Ardeola 61(2), 2014, 285-296 DOI: 10.13157/arla.61.2.2014.285

POPULATION DYNAMICS OF A COLONY OF LITTLE EGRETS *EGRETTA GARZETTA* AT AN ESTUARY IN NORTHERN SPAIN

DINÁMICA DE POBLACIÓN DE UNA COLONIA DE GARCETA COMÚN *EGRETTA GARZETTA* EN UN ESTUARIO EN EL NORTE DE ESPAÑA

Aitor GALARZA[1] and Juan ARIZAGA[1] *

SUMMARY.—The population of little egrets *Egretta garzetta* in Spain is over 20,000 adult breeding birds, making it one of the largest in Europe. Apart from its population size and population trends, the parameters associated with the dynamics (e.g., survival) of the species in Spain are virtually unknown. Our aims were to develop models to assess (1) the colony growth rate, and (2) apparent survival rate of a colony of little egrets breeding in northern Iberia. We used capture-recapture data of little egrets ringed as chicks within the colony, of normally < 30 adult breeding pairs, over a 14-year period starting in 1999. Colony size was observed to be increasing in a linear tendency broken by specific catastrophic events: a very strong hailstorm in 2004 and a pair of peregrines *Falco peregrinus* that killed several adults in 2005. By 2012, the colony had still not reached the size that it was before the decrease, so it can be concluded that sporadic catastrophic events can have a significant effect on colony size and subsequently population size, especially in small colonies. Annual apparent survival (±SE) was constant and differed between age classes (first-years: 0.15 ± 0.05; adults: 0.78 ± 0.06). Our survival estimate was relatively high compared with other little egret populations, especially for adults. This result, however, may not necessarily apply to other colonies given our small sample size and the lack of data on other factors that also affect the dynamics of the study population.

Key words: herons, Iberia, population size, survival, Urdaibai, waterbirds.

RESUMEN.—La población de garcetas comunes *Egretta garzetta* en España se estima en unos 20.000 individuos nidificantes, lo que la convierte en una de las mayores de Europa. Aparte de su tamaño y tendencia de población, los parámetros que determinan su dinámica en España (e.g. la supervivencia) se desconocen. El objetivo de este estudio es estimar, mediante modelización, (1) la tasa de crecimiento y (2) la supervivencia (aparente) de una colonia situada en un estuario en el norte de España. Para esto último se ejecutaron modelos de captura-recaptura basados en el anillamiento de pollos en la colonia de estudio (cuyo tamaño no superó, normalmente, las 30 parejas de adultos nidificantes) a lo largo de un periodo de 14 años (1999-2012). El tamaño de la colonia aumentó de manera lineal, si bien esta tendencia se vio interrumpida por un episodio de carácter catastrófico en 2004 (granizada) y otro en 2005 (una pareja de halcones peregrinos *Falco peregrinus* mató varias aves adultas). En 2012, la colonia estaba todavía por debajo del tamaño que tenía antes del primer evento catastrófico. La supervivencia inter-anual aparente (±SE) no varió inter-anualmente pero sí según la edad (jóvenes: 0,15 ± 0,05; adultos: 0,78 ± 0,06). En comparación con otras colonias

[1] Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11, E20014 Donostia-S. Sebastián, Spain.

* Corresponding author: jarizaga@aranzadi-zientziak.org

de garcetas, la supervivencia en Izaro fue alta, especialmente en adultos, si bien esta conclusión ha de considerarse cautamente debido al bajo tamaño muestral y a que no disponemos de datos sobre otros factores que también afectan a la dinámica de la población estudiada.

Palabras clave: aves acuáticas, garzas, Iberia, superviviencia, tamaño de población, Urdaibai.

Introduction

The investigation of population dynamics is a fundamental component of conservation and population ecology studies. It includes not only the establishing of population trends, which are generally easier to determine, but also the assessment of additional demographic parameters such as survival (Newton, 1998), that normally require long-term capture-recapture studies (e.g., Chase *et al*., 1997; Peach *et al*., 1999; Tavecchia *et al*., 2001, 2007). Apart from survival, there are other parameters that must be assessed to obtain a complete comprehension of the demography and dynamics of a population (Margalef, 1998; Newton, 1998), such as productivity, colony site fidelity, breeding age, immigration and emigration. Most herons are long-lived colonial waterbirds, many of which have shown and or are still experiencing increasing population trends in Europe (Marion *et al*., 2000). Being long-lived, the growth of these populations could be driven by high annual adult survival (Cézilly, 1987), which in herons has been shown to range from 0.55 to 0.75 (e.g., Freeman and North, 1990; Hafner *et al*., 1998).

