to terrestrial predators. We expected that the badger would prey freely on nests (both eggs and chicks) negatively affecting some breeding parameters (such as clutch size and breeding success), since gulls have no effective mechanisms of defense against terrestrial predators. If predation occurred, it would trigger breeding dispersal, since gulls, despite being mainly philopatric, are known to abandon their natal colony after breeding failures instigated by events such as this (Greenwood and Harvey 1982; Birkhead and Furness 1985; Croxall and Rothery 1991; Cairns 1992). We also expected that dispersal would be higher in new breeders than in more experienced breeding birds, which have had more opportunities at the site to assess its suitability (Parsons and Ducan 1978; Coulson and Néve de Mévergnies 1992; Danchin and Monnat 1992). Finally, as recorded in other colonial seabirds, we tested the prediction that if dispersal occurs, it would be higher in females than in males (Greenwood and Harvey 1982; Clarke et al. 1997).

Methods

Study area and the trawling moratorium

Data were collected between 1992 and 1997 in a colony of Audouin's gull nesting on the Punta de la Banya (Ebro Delta Natural Park, NE Spain: 40°37'N, 00°35'E). The colony holds 75% of the total world population, and since its establishment in 1981 has increased at an average 64% growth rate (Oro 1998). The habitat is a flat sandy saltmarsh of 2500 ha with several dunes covered by halophilous vegetation, where the gulls breed (hereafter called subcolonies). This is the only colony of Audouin's gull located on the mainland, although the site is a peninsula connected to the rest of the delta by a narrow sand bar 9 km long. Thus, about 90% of the perimeter of the peninsula is surrounded by the sea. Normally, no terrestrial predators are present in the colony (see below for details about the entry of a badger in 1994), and only yellow-legged gulls *L. cachinnans* prey regularly upon Audouin's gulls, both adults and nest contents.

A trawling moratorium was established from 1991 to allow the fish populations to recover from trawler overfishing, although the situation was far from collapse (Alvarez 1990). The moratorium affected an area extending 220 km along the coast out to the limit of the continental shelf (60 km) (see Oro et al. 1996b for more details). The moratorium operated each year for 2 months, always during the breeding season of Audouin's gulls. In some years, the moratorium overlapped with the laying stage of the gulls (April–May), in others with the incubation and first weeks of the chick-rearing stage (May–June), and in others only with the chick-rearing stage (June–July). Discard availability was estimated using statistics of fish catches from fishermen's guild bulletins, since the amounts of fish discarded are highly correlated with the size of commercial catches (Oro and Ruiz 1997).

Collection of data

Adult survival of Audouin's gull in this colony (i.e., local annual adult survival) was estimated by mark-recapture (Lebreton et al. 1992, 1993). Fledglings have been ringed since 1988 with an engraved plastic ring carrying a unique three digit code (Oro and Martinez 1994). From 1988 to 1994, 4595 chicks were ringed in the colony (range = 360–1035 each year). The year of resighting indicated the age of the individual, enabling assessment of the effect of age on survival. From 1992 to 1997, ringed gulls were resighted in the colony during the breeding season (from March to July), using a telescope from a distance up to 150 m. From the overall 11,032 resightings, we excluded (a) resightings of the same rings in the same breeding season, (b) immature birds (less than 3 years old; Oro and Martinez 1994), and (c) birds ringed in other colonies (because only local adult survival was estimated). This left resightings of 2191 adult individuals which could be treated as recapture data (Lebreton et al. 1992). Copulatory and courtship feeding behavior was recorded whenever possible to sex some individuals: in total, 142 gulls were identified as males and 170 as females, and they were used to assess the effect of sex on survival. To limit confusion between death and permanent emigration (i.e., birds leaving the colony permanently, which are considered dead), the first resighting as a breeder at the Ebro Delta was considered as its initial capture (Pradel et al. 1997). The number of visits to the different subcolonies varied according to their size (i.e., the number of pairs in each subcolony) to distribute the effort of reading rings uniformly through the colony and thus limit heterogeneity in resighting probabilities (Prévot-Julliard 1996; Pradel et al. 1997). In all years, all subcolonies were checked for ringed birds.

