

Lessons from a failed translocation program with a seabird species: Determinants of success and conservation value

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ARTICLE INFO

Article history:

Received 20 September 2010

Received in revised form 25 November 2010

Accepted 28 November 2010

Available online 21 December 2010

Keywords:

Conservation
Chick translocation
Dispersal
Ecological trap
Metapopulation
Release site
Survival

ABSTRACT

Conservation diagnosis of ex situ techniques (e.g. releasing chicks by hacking) cannot be evaluated without quantitative assessment of the fate of individuals, mainly their survival and recruitment. Here we use a long-term monitoring at a large spatial scale of a hacking programme (i.e. chick translocations) for Audouin's gulls in an uninhabited site so as to establish a new breeding patch and reinforce the metapopulation. The success of the programme relied on the assumption that birds tend to recruit to the site where they fledge (i.e. they were philopatric). Multi-state capture-recapture models applied to a large dataset (more than 43,500 resights at 30 colonies during 1999–2010) were used to evaluate the survival of released chicks and the probability of being philopatric. Adult survival was high, but juvenile survival was lower than that of wild gulls, suggesting that there was a cost associated with hacking only during their first year of life. As expected, most released birds returned to the hacking site, but very few (including immigrants from abroad) attempted to breed here. Dispersal was inversely correlated with distance from the hacking site and positively associated with the population size of the patch (i.e. conspecific attraction). Even though most hacking procedures met the ecological conditions to succeed, results clearly showed that the program failed to establish a new breeding site. The ability of prospecting and the attraction made by conspecifics at established sites may be a constraint for the success of hacking programs, particularly for social and nomadic species.

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1. Introduction

Most seabird species are necessarily structured in metapopulations, owing to the patchy nature of their breeding sites, typically oceanic or coastal islands, and their social aggregation in colonies, connected by dispersal processes and subjected to extinction–colonization turnover (e.g. Oro, 2003). Hence, the availability of a large web of occupied patches, with several local populations connected by dispersal, is a desirable conservation goal (Gilpin, 1980; Smith and Peacock, 1990). Conversely, an undesirable situation from a conservation perspective occurs when only one or a few of the metapopulation patches host the bulk of the individuals of a given species. Some extreme examples include some seabirds, such as Amsterdam albatross *Diomedea amsterdamensis* and Short-tailed Albatross *Diomedea albatrus*, with a single colony, and Heermann's gull *Larus heermanni*, whose largest colony holds

95% of the species world population; in these cases a local perturbation could threaten the whole species. Thus, at the scale of species range, a potential conservation aim, when recovering an endangered organism, is to increase occupation rates of empty metapopulation patches and thus reduce the chances of extinction (e.g. Doak and Mills, 1994; Hanski, 1999; Vuilleumier et al., 2007). Consequently, reintroductions, defined as the release of animals to reinforce or to re-establish extinct local populations, and introductions, in which release targets the establishment of new local populations of endangered flora and fauna, are proper conservation tools often used for management purposes (Sutherland, 2000; van Wieren, 2006).

To aid in the establishment of new metapopulation patches, several management techniques can be applied, such as social attraction or the translocation of nestlings from source sites followed by captive-rearing and release at fledging time (hereafter hacking). This latter technique is based on the principle that birds experience two types of behavioural imprinting during their lives: a species imprinting after hatching, and a site-specific imprinting when fledging. These features are life-history traits shaped by evolution, and evolutionary theory can be applied for conservation

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purposes (e.g. Martínez-Abraín and Oro, 2010). Hacking has been most commonly applied to raptor species in the last decades, taking advantage of their highly philopatric habits (Sherrod et al., 1982; Dzialak et al., 2006), and several pilot experiences have also been implemented on many seabirds species (Kress, 1997; Gummer, 2003), waders (Roche et al., 2008), and game birds (Buner and Schaub, 2008). However, the fate of individuals released in hacking programmes has seldom been evaluated with reliable conservation diagnoses (Hull et al., 1998; Sarrazin and Legendre, 2000; Nicoll et al., 2004; Buner and Schaub, 2008).

Based on the premises mentioned above (i.e. the importance of empty patches in asymmetric metapopulations and the availability of management techniques for relatively philopatric species) a hacking program was launched on a small western Mediterranean island to help reinforce the western Mediterranean metapopulation of the vulnerable Audouin's gull (*Larus audouinii*). The distribution range of the species is very particular, with a single colony hosting 60% of total world population, which is by itself a cause of conservation concern. The availability of suitable breeding patches in the Mediterranean has decreased since historical times due to the human occupation of coastal habitats and loss of marshes and wetlands (Blondel and Aronson, 1999; Coll et al., 2010); as a result, the need for increasing the colonization rate of empty patches in this region is even higher. Here, we report on the results of that experience and identify the key factors for diagnosing the success of the hacking programme. To obtain a reliable conservation diagnosis we focussed on demographic analyses of two key parameters for animals being translocated: (1) survival of chicks released in the wild, to assess the viability of such individuals and (2) recruitment and dispersal to the hacking site, to quantify the degree of success in establishing a viable local population. Dispersal was estimated at a large spatio-temporal scale covering 90% distribution of the world population, i.e. encompassing most of the dispersal potential events. At the same time, we assessed whether some variables influenced dispersal to other sites in order to understand the reasons of why some individuals did not behave as philopatrics, in other words, the factors (at ecological and evolutionary levels) of the potential failure of the programme. One of these factors was distance (see Oro and Pradel, 1999), because having close patches to the hacking site may have attracted some released birds preventing to behave as philopatrics. Furthermore, an ecological factor used by Audouin's gulls and many other social species to select habitat for being philopatric or dispersers is conspecific attraction, because larger number of conspecifics may inform about a patch of higher quality (Stamps, 1988; Martínez-Abraín et al., 2001; Oro and Ruxton, 2001; Serrano et al., 2004). Thus, the success of the hacking programme was evaluated by testing whether philopatry to the natal site was stronger than dispersal to already occupied patches exerting conspecific attraction.