The little egret *Egretta garzetta* is a widespread species, breeding in Europe, Asia and Africa as well as in Australia (Kushlan and Hancock, 2005). In Europe, it is mainly a circum-Mediterranean breeding bird (Hagemeijer and Blair, 1997), with an increasing population tendency (e.g., Hafner and Fasola, 1997) linked to the colonisation of areas where the species was absent until recently(e.g., Garrido *et al*., 2012). Since the mid-20th century it has spread to the milder Atlantic areas, mainly in Iberia, France and the southern parts of the British Isles (Marion *et al*., 2000; Holling, 2010; Garrido *et al*., 2012). In Iberia, this colonisation phenomenon is well represented across the Northern Atlantic coast, where the species was first recorded breeding during the 1990s (Garrido, 2003). Currently, this coastal population is assessed to be 200 birds in total (Garrido *et al*., 2012): all the colonies are on islands, near estuaries where the birds forage (A. Galarza, pers. obs.).

The population of little egrets in Spain is one of the largest in Europe (Marion *et al*., 2000). It comprises over 20,000 adult breeding birds (Garrido *et al*., 2012). Apart from its size and trends (Garrido *et al*., 2012), the parameters associated with the dynamics (e.g., survival, etc.) of this population remain virtually unknown. Furthermore, little is yet known about the dynamics of the Atlantic European colonies. The colonisation of this area and the increasing population trend may be due to a high survival rate in adults, as has been reported for a population in southern France (Hafner *et al*., 1998). Alternative hypotheses are possible too. Thus, a colony is likely to show stability or even experience growth by having a high turnover of breeding adults even if adult survival is low (Newton, 1998, 2013). Furthermore, high adult survival needs to be accompanied by high site fidelity in order to reach constancy in size or growth.

The aims of the present study were (1) to explore models fitting colony growth rate and (2) to estimate the apparent survival of a colony of little egrets breeding at one of the main estuaries in northern Iberia. In particular, we focused on the single colony that exists in the Urdaibai marshes. This is the only colony on the Basque coast and one of the few in coastal northern Iberia (Garrido *et al*., 2012). It is also the first study in which apparent survival is analysed for a Spanish little egret colony.

METHODS

Sampling area and protocol

The study was carried out at a little egret colony on Izaro island (43º 25' N, 02º 41' W; Basque coast, northern Spain), *c*. 1-km offshore from the Urdaibai marshes (fig. 1). Izaro is a small islet of approximately 3.2 ha, and has a maximum elevation of 46 m. The island is mostly flat and bare, with some vegetation patches dominated by tree mallow *Lavatera arborea* and sea beet *Beta vulgaris* with some tamarisks *Tamarix gallica* also present. Izaro is a breeding site for two seabird species: the European storm-petrel *Hydrobates pelagicus* and the yellow-legged gull *Larus michahellis* (Franco *et al*., 2004). The yellow-legged gull colony, of 1,200-1,600 breeding pairs, is the largest in the region (Arizaga *et al*., 2009). The little egret colony on Izaro was discovered in 1998 (Galarza, 1999) but was probably founded earlier, coinciding with the colonisation of other European Atlantic zones during the 1990s (Bargain, 1993; Debout, 1997; Lock and Cook, 1998; Álvarez-Balbuena *et al*., 2000). Initially, little egrets nested on the ground but over time they built their nests in sea beet and tree mallow. Since 2006 they settled in a small tamarisk patch.