In 1994, a badger entered the colony probably via the sandy bar connecting the peninsula to the mainland. The presence and movements of the badger throughout the colony were easily detected by its tracks in the sand, which were checked daily from March to July. The badger was first detected in mid March, 4 weeks before Audouin's gull started to lay; it stayed constantly in the area until mid July, after the chicks fledged. The daily surveys of the tracks and food remains allowed us to assess whether the badger preyed only on eggs and chicks, or on adults as well.

Modeling adult survival

Adult survival rate was estimated using techniques of mark-recapture analyses (Lebreton et al. 1992, 1993). To model survival probabilities in relation to related biological assumptions, the procedures and notations of Lebreton et al. (1992) were followed. We started from the CJS model (ϕ_t, p_t), where ϕ is the local survival rate, p is recapture probability (i.e., resighting) and t is time. The fit of this model was assessed by means of a goodness-of-fit test (GOF) using the program RELEASE (Burnham et al. 1987): the component tests within TEST2 and TEST3 were examined to identify the nature of the violation (see Burnham et al. 1987; Pradel et al. 1997). Since the initial CJS model did not fit the data (TEST2 + TEST3 was significant on one occasion, corresponding to 1994; see Results), the presence of transients (i.e., emigrants; see

Pradel et al. 1997) was assessed by estimating the parameter following the procedures of Pradel et al. (1997): $\tau(\omega, e)$ was the probability that an unmarked animal ω captured at e was a transient (we noted this probability as τ^{badger} , or τ^b , since we assumed that the transient effect was caused by the badger). Estimators of τ^b were calculated as:

$$\tau^b(\omega, e) = 1 - \frac{\phi^*(\omega, e)}{\phi(\omega, e)},$$

where $\phi^*(\omega, e)$ was the initial survival rate for transients, and $\phi(\omega, e)$ that for residents.

Additional models with a transient effect [denoted (τ^b, ϕ, p), see notation in Pradel et al. 1997] were then constructed, which were fitted by the maximum-likelihood method using the program SURGE 4.2 (Cooch et al. 1996). The model with the lowest value of the Akaike information criterion (AIC) was accepted as the most parsimonious model (Lebreton et al. 1992; Anderson et al. 1994). Models were then constrained by ecological hypotheses based on factors that, in our view, could affect transience, survival or capture probabilities (Table 1). The possibility that discard availability affected survival rates was also considered in the models as a logit-linear constraint (Lebreton et al. 1992). Different models included variation in the parameters as a function of year, sex, and age (birds from 3 to 8 years old), and the badger effect, expressed as different survival and capture rates in the year that the predator entered the colony. Unsexed birds were considered as a mixture in roughly equal proportions of males and females. This was achieved by coding the covariate sex as 0 for females, 1 for males, and 0.5 for unknown-sex individuals. The τ parameter was also constrained with some other ratios between sexes (i.e., 0.4 and 0.6) to check for a sex ratio different from 0.5. For age, two age classes were considered to achieve a reasonable sample size in each category: animals reobserved for the first time at 3 or 4 years old (age class 1), and birds 5–8 years old (age class 2). To estimate capture probability, several models were also constructed to allow for the different resighting effort made each year, measured as the number of hours spent at the colony reading rings.

Breeding parameters

From 1992 to 1997, clutch size and egg volume were recorded in a number of nests checked daily on a linear transect selected randomly in the colony (Oro et al. 1996a). On the day of laying, each

Table 1 Summary of the different (τ, ϕ, p) models built with SURGE to estimate the proportion of birds among unmarked birds that emigrated after the predator event (τ^b), survival probability (ϕ), and capture probability (p)

Model notation	Biological hypothesis
Modeling τ^b	
τ^b	Constant
τ_a^b	Dependent on two age class: ≤ 4 years (3 + 4 years) and older birds
τ_s^b	Sex dependent [unknown sex: specifically $\log \tau = (\log \tau_{\text{males}} + \log \tau_{\text{females}})/2$]
$\tau_{a* s}^b$	Age dependent for every sex (unknown sex as above within each age class)
$\tau_{a+ s}^b$	Age dependent with an additive effect of sex (unknown sex as above)
Modeling ϕ	
ϕ_t	Survival is time dependent
ϕ	Constant survival
ϕ_e	Survival is dependent on availability of trawler discards
Modeling p	
p_t	Recapture is time dependent
p_e	Recapture is dependent on effort of resightings (number of hours sampled)