2. Methods

2.1. Study species

Audouin's gull is an endemic Mediterranean species that was considered one of the most threatened gull species in the world with only 1000 pairs in the 1960s and 1970s. However, colonization of the Ebro Delta in the western Mediterranean by 36 pairs in 1981 led to an exponential population increase leading to ca. 14,000 pairs in 2005 (Tavecchia et al., 2007). In this Mediterranean area, ca. 40 colonies (median population size in 2006: 80 pairs, range 8–15,329), form a metapopulation system with breeding sites connected by high dispersal rates (Oro and Ruxton, 2001; Cam et al., 2004; Tavecchia et al., 2007) and high

extinction–colonization turnover (Martínez-Abraín et al., 2003a; Oro, 2003). Although it had been traditionally considered an island species, successful colonization of the Ebro Delta saltmarshes and several salt pans showed that such habitats are most likely their optimal breeding sites. In fact, the Ebro Delta alone holds ca. 75% of breeding pairs in that metapopulation. Philopatry to the breeding site is considered to be relatively high (ca. 90%, Cam et al., 2004), although the species is also highly nomadic with relatively high natal and breeding dispersal among local populations (Martínez-Abraín et al., 2001; Oro and Muntaner, 2001; Oro, 2003; Cam et al., 2004; Tavecchia et al., 2007). Breeding success and survival may be affected especially by terrestrial mammals (e.g. badgers, foxes) and to a lesser extent by aerial facultative predators such as yellow-legged gulls *Larus michahellis*, but also by availability of small pelagic fish and fishing discards, their main foraging resource (Oro et al., 1999; Martínez-Abraín et al., 2003b; Tavecchia et al., 2007). Audouin's gulls are known to recruit at the age of three at the earliest; they typically migrate to tropical latitudes of the eastern Atlantic during their first year (Oro and Martínez-Vilalta, 1994).

2.2. Study site

Hacking of Audouin's gull chicks was performed on the Island of Benidorm, a 6.5 ha limestone outcrop located ca. 3 km off the eastern coast of the Iberian Peninsula (Fig. 1). The island has a Mediterranean climate with a vegetation cover composed mainly of shrubs from semi-arid zones, nitrophilous herbaceous plants and exotic vegetation, mainly *Opuntia maxima*; this is the typical island habitat of most colonies of the species (more than 90% from ca. 60 sites occupied sites in the whole Mediterranean), except a few breeding sites (five sites in total) located in salt marshes and salt pans (Oro, 1998; own data). Size of the island was considered suitable for the hacking, since it was well within the range of most colonies of the species (median surface = 5.6 ha; range = 0.036–2409,000 ha; $N = 56$). The island has no terrestrial predators, but it holds a colony of yellow-legged gulls, which increased from ca. 350 pairs in 2000 to ca. 676 pairs in 2009 following the island's legal and effective protection (Martínez-Abraín et al., 2004). Benidorm is located in the Ibiza channel, an area with a relatively high oceanographic productivity, with high densities of small pelagics and a large fishing fleet generating considerable amounts of discards (Martínez-Abraín et al., 2002; Louzao et al., 2006).

2.3. Management techniques

Gull chicks were taken from the Ebro Delta colony, the largest colony of the species. The Ebro Delta was visited in late may, when oldest chicks have ca. 2 weeks of age; only these chicks were taken and only one at each brood, selected at random. Chicks were transported immediately by car to a fauna rehabilitation centre in a 2 h trip from the colony. The chicks remained for ca. 3 weeks in the centre, where they were fed 2–3 times per day with sardines, their main natural prey. After this period, chicks were again transported in small cages by car and boat to the hacking site in a trip lasting 2 h. An average of 33 ± 11 chicks (mean \pm SD; $N = 8$ cohorts) was released annually from 1999 to 2006; after being in the hacking cage during a mean of 18 ± 5 days. While stay in the cage, chicks were also fed with sardines once a day. Overall, 261 chicks aged 50–60 days (i.e. the age at which the chicks abandoned the cage, which was progressively opened to allow chicks to escape) were released during that time period. Upon release, 76% of gull chicks were weighed to the nearest gram on a digital scale, because weight could influence the survival of fledglings (e.g. Magrath, 1991). Weight was used as a proxy for body condition of released gulls, since we had no structural measures to build a usual body condition