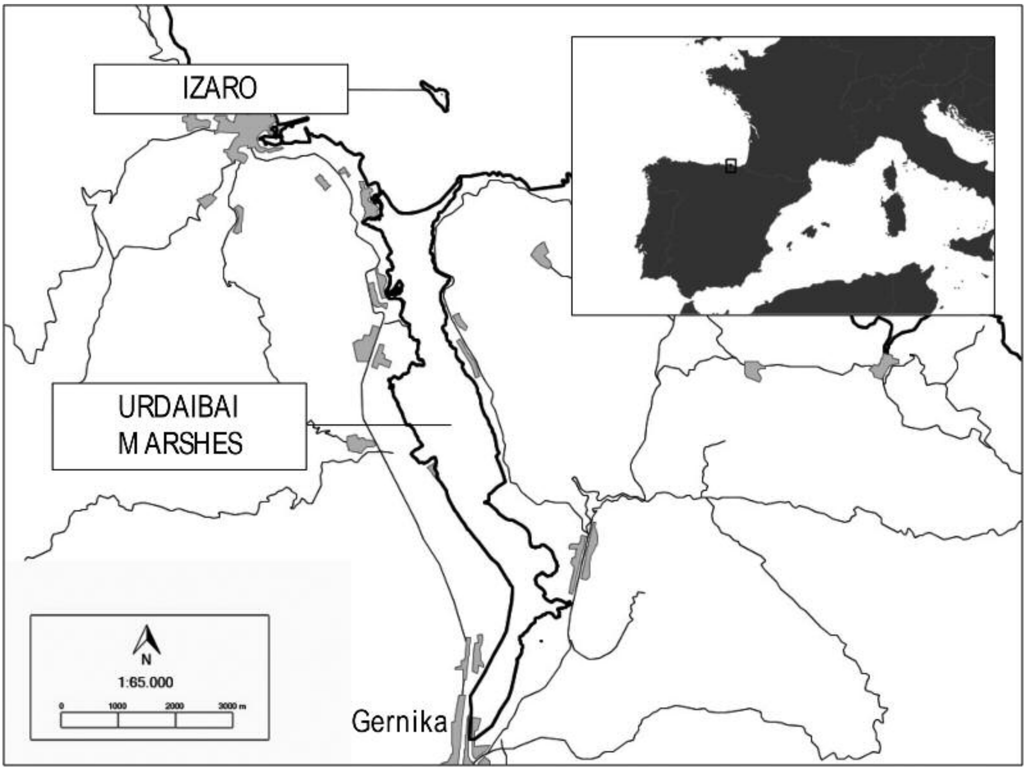

FIG. 1.—The location of Urdabai in the North of Spain and of the little egret colony on Izaro Island.
[Localización de Urdaibai en el norte de España y de la colonia de garceta común en la isla de Izaro.]

The chicks hatched within this colony were ringed from 1999 up to 2012. In total, 344 chicks were marked in the nest at *c*. 20 days old with a yellow darvic ring, bearing a black code of 2-3 characters. Due to the within-year hatching asynchrony (Hafner *et al*., 1994), chicks were normally ringed over several visits (mean ± SD, 5.8 ± 1.8 visits/year; range: 2-9). Ringing was carried out from May to July annually. We were unable to ring all the chicks hatched each year because of logistic limitations: in particular access to the island was frequently impossible due to the inclement weather conditions. We estimate that *c*. 60% of the chicks were ringed each year.

During visits to the colony we also looked for previously ringed little egrets, to obtain "recaptures" of recruits within the colony. Outside the breeding season, we surveyed the Urdaibai marshlands for ringed little egrets, and compiled sighting data obtained from birdwatchers who had reported the marked birds. These sightings came from a wide geographic area. Overall, 233 sighting events relative to 82 individual little egrets were recorded. The most distant was a first-year bird seen in January at a locality in La Coruña province, in north-western Spain, 515 km west of Urdaibai.

During visits to the colony we also surveyed the number of active nests and this data was used to assess the colony size. This was not an absolute count since using this approach we were not able to survey possible colony turnover and/or re-nesting. Each year the nests were all individually tagged with a numbered flag. We used this method because counting breeding pairs directly was difficult. The birds flew when we approached the colony and could not be easily surveyed at a distance, due to the topography of the islet. Little egrets are single brooded (Harrison, 1975) and therefore using active nests to count breeding pairs can be an accurate way of estimating breeding colony size. Strong winds, especially in winter, destroy all nests from one year to the next, so nests from other (previous) years are completely excluded from our annual nest count.

The population size of little egrets at Urdaibai was also surveyed during the winter, with counts being carried out at the winter roosts during the first half of January. All the little egrets present at Urdaibai used a single roosting site in winter. Until 2005 the roost was situated at the colony on Izaro. In 2005, a peregrine *Falco peregrinus* pair bred on Izaro and from the winter 2006 onwards the roost was in an area of oak trees *Quercus* spp., within the lower marsh.

Colony size analyses

Trends in breeding colony size were analysed using TRIM software (Pannekoek and Van Strien, 2001). Three alternative models were tested: no time effect (i.e. stable population), linear tendency (i.e. population increasing or decreasing assuming a constant slope for the whole temporal series), and linear-switched tendency (i.e. temporal variations in population trends). Two catastrophic events were reported in the colony during the study period: in 2004, a hailstorm destroyed 14 nests and killed 10 adults; in 2005, a Peregrine pair bred on the island and killed at least 10 more adult birds. Therefore, we tested for the occurrence of a change in the slopes for the periods: 1999 to 2004, 2004-2005 (hailstorm effect), 2005-2006 (Peregrine effect), and 2006 to 2012.

The small sample size-corrected Akaike values (AICc) were used to rank the fit of models to data (Burnham and Anderson, 1998). Models with an AICc difference less than 2 were considered to fit the data well (Burnham and Anderson, 1998).

To test to what extent the winter population size within the region (defined as the Urdaibai marshlands) was correlated with the size of the breeding colony a Pearson's correlation test was done on the data on the population size in the colony and the population size in the subsequent winter.

Survival analyses

To estimate survival we used Cormack-Jolly-Seber (CJS) models, which allow separate estimation of survival (ϕ, probability that a bird captured in *t* is still alive in *t*+1) and recapture probability (*p*, probability that a bird captured in *t* and still alive in *t*+1 is recaptured in *t*+1). To achieve our stated goals, two analytical datasets were used, to estimate the apparent (1) annual survival at the colony and (2) survival of juvenile (first-year) birds during their first year of life.