egg was measured with callipers (length and maximum width to ± 0.1 mm). The number of nests checked was 107 in 1992, 211 in 1993, 216 in 1994, 182 in 1995, 68 in 1996, and 140 in 1997. Each year, two fence enclosures surrounding about 80 nests were also used to record the number of chicks fledged per pair as a measure of breeding success. The fences were built before the hatching period, and the number of nests within the fences was counted. During the hatching period, the fences were visited at 2-day intervals until all fertile eggs had hatched. Before the fledging period, the number of fledglings within the fence was counted and the breeding success was obtained as the average number of chicks fledged per pair. We assessed the relationship between discard availability (see above) and (a) average volume in a clutch and volume of the first egg, since they are good estimators of physiological body condition of females (Ruiz et al. 1996), (b) clutch size and (c) breeding success. To analyze the correlation between breeding parameters and food availability, the fishery catches of April (just before laying) were used for egg parameters and clutch size, while the catches of April, May, and June were summed to analyze the relationship between food supply and breeding success. Data on clutch size and breeding success collected in 1991 using the same methodology were also included in the analysis (Oro 1998). Two-tailed Spearman rank correlations were carried out using program SPSS v6.1.2.

To assess the effects of the badger predation in 1994, a specific approach was used. Since nest content was recorded while the census of the number of nests was performed (ca 10 days before hatching), we were able to compare clutch size (as number of eggs not predated in a nest) in subcolonies the badger had not yet entered with subcolonies in which the badger had already preyed on some nests. The number of broken eggs was recorded during the nest census and one nest was considered predated when at least one egg was broken, to estimate a minimum number of nests predated. Eggs predated by yellow-legged gulls were differentiated from those predated by the badger since the badger always broke the eggs totally, whereas yellow-legged gulls just make a hole to feed on the egg content. Thus, we only considered eggs predated only by the badger, although this rate was probably underestimated since many eggs were probably predated opportunistically by yellow-legged gulls after being deserted. In relation to the breeding success, the results between two fences were compared, one predated and the other not predated by the badger. Nests at both fences initiated the clutches at approximately the same time (median hatching date in the two fences: 25 May and 26 May). Likelihood ratio (*G*-test) and chi-square tests were used to compare clutch size and breeding success between predated and nonpredated subcolonies.

Results

Adult survival

Program RELEASE showed that the CJS model (ϕ_t, p_t) did not fit our data (TEST2+TEST3: $\chi^2_{20} = 49.52$, $P = 0.003$). However, all the discrepancy lay in only one component, namely the 2×2 contingency table which compared the fate of animals captured in 1994 depending on whether they were already marked and seen again after 1994. We interpreted this result as emigration of birds new to the colony in 1994 as a consequence of predation by the badger in that year. Including a proportion of emigrating birds among those captured in 1994 and previously unmarked led to an acceptable model (GOF test: $\chi^2_{18} = 25.28$, $P = 0.117$). This model, denoted as (τ^b, ϕ_t, p_t), was used as a starting point for model selection with SURGE.

If birds that had already bred in this colony had also emigrated as a consequence of predation by the badger, the survival of birds marked previously from 1994 to 1995 should have been lower than in other years [model (τ^b, ϕ_t, p_t)]. In fact, the estimate of survival in that year was one of the highest recorded [estimate (SD) = 0.92 (0.02)]. We thus considered that experienced birds within the colony were not affected, with constant survival in all years [model (τ^b, ϕ, p_t)]. This model showed the lowest AIC value (see Fig. 1). We also checked that emigration of newly marked individuals was limited to 1994 [model (τ_t^b, ϕ, p_t)]. Another specific assumption concerning the effect of the badger was that birds new to the colony in 1994 could have emigrated only temporarily after the predation event and returned after 1 or 2 years away from the colony. In that case, the capture rates of those birds should be lower than the capture rates of other birds in 1995, 1996, and 1997. We did not find such effects. We then tested for differential emigration of young and older birds and of males and females. Neither the age nor the sex effect were retained (τ^b, ϕ, p_t), although the model with an effect of age on τ^b showed a very similar value of AIC (Fig. 1). Thus, we selected the model (τ_a^b, ϕ, p_t) which indicated a tendency for younger breeders to emigrate in greater numbers than older breeders (see estimates of τ^b and ϕ in Table 2). Recapture probability estimates ranged between 0.494 and 0.800 under the selected model.