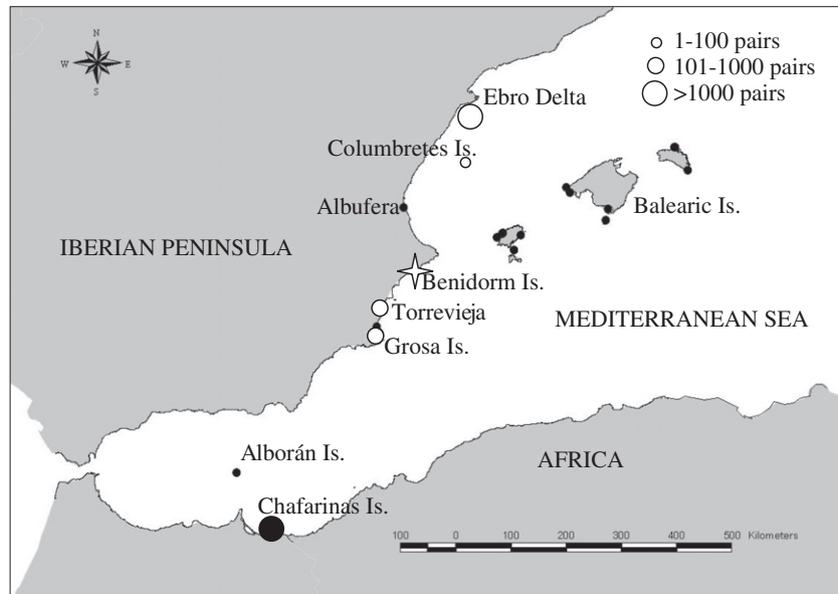


Fig. 1. Map of the study area showing Benidorm Island (where the hacking was performed during 1999–2006) and the location of the other main breeding sites cited in the text. White dots show the breeding sites where birds from the hacking programme were resighted during 2000–2009. Size of the dots shows the relative density of the colonies.

index; although we did not know the age of the chicks with accuracy, weight was well already in the asymptotic part of the growth curve, which is attained at 27–30 days of age (Villuendas and Sarzo, 2003). Males and females were considered separately to account for differences in weight resulting from structural reasons (i.e. females are smaller than males in this species). The sex of most chicks released between 1999 and 2001 was determined by molecular techniques (see Genovart et al., 2003).

Chicks were marked with darvic rings with an alphanumeric code for monitoring purposes, following the same protocol carried out in most colonies over the years (e.g. Cam et al., 2004; Tavecchia et al., 2007). To determine whether one sex returned at Benidorm Island more than the other, a CMR multi-state approach (see below) could not be used because of the excessive number of estimable parameters in such a model. Instead, we used contingency tables (assuming that detection probability was equal between males and females) together with the chi-square statistic to run homogeneity tests.

A small group of impaired adult Audouin's gulls (between 2 and 6 depending on the years) together with a number of artificial decoys (between 24 and 41 depending on the years), were also placed close to the hacking cage each year in order to facilitate the colonization of the island through social attraction.

Returning birds were monitored by a team of three wardens with a daily presence on the island during the breeding period. Resightings were limited to the breeding season at most breeding sites (see Fig. 1), and were performed from distance using telescopes. A total of 247 resightings of released birds were performed during 2000–2009, resulting from the monitoring effort performed at 30 colonies and at the main resting sites of the species that totalize 5674 h of fieldwork. When a marked bird was seen at multiple sites in a single season, we only considered the resighting confirming its reproduction and deleting the other resightings for analysis; the two cases when this was not possible were not considered.

2.4. Capture–recapture analysis

The probability of survival and recruitment was estimated by capture–recapture modelling (CRM, see Lebreton et al., 1992) using

data on the 261 birds released and monitored at the breeding sites (247 resightings). The main hypothesis tested with CRM was that birds return to their natal site to reproduce more than they dispersed for breeding at other sites. Then, once accepted or rejected the main hypothesis, the CMR models allowed us to test alternative hypotheses to find out what were the proximal factors potentially influencing the behaviour of individuals released during the hacking programme (e.g. dispersal probability decreased with distance to the release site; see Oro and Pradel, 1999), and dispersal increased with population density at other sites, i.e. with conspecific attraction. Sex was not included in CRM analysis because only ca. 35% of chicks were sexed (so we would had to include three sexes to include the unsexed individuals) and thus to avoid overparameterization (i.e. trying to estimate an excessive number of parameters), since models already took into account time, colony and age (noted by 't', 'r' and 'a' respectively). Body condition of chicks was either included because ca 25% of chicks were not weighted. Models included three types of parameters for each colony, noted and defined as follows:

- Φ_t^r : the probability that a bird in colony r at time t survived until time $t + 1$ (i.e. survival probability)
- Ψ_t^{rs} : transition probability conditional to the fact that a bird in colony r at time t was in colony s at time $t + 1$, given that the individual survived from time t to time $t + 1$ (Lebreton and Pradel, 2002).
- p_t^r : the probability that a bird was resighted at time t in colony r , given that it was alive and present in the population at time t (i.e. recapture probability).