To estimate the apparent annual survival we considered a matrix with all the little egrets ringed as chicks at the colony and the "recaptures" (i.e., little egrets seen at the colony and ringed previously as chicks at this same colony). Since we considered resightings of live little egrets within the colony, this was an assessment of local survival rates. The data used in this matrix were obtained over a three-month period (May-July) each year (see Supplementary Electronic Material). The size of the matrix was 344 rows (ringed chicks) × 14 columns (years). Before starting to select models we explored the fit of data to CJS assumptions. To accomplish this we used a goodness-of-fit (GOF) test. A GOF test on a CJS model, where both ϕ and *p* varied with time [ϕ(t) *p*(t)], was carried out with U-CARE software (Choquet *et al*., 2001). Our data fitted the global CJS assumptions (global test: χ^2 = 24.38, *df* = 19, *P* = 0.182), but the specific test to detect transients was significant (*Z* = 4.12, *P*< 0.001). The specific Test to detect trap-dependence was non-significant (*Z* = 0.11, *P* = 0.915).

We thus identified a basic starting model with transients [$\phi(t_1,t_{rest})$ *p*(t)] to start model selection. Alternative models tested here were those that considered all the possible combinations of constant or year-associated (t) variations in ϕ and *p*. Such models did not account for the presence of transients, but were run to test how better models considering transients fitted to data. In models where transient birds were considered, we calculated the proportion of transients as: $1-[\phi(t_1)/\phi(t_2)]$, where $\phi(t_1)$ is the survival of previously unmarked little egrets, and $\phi(t_2)$ is that of previously marked individuals (Pradel *et al*., 1997).

To estimate the apparent monthly survival of first-year birds we considered a matrix with the data of all the chicks ringed in the colony and the sighting data obtained everywhere once the chicks left the colony, until April of the following year (see Supplementary Electronic Material). The unit of time used for the analyses was "month". This resulted in a matrix of 344 rows (ringed chicks) × 11 columns (months; no sighting data were obtained for February). Because the chicks were ringed over a long period (3 months), and survival can differ in relation to hatching date (Newton, 2013), we considered cohort models. In particular, we considered three cohorts corresponding to chicks hatched in May, June or July. Moreover, the GOF revealed that, overall, the data did not fit the CJS assumptions (global test: χ^2 = 47.63, *df* = 18, *P* < 0.001), due to the presence of transients (*Z* = 5.28, *P*< 0.001). The specific Test to detect trap-dependence was non-significant (*Z* = 1.68, *P* = 0.09).

Corrected Akaike values (AICc) were used to rank the fit of models to the data (Burnham and Anderson, 1998). Models with an AICc difference < 2 were considered to fit the data equally well. We used MARK 7.1software (White and Burnham, 1999) to run the CJS models.

Results

Population size

The colony size during the breeding period ranged from 5 (2006) to 32 breeding pairs (2003) (fig. 2). This colony experienced remarkable annual variations, firstly increasing during the period 1999 to 2003, then decreasing and subsequently crashing in 2006 before increasing again until the end of the study. Models assuming either no-time effect or linear tendency on the population size growth did not fit our data (table 1), so they were not good candidates for explaining our population size variations. In contrast, the switched linear model fitted data well (table 1), assuming a slope change in 2004 (Wald statistics: 8.64, *P* = 0.003), no change in 2005 (Wald statistics: 0.62, *P* = 0.433), and one additional change in 2006 (Wald statistics: 16.24, *P*< 0.001). Therefore, the slopes (± SE) for each period were: 1999-2004: +0.04 ± 0.03; 2004-2005: -0.55 ± 0.19; 2005-2006: -0.85 ± 0.23, and 2006 to 2012: +0.16 ± 0.04. Thus, during the catastrophic events from 2004 and 2005, the colony had an average decline of 70% per year.

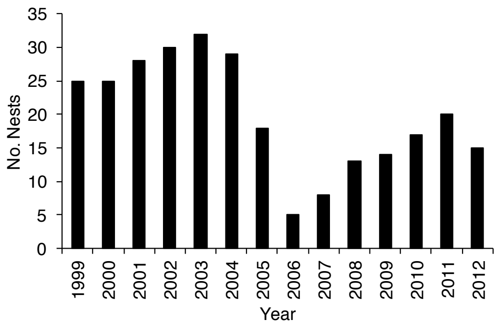

FIG. 2.—Annual variations in colony size of little egrets breeding on Izaro island.
[Variaciones anuales del tamaño de la colonia de garcetas comunes durante el periodo de cría en la isla de Izaro.]

Population size during the winter at Urdaibai ranged from 23 (2007) to 61 (2003) individuals and was positively correlated with colony size during the following breeding season (r^2 = 0.65, *P*< 0.001; fig. 3).