Breeding parameters

Food availability, expressed as the volume of commercial catches by the fisheries around the colony, significantly influenced average egg volume in a clutch, volume of first egg laid (A_{egg}) in the clutch, clutch size, and breeding success (Fig. 2). When we took into account the volume of commercial catches of months prior to the breeding season (from January to March), correlations with breeding parameters were in all cases non significant ($P > 0.05$). Egg-related parameters were greatly affected in 1992, when the trawling moratorium coincided with the pre-laying and laying stages (Fig. 2). In the other years, the moratorium coincided with other breeding stages, such as incubation and the early chick-rearing stage, or the whole chick-rearing stage.

Clutch size was significantly higher in the subcolonies where the badger did not enter (mean = 2.77, SD = 0.13, $n = 2465$ nests) than in the predated subcolonies (mean = 2.67, SD = 0.04, $n = 800$ nests) ($G_3 = 25.0$, $P < 0.001$). Of the 10,143 nests censused in 1994, 3% suffered predation (at least one egg lost), although this rate was probably underestimated since it did not account for the nests predated in the last week of incubation, nor for the unpredated nests which were deserted after the entry of the badger to the subcolony. Breeding success (number of chicks fledged as a percentage of eggs laid) was significantly higher in subcolonies that did not suffer predation by the badger (23%) than in those that did

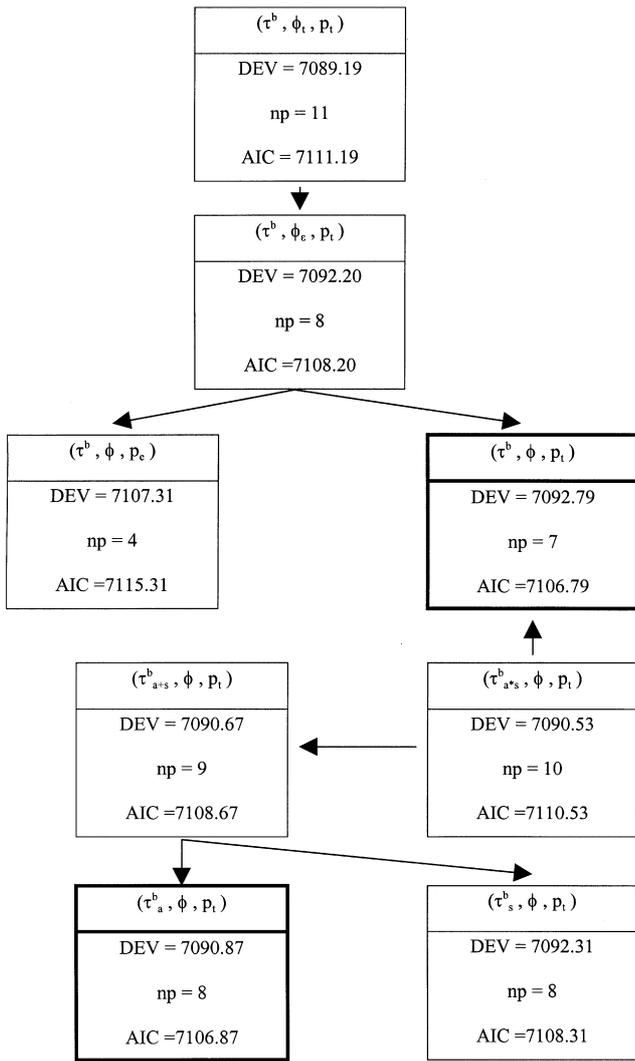


Fig. 1 Core of capture-mark-recapture models around the selected model (*bold*) for Audouin’s gulls from the Ebro Delta. Effects considered are sex (*s*), time (*t*) and age (*a*). *rDEV* (*DEV*) = relative deviance as given by program SURGE. *np* = number of identifiable parameters. *rAIC* (*AIC*) = relative Akaike information criterion computed as $rDev + (2 \times np)$; *rDev* and *rAIC* differ by an unknown constant (for a given dataset) from the true deviance and AIC. The two models with the lowest AIC are the best compromise between parsimony and description of the data (*bold models*). The *arrows* point to nested models. All the models were tested with the τ parameter constrained with a 0.4 and 0.6 ratio between the sexes and they yielded significantly higher *rAIC* and are not shown