Since the breeding status of most birds was unknown, we defined recruitment as the probability of moving to a breeding site: in the case of Benidorm, the probability of returning to the hacking site (i.e. local recruitment), and in the case of established colonies, the probability of dispersing (i.e. emigration). To avoid overparameterized models we limited the number of sites to the following: Benidorm, Ebro Delta area (including a few resightings at Columbretes Islands) and southern neighbouring colonies (grouping the Torrevieja salt pans and Grosa Island). The other

Table 1
Modelling survival (Φ' for juveniles and Φ for older gulls) and dispersal (Ψ) probabilities of Audouin's gull from a hacking programme at Benidorm Island during 1999–2009 using multi-site CMR models. The effects considered were yearly variation (denoted by 't'), colony ('r'), population size ('P') and distance ('d'). The symbol '*' was used to show the interaction term between the effects, whereas the symbol '+' was used in models with a parallel variation; when no effects were considered (i.e. constant parameter) then the symbol '.' was used. K = number of identifiable parameters; DEV = relative deviance of each model; AICc = AIC value for each model corrected for sample size; Δ_i , the AIC difference between the current and lowest AIC model; w_i , Akaike weight. The model selected is in bold; model 1 was the umbrella, more general model (see text).

Model	Considered effects in Φ , Ψ , and P				K	Dev	AICc	Δ_i	w_i
	Φ'	Φ	Ψ	P					
1	t*r	t*r	r	t*r	69	1358.287	1496.287	28.966	0.00
2	t*r	t*r	r	r	39	1443.693	1521.693	54.372	0.00
3	t*r	t*r	r	.	41	1489.384	1571.384	104.063	0.00
4	t*r	t*r	r	t	47	1409.797	1503.797	36.476	0.00
5	t*r	t*r	r	t+r	50	1407.566	1507.566	40.245	0.00
6	r	t*r	r	t*r	64	1371.520	1499.520	32.199	0.00
7	t	t*r	r	t*r	47	1408.287	1502.287	34.966	0.00
8	.	t*r	r	t*r	62	1371.810	1495.810	28.489	0.00
9	t+r	t*r	r	t*r	67	1358.287	1492.287	24.966	0.00
10	.	r	r	t*r	40	1392.215	1472.215	4.894	0.06
11	.	t	r	t*r	45	1388.985	1478.985	11.664	0.00
12	.	.	r	t*r	38	1396.221	1472.221	4.9	0.06
13	.	t+r	r	t*r	48	1384.714	1480.714	13.393	0.00
14	.	.	.	t*r	33	1444.746	1510.746	43.425	0.00
15	.	.	P	t*r	34	1401.567	1469.567	2.246	0.13
16	.	.	d	t*r	34	1402.340	1470.340	3.019	0.25
17	.	.	P+d	t*r	35	1397.321	1467.321	0	0.50

colonies (see Fig. 1) were Albufera, Alborán, Chafarinas and those from the Balearic archipelago, which were also grouped; in these colonies there were no resightings of released birds over the years. Transient probabilities from one site to another equalled dispersal (Pradel et al., 1997). Time variation in transition probabilities was not considered in the models to avoid an excessive number of non-estimable parameters, and also because we only tested the hypothesis that recruitment probability was higher at Benidorm than at the other sites. The potential effects of distance and population size as a proxy of conspecific attraction (noted in the models by 'd' and 'P' respectively) on dispersal were also tested. We performed a GOF of a general multi-state model, the Arnason–Schwarz model (see Pradel et al., 2003). The GOF test was carried out using the U-CARE program (Choquet et al., 2005). All CMR analyses were carried out using M-SURGE (Choquet et al., 2004) and model selection was performed using AICc values (i.e. AIC values corrected for small sample sizes) following standard procedures (Lebreton et al., 1992; Burnham and Anderson, 2002).

3. Results

3.1. Wintering and migration of released gulls

Fourteen individuals (5.4% from the total released) were reported from the traditional wintering headquarters of the species in Atlantic Africa (i.e. Mauritania, Morocco, Senegal), suggesting that gulls were capable of long-distance migration (ca. 4000 km) after release. This percentage was very similar (4.7%) to that of control birds marked in other colonies and resighted in those areas during the same period. Additionally, 22 immature gulls, i.e. younger than first-breeding age – 3 year old – (8.4% from the total released) were resighted in coastal wetlands of the southern Iberian Peninsula during the summer, suggesting that they had followed the same southward migration route as wild-ranging individuals, probably joining flocks of wild conspecifics.

3.2. Survival, recruitment and dispersal

The fit of the more general Arnason–Schwarz multi-site model was good despite the suspected age-structure in survival, transition and recapture probabilities (TEST3G $\chi^2_{31} = 36.55$; $P = 0.23$; TESTM $\chi^2_6 = 4.0$; $P = 0.62$; LRT (JMV vs. AS) $\chi^2_{37} = 40.6$; $P = 0.32$).