Survival models

The apparent annual survival at the colony was not constant but it was age-dependent (table 2). The best model was the one which included "transients" (table 2), with an apparent annual survival estimate of 0.15 ± 0.05 (mean ± SE) from hatching to the next year, and of 0.78 ± 0.06 for the subsequent years. The percentage of transients: birds that were never seen after being ringed, having either died or

TABLE 1

Goodness of fit of main models explaining the little egrets' breeding population tendency from 1999 to 2012.
[Bondad de ajuste de diferentes modelos utilizados para determinar la tendencia de la población de garcetas nidificantes en Izaro entre 1999 y 2012.]

Models	χ2	P	AICc
No time-effect	46.71	< 0.001	+25.45
Linear	29.29	0.004	+9.61
Linear-switched slopes	4.40	0.883	-13.41

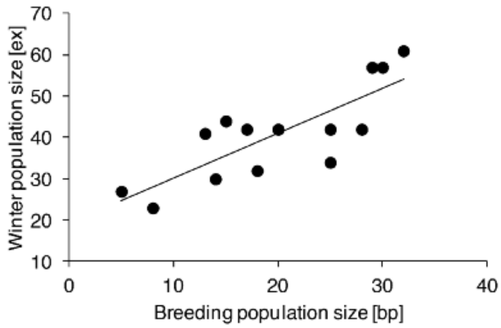

FIG. 3.—The little egret colony size during the breeding season is positively associated with the population size during the following winter at Urdaibai.
[El tamaño de la colonia durante el periodo de cría se correlaciona de manera positiva con el tamaño de la población en el siguiente invierno en Urdaibai.]

left the area definitively, was 80.6%. This percentage includes emigration and juvenile (first-year) mortality. The *p* ("recapture" probability) value was found to differ from year to year, ranging from 0.06 ± 0.06 to 0.40 ± 0.22.

The apparent monthly survival of first-year birds varied between cohorts and was lower for the first month of life (table 3; fig. 4). The first model fitted our data better than models considering a simple cohort or age-dependent effect (table 3). We obtained a constant *p* of 0.21 ± 0.03.

Recruitment and age of first breeding

Of 344 chicks ringed overall, 20 (5.8%) were seen as breeders within our colony in subsequent years. Of those, six (30%) were recruited into the colony as second-calendar year birds, i.e. ringed as chicks a year before they were seen as breeders in Izaro. Returning birds are likely to have been underestimated, given the low probability of resightings (see above for details). The most extreme case was a bird that was not seen until seven years after ringing.

TABLE 2

Ranking of CJS models used to estimate the annual apparent survival of little egrets breeding at Urdaibai. Data used were obtained at the colony on Izaro.
[Modelos CJS utilizados para estimar la supervivencia anual aparente de las garcetas que se reproducen en Urdaibai. Para ello han sido utilizados datos obtenidos en la colonia de Izaro.]

Models	AICc	ΔAICc	AICc weight	No. Parameters	Deviance
1. $\phi(t_1,t_{rest}), p(t)$	273.94	0.00	1.00	15	86.42
2. $\phi, p(t)$	285.95	12.01	0.00	14	100.61
3. ϕ, p	290.36	16.41	0.00	2	130.23
4. $\phi(t), p$	294.04	20.09	0.00	14	108.70
5. $\phi(t), p(t)$	303.40	29.46	0.00	26	90.91

t_1 = survival from hatching year to the following year (i.e., first-year survival); t_{rest} = survival from one year to the next, excepting t_1; t = survival (or *p*) from one year to the next.

TABLE 3

CJS models used to assess the apparent monthly survival of first-year little egrets hatched at Urdaibai. Data used comprise all sightings once the birds had left the colony.
[Modelos CJS utilizados para estimar la supervivencia mensual aparente en garcetas comunes nacidas en Urdaibai. Para ello han sido utilizados todos los datos (avistamientos) de aves en su primer año de vida.]

Models	AICc	ΔAICc	AICc weight	No. Parameters	Deviance
1. $\phi[\text{coho}\times(t_1,t_{rest})]$, *p*	778.74	0.00	1.00	7	146.17
2. $\phi(\text{coho})$, *p*	791.12	12.39	0.00	4	164.72
3. $\phi(t_1,t_{rest})$, *p*	797.03	18.30	0.00	3	172.67
4. $\phi(t)$, *p*	810.29	31.55	0.00	11	169.37
5. ϕ, *p*	812.88	34.15	0.00	2	190.55
6. ϕ, *p*(t)	822.84	44.11	0.00	11	181.92
7. $\phi(t)$, *p*(t)	824.34	45.60	0.00	20	164.03

t_1 = first-month survival; t_{rest} = survival from a given month to the next, excepting t_1; t = survival (or *p*) from one month to the following one; coho = cohort (we considered three cohorts, comprising chicks hatching in May, June or July).