Fig. 2 Effects of discard availability (as commercial catches, see Oro and Ruiz 1997) on some breeding parameters: volume (in ml) of first egg in a clutch (**a**); average volume (in ml) in a clutch (**b**); clutch size (as number of eggs per nest) (**c**); breeding success (as number of chicks fledged per nest) (**d**). For the egg-related parameters, only catches of the month prior to laying (April) are considered, whereas for breeding success, the catches of the whole reproductive season (April–July) are taken into account. Results of the Spearman rank correlations are shown for each pair of variables

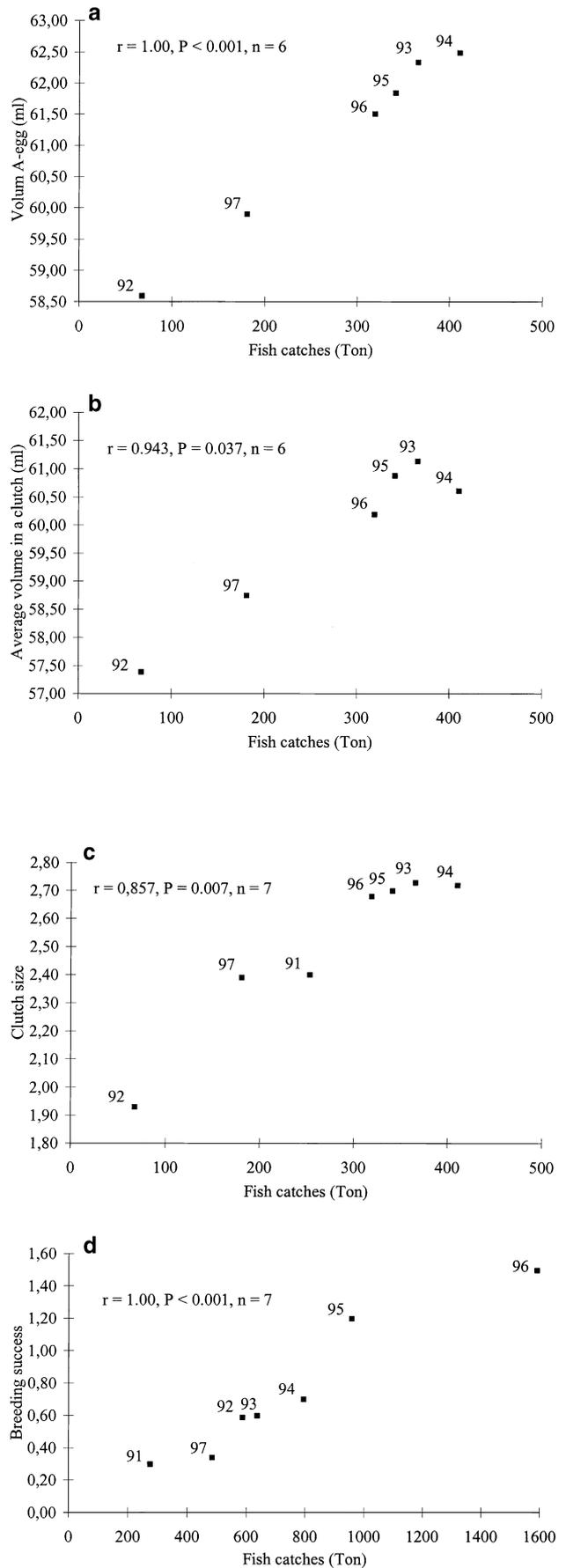


Table 2 Summary of estimates of adult survival (ϕ) and the proportion of dispersed birds after the predator event (τ) depending on age, under the model (τ_a^b , ϕ , p_i)

		95% confidence interval	
τ^b	3–4 years old	0.139	0.050, 0.227
	>4 years old	0.077	0.004, 0.150
ϕ		0.908	0.892, 0.922

(6%) ($\chi^2_1 = 8.5$, $P = 0.003$). No corpses of adult Audouin's gull predated by the badger were found, confirming that the predator only preyed on eggs and chicks.