However, a deeper insight into the subcomponents of the GOF showed an age-structure for survival but not for recapture (TEST 3G.SR $\chi^2_5 = 11.7$; $P = 0.04$; TEST M.ITEC $\chi^2_4 = 2.9$; $P = 0.57$ respectively). Thus, the starting multi-site model was $\Phi'(t*r)\Phi(t*r)/\Psi(r)/p(t*r)$, i.e. including a two-ages class in survival (Φ' for first-age class and Φ for the rest of age-classes, see model 1 in Table 1), and with no overdispersion. We first tried to improve the fit of the starting model by modelling recapture probability; none of the models (models from 2 to 4 and the one including an additive effect of colony and time – model 5) yielded a lower AICc value, so we kept the initial structure in such parameter. Then we modelled survival probabilities for juveniles: the model that considered that juvenile survival was constant (model 8) was selected rather than the one with an additive effect of time and colony (model 9) even though the later had a slightly lower AICc value because the lower

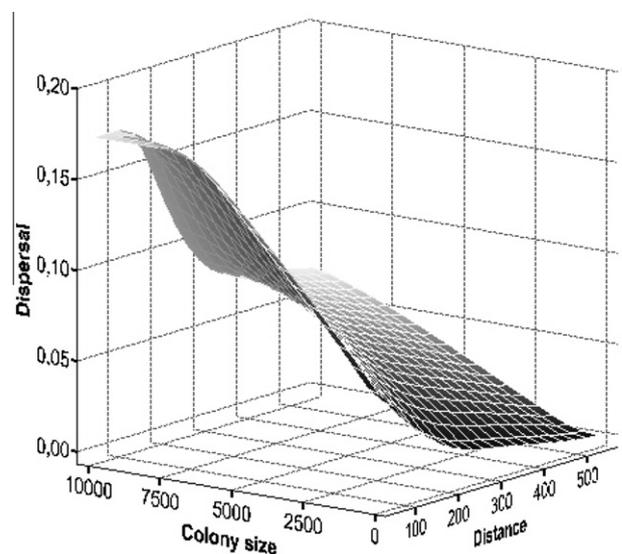


Fig. 2. Dispersal probabilities of Audouin's gull chicks released at Benidorm Is. and moving to other patches in the metapopulation (see Fig. 4) depending on their population density and the distance from the hacking site. Dispersal increased monotonically to larger colonies at shorter distances from the hacking site. We adjusted a smoothing regression surface using a loess method by iteration of weighted least-squares on the data.

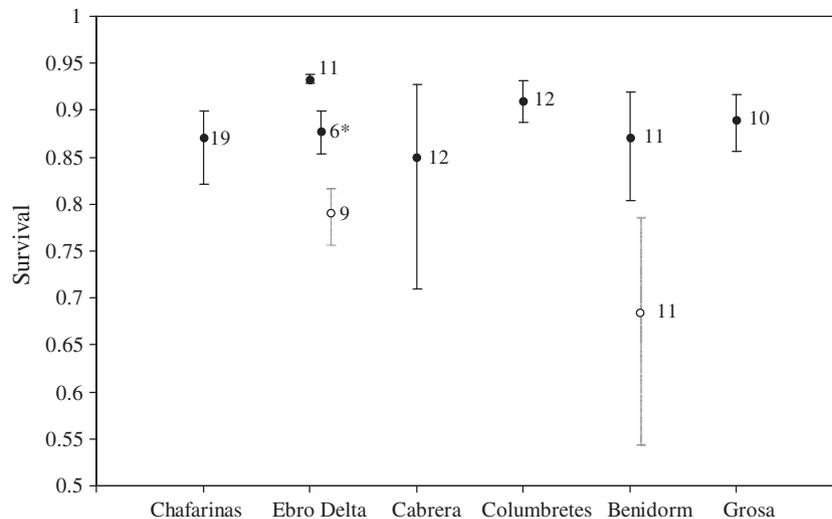


Fig. 3. Estimates of survival of Audouin's gull (mean and 95% CIs) released at Benidorm are drawn from the hacking programme and compared to estimates from other colonies in the western Mediterranean metapopulation (see Fig. 1). Open dots are estimates for juvenile birds (survival of the first year of life) and solid dots are estimates for older gulls (immatures and adults). The labels next to the estimates show the number of years of monitoring. Survival from other colonies came from the literature and unpublished data, and they were estimated using the resightings made at each colonies and CMR modelling (see methods) (Oro, 1998; Oro et al., 1999, in press; Oro and Muntaner 2001; Tavecchia et al., 2007). Ebro Delta* = estimate of survival in years with carnivore predation.

number of parameters of the former; we also kept the model that had a constant survival for the second age-class (model 12) for the same reason. We finally modelled transition (i.e. dispersal) probabilities testing also for the potential factors of population size (P) and distance (d): the inclusion of an additive effect of the two factors (model 17) was the finally selected model, with a 50% weight of all the models; distance had a slightly higher influence on dispersal than population size (models 16 and 15 respectively, Table 1 and Fig. 2).