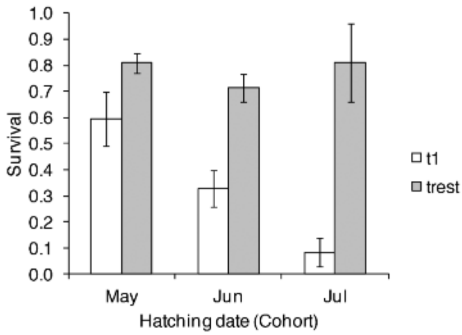

FIG. 4.—First-year apparent monthly survival (±SE) of little egrets from Izaro. Values obtained from model one in table 3. Data series: t_1, first-month survival; t_{rest} = survival from a given month to the next, excepting t_1.
[Supervivencia mensual aparente durante el primer año (±SE) en garcetas marcadas (anilladas) como pollos en Izaro. Valores calculados a partir del primer modelo de la tabla 3. Series de datos: t_1, supervivencia del primer mes de vida; t_{rest} = supervivencia mensual, excepto t_1.]

DISCUSSION

A little egret colony founded during the 1990s on a small islet close to Urdaibai in the North of Spain was showed large variations in size from year to year. Overall the colony was small, which is typical of little egret colonies situated on small islands along the north coast of Spain (Garrido *et al*., 2012). Furthermore, a very strong relationship between the sizes of the breeding and wintering populations suggests that the Urdaibai birds are resident and that winter immigration is probably rare in the region.

The increasing population tendency registered from 1999 onwards was dramatically cut by two catastrophic events: a very strong hailstorm in 2004 and a pair of Peregrines that bred on Izaro in 2005. Even by 2012 the colony had been unable to recover its former numbers.

Such a strong negative impact on the colony was due to the fact that many adults died during these events. This supports the idea that adult survival is of key importance for population dynamics in little egrets (Hafner *et al*., 1998), as seen in other waterbirds (Cézilly *et al*., 1996). A rapid recovery after the crash was probably due to the capacity of little egrets to breed just one year after hatching (Hafner *et al*., 1998), rather than to a high immigration rate. CJS models, however, seemed to be unsuccessful in detecting this mortality. In part, this might have been due to the relatively low resighting probability.

The annual apparent survival rate was 0.15 for hatch-year birds and 0.78 for adults. The best models considered that these apparent survival rates were constant over time. We cannot fully reject the possibility that some time-associated covariates, such as winter temperatures or rainfall, may have affected the annual apparent survival (e.g., Cézilly *et al*., 1996). However, using larger sample sizes, other authors found no effect of a winter cold index on apparent adult survival rates in a little egret population (Hafner *et al*., 1998). This supports the theory that those populations that occupy a climatically mild area: the Mediterranean and Atlantic zones in southern Europe, are able to respond successfully to a severe winter (Hafner *et al*., 1998). Indeed, the effect of winter severity on survival and breeding population size of grey herons *Ardea cinerea* was observed for areas with freezing events during the winter (North, 1979). The size of the little egret colony may also be affected by spring rainfall, since this affects the extent of available foraging habitat during the breeding season (Bennets *et al*., 2000; Fasola *et al*., 2010). However, this phenomenon cannot be extrapolated to estuaries in the North of Spain, where food availability is much more influenced by tidal patterns.

The apparent survival rate of first-year birds in a population of little egrets breeding in the Camargue (France) varied annually, ranging from 0.065 to 0.552, with most years varying between *c*. 0.10 and 0.30 (Hafner *et al*., 1998). Therefore, our mean apparent survival rate was towards the lower end of the range reported for the Camargue, for unknown reasons.

We observed that chicks ringed late in the season were more likely to die during the first few days post-fledging. This phenomenon is common in several bird species, where survival rates are lower in second broods, in chicks with the last hatching rank in a nest (although this has not been demonstrated for little egrets; Hafner *et al*., 1998) or in chicks from late broods. The underlying causes require investigation in detail, in particular to determine whether reduced survival is promoted by biologically-associated causes of breeding late (e.g., late chicks come from poor-quality parents or food availability may decline late in the season), in part by possible sibling completion between the oldest and youngest chicks, or by external causes that would only affect late chicks (e.g. increasing disturbance in foraging areas later in the season).

Our estimate of an apparent survival rate of 0.78 in adults was slightly higher than the rate reported for a population breeding in the Camargue (Hafner *et al*., 1998), and it is also at the higher rate of the range reported in grey herons (Freeman and North, 1990). Actual survival is likely to be even higher, since our value of 0.78 incorporated possible emigration from the area. Therefore, it can be concluded that little egrets breeding/living in our zone (Urdaibai) seem to experience environmental conditions of a sufficient standard to allow very good survival prospects.

Although our results show high adult survival they are insufficient to conclude that population growth in our area is independent of survival, given the lack of data on such factors as productivity and rates of immigration/emigration that may also affect the dynamics of the study population.