Discussion

Food availability and the trade-off between reproduction and survival

Life history theory predicts that in long-lived species, environmental stress will affect fecundity before affecting adult survival (Benton and Grant 1996). Pons and Migot (1995) demonstrated that a decrease in food availability affected clutch size and breeding success in a colony of herring gulls, whereas adult survival did not change significantly. Discards from trawler fisheries may represent up to 73% of biomass in the diet of Audouin's gull breeding at the Ebro Delta (Oro et al. 1997). Before the start of the trawling moratorium in 1991, the amounts of discards available were about four times higher than the energetic demands of the seabird community breeding there (Oro and Ruiz 1997). This may explain the high breeding success of 2.01 chicks/pair recorded in 1990, which is the highest ever recorded for the species (see Oro et al. 1996a,b; Oro 1998) and is very high even when compared with other Laridae (e.g., Spaans 1971; Pierotti 1982; Pons and Migot 1995; Wanless et al. 1996). As expected (see also Ricklefs 1990), our study showed that increased food availability enhanced the breeding performance of the nesting gulls (see also Oro et al. 1996b), whereas adult survival was constant and independent of changes in food supply. Suitable ecological conditions at the Ebro Delta (protection against human disturbance, habitat suitability, low levels of interspecific competition with yellow-legged gulls, and high food availability; Oro et al. 1996a,b) have probably contributed to low variability in adult survival, in contrast to that recorded in some long-lived species living in highly variable environments (e.g., Kanyamibwa et al. 1990; Chastel et al. 1993; Coulson et al. 1997). The estimated adult survival rate in Audouin's gull (91%) is very close to those recorded for other gull species (88% in herring gull: Pons and Migot 1995; Wanless et al. 1996; 91% in lesser black-backed gull: Wanless et al. 1996; 90% in common gull *L. canus*: Rattiste and Lilleleht 1995; 91% in California gull: *L. californicus*: Pugsek et al. 1995; 90% in black-headed gulls *L. ridibundus*: Prévot-Julliard 1996). Neither age (varying from 3 to 8 years) nor sex had a significant effect on Aud-

ouin's gull survival, confirming previous results for other gull species (Pons and Migot 1995; Pugsek et al. 1995; Rattiste and Lilleleht 1995; Prévot-Julliard 1996; Wanless et al. 1996). However, future analysis involving older age classes might detect a senescence effect (i.e., a decline of survival with older age), as recorded in other Laridae (Aebischer and Coulson 1990; Pugsek et al. 1995).

Consequences of the predator event

Most of the predictions about the effects of the predatory event on breeding performance and breeding dispersal were supported by our results. In 1994, the badger caused not only a significant decrease in productivity, but also drove a relatively large number of Audouin's gulls to disperse, which probably affected the population dynamics of the colony. Several studies on seabird nest predation by carnivores have shown that when predation continues over many years, the number of breeding pairs may decline (Kadlec 1971; Southern et al. 1985). Our results suggest that a decrease in breeding numbers caused by nest predation over several breeding seasons may be due to a negative balance between breeding dispersal and recruitment together with the effects of low reproductive success over time. In this study, colony size in 1995 still increased by 2%, suggesting that the increase in the number of breeding pairs despite the badger event was probably a result of the buffering effect of recruitment, compensating for 10% of the dispersing breeders. Minimizing the risk of breeding failure from predation is one of the decision processes involved in dispersal, and birds often move to a new breeding site following a poor or unsuccessful breeding attempt (Danchin and Monnat 1992; Nager et al. 1996; Wiklund 1996; but see Korpimäki 1993). An average 10% of breeding adults left the Ebro Delta after the predation event, probably to breed in another colony. Results confirmed the prediction that dispersal was greater in younger breeders than in more experienced birds, supporting the hypothesis that breeding experience may affect philopatry to the colony site (Beletski and Orians 1991). However dispersal was not significantly higher in females than in males as has been found in many other bird species (e.g., Greenwood and Harvey 1982; Clarke et al. 1997).

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