Average survival (from the model 17; see Table 1) during 1999–2010 was 0.685 (95% CI: 0.545–0.787) and 0.871 (95% CI: 0.803–0.920) for juveniles and older gulls respectively (Fig. 3). The only existing estimation of juvenile survival from the Ebro Delta colony was higher than that of birds released from hacking at Benidorm (z -test = 4.0; $P < 0.05$). Adult survival was similar to that in most other colonies (Ebro Delta with predation, z -test = 0.65; $P > 0.05$; Columbretes, z -test = 1.78; $P > 0.05$; Chafarinas Islands z -test = 0.02; $P > 0.5$; Cabrera archipelago z -test = 1.01; $P > 0.5$; Grosa, z -test = 1.69; $P > 0.05$), except for the Ebro Delta estimation that was significantly higher (z -test = 6.15; $P < 0.005$, Fig. 3).

Dispersal probabilities increased with population size and decreased with the distance from the hacking site. Most surviving birds were resighted at Benidorm (probability of returning to the site: 0.77; SE = 0.03; Fig. 4); 23% of individuals (0.23; SE = 0.04) dispersed only to the other breeding areas relatively close and with large population sizes: the Ebro Delta-Columbretes and the Torreveja-Grosa systems. Once dispersed to those sites, only 9% of the birds returned to Benidorm Island (Fig. 4). There was no dispersal detected to the other four colonies, because of their low population sizes or the large distance from Benidorm. Despite the high philopatry of released birds to Benidorm, no breeding attempts of recruiting birds were detected until 2005; since then to 2007, 13 pairs attempted breeding close to the hacking cage, but none raised successfully a chick; in 2008 and 2009 no breeding attempts occurred, and three pairs bred in 2010, with a single fledgling at the end of the season. All resightings of marked breeders in the hacking site during those years showed that only six released birds (from the total 261) attempted breeding here. Most of these birds (five out of six) dispersed in subsequent years and were

observed breeding at the other two patches (see above). Other 18 birds were also observed breeding at those patches from a total of 143 different individuals resighted over the years.

3.3. The influence of sex and body condition

Although chicks collected at the Ebro Delta colony were randomly selected, it turned out that we released a larger number of females (22 males vs. 61 females for the period 1999–2001 for which information on sex of individuals was available). Despite so, the frequencies of males and females observed returning at least once to Benidorm were similar (Fisher's exact test, $P = 0.249$). Weight of released chicks from hacking (552.6 g, SE = 3.7;

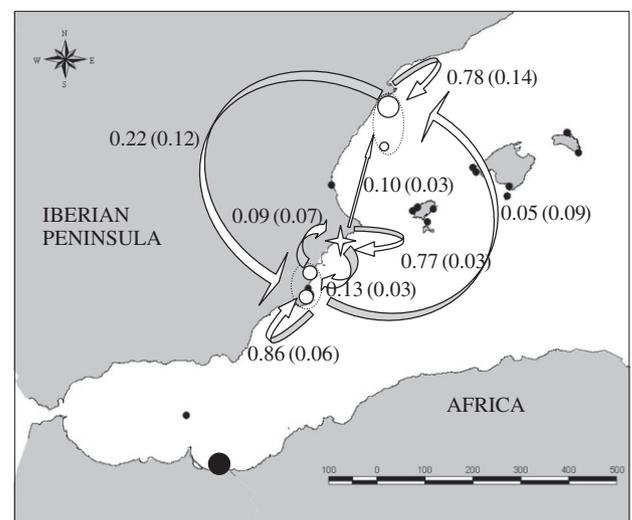


Fig. 4. Mean transition probabilities (SE in brackets) of released chicks from a hacking programme at Benidorm Island (shown by a star) during 1999–2009 between the three breeding areas; labels of sites are shown in Fig. 1. Estimates came from the best model in Table 1. Transition probabilities from a patch r in a given year t include the probabilities to disperse to patch s (i.e. dispersal) and that of staying at patch r (i.e. philopatry). Patches were grouped in breeding areas by vicinity (see text). Note that the probability of dispersing from the Ebro Delta area to Benidorm was 0.

$N = 198$) was significantly higher than that of wild-reared fledglings from the Ebro Delta (data from Oro et al., 1996: 526.6; SE = 9.1; $N = 22$) ($t = 2.24$; d.f. = 218; $P < 0.05$), even though hacking chicks were biased to slighter, smaller females. Returning females were heavier at release than non-returning females (mean \pm SE: 551.7 \pm 14.9 g vs. 528.2 \pm 3.8 g; $t = -2.182$; d.f. = 59; $P < 0.05$), but such a trend – likely because a lack of power – was not found for males (631.5 \pm 11.8 g vs. 611.2 \pm 9.5 g; $t = -1.309$; d.f. = 32; $P > 0.05$). A logistic regression showed no evidence against the null hypothesis that either sex, weight, or the interaction between the two variables was different between returning and non-returning gulls to Benidorm (null deviance 102.824 on 94 d.f.; residual deviance 92.421 on 91 d.f.).