Possible reasons why the little egret population in the North of Spain is rather small should be investigated specifically. From our investigations we can suggest that breeding site availability may be limited, fidelity to breeding sites is relatively low and/or the northern Spanish estuaries may offer foraging habitats of the same quality as wetlands in the rest of Spain, especially those within the circum-Mediterranean region (Ebro, Albufera de Valencia) and the surroundings of Doñana, which hosts the largest colonies of herons in Spain (Garrido *et al*., 2012). Whereas the extensive southern European wetlands offer ricefields that permit a high carrying capacity (Fasola and Ruiz, 1996; Kazantzidis and Goutner, 1996; Prosper and Hafner, 1996), little egrets breeding in estuaries in northern Spain forage in small tidal areas with limited foraging habitat availability. Furthermore, little egrets in such estuaries are strongly territorial (A. Galarza, pers. obs.), thus reducing potential habitat availability still further.

Recruitment rate at age one was 30%, i.e. almost 10% higher than in the Camargue (Hafner *et al*., 1998). However, this difference must be considered cautiously, due to the low probability of resighting at that site and the very small sample sizes. Differences in the age of first breeding could be the result of different individual strategies (Cam *et al*., 1998) and/or the result of several constraining factors, such as a shortage of breeding sites or mates (Curio, 1983). We hypothesise that the high recruitment rate at age one may be due to the ready availability of sufficient breeding sites, given the relatively small size of this new and increasing colony.

In conclusion, the colony of little egrets at Urdaibai is small and hence very vulnerable to sporadic catastrophic events. Apparent annual survival was observed to be reasonably high in adults, and low for first-year birds. Additional monitoring would be useful in order to study the development of the colony and the role of potential factors regulating the population of little egrets breeding at Urdaibai and in other estuarine areas of northern Spain. The small sample sizes of our colony may preclude us from applying our conclusions to other areas, compelling us to consider our results with caution.

ACKNOWLEDGEMENTS.—We are grateful and indebted to the many volunteers that assisted us in the field and especially to T. Díaz, E. Díez, I. García, J. Hidalgo, F. Martínez, M. Martínez-Madrid and P. Pérez. We also wish to thank the numerous birdwatchers that shared data on sightings. Ringing activities were authorised by the Biscay Council. The comments of three referees were of great value in improving an earlier version of this work.

BIBLIOGRAPHY

ÁLVAREZ-BALBUENA, F., VIGIL A., ÁLVAREZ, C. M., CARBALLAL, M. E., GARCÍA, E. and GARCÍA, J. A. 2000. *Aves Raras y Escasas en Asturias*. Coordinadora Ornitoloxica d'Asturies. Avilés.

ARIZAGA, J., GALARZA, A., HERRERO, A., HIDALGO, J. and ALDALUR, A. 2009. Distribución y tamaño de la población de la gaviota patiamarilla *Larus michahellis lusitanius* en el País Vasco: tres décadas de estudio. *Revista Catalana d'Ornitologia*, 25: 32-42.

BARGAIN, B. 1993. Oiseaux de Bretagne. *Pen Ar Bed*, 150: 12-14.

BENNETS, R.E., FASOLA, M., HAFNER, H. and KAYSER, Y. 2000. Influence of environmental and density-dependent factors on reproduction of little egrets. *Auk*, 117: 634-639.

BURNHAM, K. P. and ANDERSON, D. R. 1998. *Model Selection and Inference. A Practical Information Theoretic Approach*. Springer-Verlag. New York.

CAM, E., HINES, J. E., MONNAT, J. Y., NICHOLS, J. D. and DANCHIN, E. 1998. Are adult nonbreeders prudent parents? The kittiwake model. *Ecology*, 79: 2917-2930.

CÉZILLY, F. 1987. Demogrpahic studies on wading birds: An overview. *Waterbirds*, 20: 121-128.

Cézilly, F., Viallefont, A., Boy, V. and Johnson, A. R. 1996. Annual variation in survival and breeding probability in greater flamingos. *Ecology*, 77: 1143-1150.

Curio, E. 1983. Why do young birds reproduce less well? *Ibis*, 125: 400-404.

Chase, M. K., Nur, N. and Geupel, G. R. 1997. Survival, productivity, and abundance in a Wilson's warbler population. *Auk*, 114: 354-366.

Choquet, R., Reboulet, A. M., Pradel, R. and Lebreton, J. D. 2001. *U-care (Utilities: Capture-Recapture) User's Guide*. CEFE/CNRS. Montpellier.

Debout, G. 1997. Évolution récente du status de l'Aigrette garzette en Normandie. *Le Cormoran*, 10: 43-48.

Fasola, M., Rubolini, D., Merli, E., Boncompagni, E. and Bressan, U. 2010. Long-term trends of heron and egret population in Italy, and the effects of climate, human-induced mortality. *Population Ecology*, 52: 59-72.

Fasola, M. and Ruiz, X. 1996. The value of rice fields as substitutes for natural wetlands for waterbirds in the Mediterranean Region. *Colonial Waterbirds (Special Publication)*, 1: 122-128.

Franco, J., Etxezarreta, J., Galarza, A., Gorospe, G. and Hidalgo, J. 2004. Seabird populations. In, A. Borja and M. Collins (Eds.): *Oceanography and Marine Environment of the Basque Country*, pp. 515-529. Elsevier Oceanography Series 70. Amsterdam.