4. Discussion

Although hacking has been one of the most commonly used management techniques for recovering decimated bird populations in recent decades (Van Wieren, 2006), the success of these programmes (i.e. the establishment or reinforcement of populations) has not always been evaluated. As a rule, re-establishment techniques (including translocations, reintroductions and reinforcements) generate poor results (i.e. they fail to recover populations) (Wolf et al., 1998). Nevertheless, in recent years, several reliable quantitative studies on raptors, waders and game birds have estimated the crucial demographic parameters of released birds: in most cases, survival, recruitment and dispersal of such birds was found to be lower than those of individuals reared in the wild (Brown et al., 2006; Poulin et al., 2006; Buner and Schaub, 2008; Roche et al., 2008; but see Nicoll et al., 2004). Field observations suggest that some bird species perform extended parental care once chicks fledge (Oro, 1998; Gummer, 2003; Sunde, 2008), and the lack of such advantage for hacking chicks may result in a lower survival, despite that captive-reared chicks had significantly higher weight than wild-reared chicks (see also Villuendas and Sarzo, 2003). Our results, applied to a seabird species, point out the importance of taking into account a lower viability of birds released from hacking programmes compared to wild seabird populations.

Estimates of dispersal among breeding patches found here showed that released birds behaved as expected, i.e. philopatrically (see Johnson and Gaines, 1990). Most of them returned to the hacking site where they were released: annual rates of return to Benidorm (82%, see Fig. 4) were higher than normally recorded for other hacking programmes (e.g. Pomarol, 1993). Nevertheless, <3% of birds released attempted to breed – and none was successful – indicating that birds rather prospected the natal site to evaluate its breeding suitability (Cadiou et al., 1994; Dittmann et al., 2005). Furthermore most of these birds (five out of six) dispersed in subsequent years to establish at other breeding patches. These results suggested that only some of the conditions necessary for a successful establishment of released birds were met (for instance an effective protection of the site, see also Martínez-Abraín et al., 2004; Sergio et al., 2005; Haight and Gobster, 2008) but some other conditions, such as density of facultative predators (such as yellow-legged gulls) and the lack of sufficient conspecific attraction (despite the dummy adults) (see Reed and Dobson, 1993; Martínez-Abraín et al., 2001; Oro and Ruxton, 2001; Serrano et al., 2004) probably reduces the appeal of the hacking site. Released birds preferred to emigrate to other breeding patches, where the ratio with yellow-legged gull density, a good predictor of breeding success (Oro et al., 2006 and references therein), was more favourable than at Benidorm Island, and where conspecific attraction was higher. Yet, during the study, 10 new breeding patches were colonized in the study area (i.e. 26% of colonization rate), showing again the high colonization ability of the species (Oro, 1998;

Martínez-Abraín et al., 2003a). This trend was seemingly stronger for neighbouring breeding patches because dispersal is negatively associated with distance (see Oro and Pradel, 1999). Dispersal capabilities, which are often a major constraint in reintroduction programmes, especially in fragmented landscapes (Van Wieren, 2006), should not be a constraint for hacking programmes for very mobile species such as many gulls and terns, and particularly for the highly nomadic Audouin's gull (Martínez-Abraín et al., 2001).

Several hacking programs have been launched in recent decades both for burrow-nesting (e.g. puffins, shearwaters, petrels) and ground-nesting seabirds (e.g. albatrosses, shags, gannets, terns, auks), but they showed mixed success (Gummer, 2003). In some cases successful programmes were reported (Kress, 1997), but negative results are seldom published (Kotze et al., 2004) and meta-analysis for assessing the goodness of hacking and translocation techniques can be biased for this reason (Bajomi et al., 2010). The diagnosis of the Audouin's gull hacking programme is rather negative, although some results were positive: survival and dispersal, while lower than for wild-reared gulls, were sufficiently high to establish a new breeding patch in the system, and migration looked normal (see Oro and Martínez-Vilalta, 1994; Oro, 1998). The number of birds released, which is crucial in reintroduction programmes (e.g. Wolf et al., 1996, 1998; Komers and Curman, 2000; but see Wanless et al., 2002 for a success with small numbers), was probably suitable for Audouin's gull hacking: on average, 33 chicks were released annually, a productivity that would correspond to a hypothetical breeding colony of ca. 50–60 pairs, around the median colony size of the species (see above; Oro, 1998). Nevertheless there could be a potential influence of Allee effects on recruitment; although no evidences of such effects have been found, releasing more birds in fewer years could be more successful than the same number of birds diluted over a larger number of years. Habitat was also the commonest for the species: small inhabited islands with Mediterranean shrub vegetation, and food availability should be normal, with the island place in one of the most productive marine areas of the western Mediterranean (Louzao et al., 2006). Nevertheless, 11 years after the first cohort was released, only a single chick fledged at Benidorm; here, the ratio between Audouin's gulls and yellow-legged gulls, an ecological clue used by Audouin's to assess the suitability of the breeding patch (Oro et al., 2006), could have been discouraging for prospecting gulls, although 68% of natural colonisations recorded in the last 20 years ($N = 25$) occurred at sites where yellow-legged gulls occurred. Examples of intra-guild predation impacts on settlement, colony size and breeding performance can be found in several raptor species (e.g. Sergio and Hiraldo, 2008).

These results, in combination with the philopatric tendency of birds, suggest that potential local recruits were exposed to an ecological trap, with some positive clues (live and artificial decoys and the annual presence of chicks) giving misleading information on habitat quality (Battin, 2004). However, Audouin's gulls have shown to be resistant to swindle due to their evolutionary life-history (Martínez-Abraín and Oro, 2010) and have not performed a maladaptive habitat selection, avoiding a forced ecological trap (Schlaepfer et al., 2002; Battin, 2004). Large colonies of the species are already present quite close to the hacking site, and chances are high that these colonies (and particularly the closest ones; see Oro and Pradel, 1999) acted as attraction poles drawing in dispersal (Smith and Peacock, 1990; Oro and Pradel, 2000). Other negative results can be of interest for future programmes not only on Audouin's but on other birds: for instance, the number of recruiting gulls could probably have been higher if the sex-ratio of gulls released had been more balanced (Tella, 2001), since bird males showed a stronger tendency to be philopatric than females (Johnson and Gaines, 1990). Body condition also seems to be an important factor influencing the success of hacking programmes:

returning females had a better body condition at release than non-returning birds (see Lindstrom, 1999). Finally, it is important to consider the evolutionary life-history of the species: Audouin's gull is a highly nomadic species due to its evolution in unstable coastal environments (Martínez-Abraín et al., 2003a; Oro et al., in press): for such species, individuals have a high capacity to react to adverse local conditions by moving elsewhere, and lower rates of recruitment are to be expected in hackings targeting some gulls and terns compared to oceanic seabirds from more stable (i.e. temporally unchanging) environments (e.g. albatrosses, petrels, penguins, cliff nesting gulls such as kittiwakes) if the releasing site is a lower-quality patch (see Matthiopoulos et al., 2005; Igual et al., 2007). The consequences of heterogeneity in habitat quality for the demography of local populations is a pattern pointed out in recent times (e.g. Frederiksen et al., 2005; Tavecchia et al., 2008; Sanz-Aguilar et al., 2009). For hackings and similar conservation efforts (e.g. reintroductions) it seems crucial to take into account that animals will evaluate the quality of their new habitat, and this will be compared to the habitat availability and quality found around after prospecting (Boulinier et al., 1996). Individuals from any hacking will face a trade-off between philopatry and dispersing to a non-natal site, particularly when alternative sites beyond the hacking site can have higher habitat quality. This is sometimes difficult to assess because it requires detailed information on habitat quality heterogeneity in space, and particularly because source-sink systems can change also over time (e.g. Tavecchia et al., 2007; Oro et al., in press). Our study suggests that programmes targeting lower-quality habitats are likely doomed to failure, particularly for highly dispersing, nomadic animals such as our study species (Oro and Pradel, 1999; Oro and Ruxton, 2001; Cam et al., 2004).

5. Conclusions and conservation implications

Hacking has been often used as an ex situ technique for recovering threatened bird populations, but it is essential to assess its validity to optimise resources in the management of species conservation (Bajomi et al., 2010). This technique has even been proposed as an ultimate solution to avoid extinction of species facing climate warming (Hoegh-Guldberg et al., 2008) but it has also generated a strong controversial (e.g. Davidson and Simkanin, 2008). Our robust, unbiased estimates of survival and dispersal of chicks released of a threatened seabird suggest that, after paying a survival cost during their first year of life, adults survived normally and they showed a strong tendency to return to the hacking site. This suggested that the programme was successful and that birds responded as expected to the *a priori* good conditions of a hacking protocol. Nevertheless, hacking birds did not recruit to the hacking site and they dispersed to established colonies (mostly to those at shorter distances and with larger number of breeders) probably responding to conspecific attraction. Together with meeting the traditional requirements of hacking (e.g. patch habitat quality, including food availability, chick body condition, number of chicks released and their sex-ratio) it is important to know the life-history evolution of the species (Martínez-Abraín and Oro, 2010) to forecast crucial behavioural aspects related to recruitment and dispersal, which will also determine the success of the reintroduction programme. Managers have also to take into account that, at the spatial scale, there is a strong, natural heterogeneity in habitat quality, some patches being relatively good habitats but some being bad habitats (e.g. source-sink populations, see Cam et al., 2004), the last being potential ecological traps when selected for hacking programmes (Battin, 2004). Consequently birds will tend to prospect always looking for the best of the available habitats to recruit and maximise their fitness (e.g. Serrano et al., 2005). Recently, new quantitative tools to evaluate the success of hacking

and translocation programmes under typical uncertainty have been proposed (e.g. Richardson et al., 2009). Finally it is essential that negative results (i.e. failed programmes) are reported to quantitatively assess (e.g. by meta-analysis) the success of hacking programmes and their determinants.

Acknowledgements

We are indebted to all the people who have been helping with the fieldwork over the years. The study was funded by Generalitat Valenciana and grants from the Spanish Ministry of Science and Innovation (Ref. CGL2006-04325/BOS). Deborah Bonner corrected the English. Irene Pérez helped with the database management. MG and AMA were funded by I3P postdoctoral fellowships from the Spanish Ministry of Education and Science. Two anonymous referees provided helpful comment to greatly improve a previous draft.

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