Freeman, S. N. and North, P. M. 1990. Estimation of survival rates of British, Irish and French grey herons. *Ring*, 13: 139-166.

Galarza, A. 1999. Garceta común *Egretta garzetta*. Noticiario Ornitológico. *Ardeola*, 46: 150.

Garrido, J. R. (2003). Garceta común, *Egretta garzetta*. In, R. Martí and J. C. del Moral (Eds.): *Atlas de las Aves Reproductoras de España*, pp. 114-115. DGCN-SEO/BirdLife. Madrid.

Garrido, J. R., Molina, B. and del Moral, J. C. 2012. *Las Garzas en España, Población Reproductora e Invernante en 2010-2011 y Método de Censo*. SEO/BirdLife. Madrid.

Hafner, H. and Fasola, M. 1997. Long-term monitoring and conservation of herons in France and Italy. *Colonial Waterbirds*, 20: 298-305.

Hafner, H., Kayser, Y., Boy, V., Fasola, M., Julliard, A.-C., Pradel, R. and Cézilly, F. 1998. Local survival, natal dispersal, and recruitment in little egrets *Egretta garzetta*. *Journal of Avian Biology*, 29: 216-227.

Hafner, H., Pineau, O. and Kayser, Y. 1994. Ecological determinants of annual fluctuations in numbers of breeding little egrets (*Egretta garzetta*) in the Camargue, S. France. *Revue d'Ecolologie (Terre et Vie)*, 49: 53-62.

Hagemeijer, W. J. M. and Blair, M. J. 1997. *The EBCC Atlas of European Breeding Birds. Their Distribution and Abundance*. T and AD Poyser. London.

Harrison, C. 1975. *A field guide to the nests, eggs and nestlings of British and European birds*. Collins. London.

Holling, M. 2010. Rare breeding birds in the United Kingdom in 2008. *British Birds*, 103: 482-538.

Kazantzidis, S. and Goutner, V. 1996. Foraging ecology and conservation of feeding habitats of little egrets (*Egretta garzetta*) in the Axios River Delta, Macedonia, Greece. *Colonial Waterbirds (Spetial Publication)*, 1: 115-121.

Kushlan, J. A. and Hancock, J. A. 2005. *The Herons*. Oxford University Press. New York.

Lock, L. and Cook, K. 1998. The little egret in Britain: a successful colonist. *British Birds*, 91: 273-280.

Margalef, R. 1998. *Ecología*. Omega. Barcelona.

Marion, L., Ulenaers, P. and Van Vessem, J. 2000. Herons in Europe. In, J. A. Kushlan and H. Hafner (Eds.): *Heron Conservation*, pp. 1-31. Academic Press. London.

Newton, I. 1998. *Population Limitation in Birds*. Academic Press. London.

Newton, I. 2013. *Bird Populations*. Collins New Naturalist Library. London.

North, P. 1979. Relating grey heron mortality rates to winter weather conditions. *Bird Study*, 26: 23-28.

Pannekoek, J. and Van Strien, A. 2001. *TRIM 3 Manual. (Trends and Indices for Monitoring Data)*. Research paper no. 0102. Statistics Netherlands. Voorburg.

Peach, W. J., Siriwardena, G. M. and Gregory, R. D. 1999. Long-term changes in over-winter survival rates explain the decline of reed buntings *Emberiza schoeniclus* in Britain. *Journal of Applied Ecology*, 36: 798-811.

PRADEL, R., HINES, J. E., LEBRETON, J. D. and NICHOLS, J. D. 1997. Capture-recapture survival models taking account of transients. *Biometrics*, 53: 60-72.

PROSPER, J. and HAFNER, H. 1996. Breeding aspects of the colonial Ardeidae in the Albufera de Valencia, Spain: population changes, phenology, and reproductive success of the most abundant species. *Colonial Waterbirds (Spetial Publication)*, 1: 98-107.

TAVECCHIA, G., PRADEL, R., BOY, V., JOHNSON, A. R. and CÉZILLY, F. 2001. Sex- and age-related variation in survival and cost of first reproduction in greater flamingos. *Ecology*, 82: 165-174.

TAVECCHIA, G., PRADEL, R., GENOVART, M. and ORO, D. 2007. Density-dependent parameters and demographic equilibrium in open populations. *Oikos*, 116: 1481-1492.

WHITE, G. C. and BURNHAM, K. P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46: 120-139.

SUPPLEMENTARY ELECTRONIC MATERIAL

Additional supporting information may be found in the on-line version of this article. See volume 61(2) on www.ardeola.org

Table S1: M-array table of birds used to estimate the apparent annual survival.

Table S2: M-array table used to estimate first-year birds' survival.

Received: 8 October 2013
Accepted: 16 June 2014

Editor: José A. Masero